

How dense is dense? Toward a harmonized approach to characterizing reefs of non-native Pacific oysters – with consideration of native mussels

Alexandra Markert¹

¹ Wilhelmshaven, Germany

Corresponding author: Alexandra Markert (mar-k-art@gmx.de)

Academic editor: S. Gollasch | Received 8 December 2019 | Accepted 3 April 2020 | Published 29 May 2020

Citation: Markert A (2020) How dense is dense? Toward a harmonized approach to characterizing reefs of non-native Pacific oysters – with consideration of native mussels. *NeoBiota* 57: 7–52. <https://doi.org/10.3897/neobiota.57.49196>

Abstract

Pacific oysters *Crassostrea (Magallana) gigas* have been successfully invading ecosystems worldwide. As an ecosystem engineer, they have the potential to substantially impact on other species and on functional processes of invaded ecosystems. Engineering strength depends on oyster density in space and time. Density has not yet been studied on the extent of reef structural dynamics. This study assessed abundance of naturalized Pacific oysters by shell length (SL) of live individuals and post-mortem shells at six sites over six consecutive years during post-establishment. Individual biomass, i.e. live wet mass (LWM), flesh mass (FM) and live shell mass (SM LIVE), were determined from a total of 1.935 live oysters in order to estimate areal biomass. The generic term density attribute was used for SL-related population categories and the biomass variables LWM, FM, SM LIVE and SM. As the oyster invasion modulated resident *Mytilus edulis* beds, the study was supplemented by contemporaneously assessed data of mussels and corresponding analyses.

Interrelations of abundance and areal biomass revealed distinct linkages between specific density attributes. Most importantly, large individuals were identified as intrinsic drivers for the determination of areal biomass. Additionally, allometry of large oysters differed from small oysters by attenuated scaling relations. This effect was enhanced by oyster density as results showed that crowding forced large individuals into an increasing slender shape. The significant relationship between the density attributes large oyster and biomass enabled a classification of reef types by large oyster abundance. Reef type (simple or complex reef) and oyster size (small or large) were considered by implementing a novel concept of weighted twin functions (TF) for the relationship between SL and individual biomass. This study demonstrates that the interplay of scaling parameters (scalar, exponent) is highly sensitive to the estimation of individual biomass (shape) and that putative similar scaling parameters can exceedingly affect the estimation of areal biomass.

For the first time, this study documents the crucial relevance of areal reference, i.e. cluster density (CD) or reef density (RD), when comparing density. RD considers reef areas devoid of oysters and results from CD reduced by reef coverage (RC) as the relative reef area occupied by oysters. A compilation of density attributes at simple and complex reefs shall serve as a density guide. Irrespective of areal reference, oyster structural density attributes were significantly higher at complex than at simple reefs. In contrast, areal reference was of vital importance when evaluating the impact of engineering strength at ecosystem-level. While mussel CD was similar at both reef types, RD at complex reefs supported significantly more large mussels and higher mussel biomass than at simple reefs. Although mussels dominated both reef types by abundance of large individuals, oysters were the keystone engineers by dominating biomass.

The prominent status of large oysters for both allometric scaling and density, presumably characteristic for Pacific oyster populations worldwide, should be considered when conducting future investigations. The effort of monitoring will substantially be reduced as only large oysters have to be counted for an empirical characterization of Pacific oyster reefs. The large oyster concept is independent of sampling season, assessment method or ecosystem, and is also applicable to old data sets. Harmonization on the proposed density attributes with a clear specification of areal reference will allow trans-regional comparisons of Pacific oyster reefs and will facilitate evaluations of engineering strength, reef performance and invasional impacts at ecosystem-level.

Keywords

allometry, biogenic, ecosystem engineering, invasive species, reef complexity, reef density, reef type, reef structure

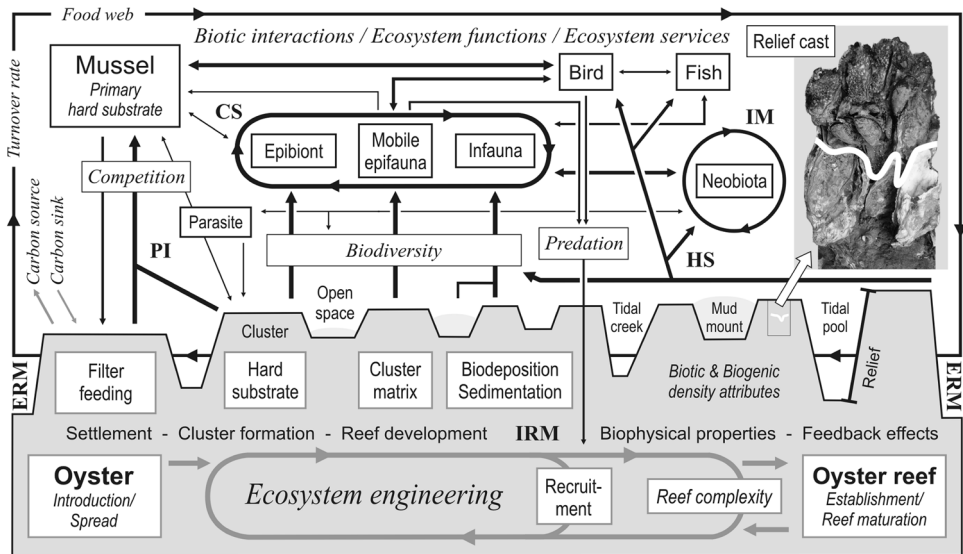
Introduction

The Pacific oyster *Crassostrea (Magallana) gigas* belongs to the most globalized marine invertebrates and is one of the most successful marine invaders worldwide. Oysters are ecosystem engineers as the creation of biogenic structure modulates the availability of resources to other species while biggest effects are attributable to oysters living at high densities, over large areas for a long time (Jones et al. 1994).

To attribute ecological and functional impacts of Pacific oysters to engineering strength in relation to density, space and time, one has to understand underlying processes of the creation of biogenic structures and the development of reef structural components due to increasing density and progressive engineering (Fig. 1). Oyster larva settles on hard substrate where the maturing oyster stays permanently attached. Due to the gregarious nature, clumps of several oysters develop from the process of repetitive settlement. Clumps enlarge by shell accretion and coalesce to oyster clusters. Increasing cluster density due to increasing numbers of live oysters and post-mortem oyster shells force the immobile filter feeder to grow increasingly vertical while a complex three-dimensional cluster matrix develops. A single cluster can cover several to some dozen square meters (Fig. 3A). Several clusters and interspersed oyster unoccupied open spaces perform as a bio-geo-morphological unit, encompassing the total area of an oyster reef. A Pacific oyster reef can reach several to some dozen hectares.

The rough surface structure of the reef reduces hydrodynamic forces which increases sedimentation above the reef and can even affect reef surroundings. High densities of oysters produce high amounts of biodeposit. Fine particles and resuspended material can accumulate in the cluster matrix and in post-mortem articulated oyster shells while individuals on top of the matrix stay clean due to small-scale turbulences at the direct interface. Progressive engineering has strongest effects on intertidal soft substrate environments. The creation of biogenic structure adds hard substrate while sediments increasingly enrich with organic matter. Fine particles and re-suspended material can accumulate in open spaces, i.e. reef areas devoid of oysters, and mud mounts may develop over time. Shells of oysters that died from burial at the bottom of clusters increasingly anchor the biogenic structure as clusters grow in height by vertical shell accretion and by raise of the sediment surface. Increasing rigidity, height and continuity of the system increase small scale tidal flow and intra-reef creeks along clusters or deep tidal pools between clusters can develop over time (Fig. 3A). These reefs harbor submerged sub-habitats even during low tide. The relief of intertidal soft-sediment Pacific oyster reefs can reach several meters (pictured in Folmer et al. 2017, Fig. 2).

Ecosystem engineering effects of introduced Pacific oysters have been discussed by Ruesink et al. (2005) while the authors stressed major gaps in knowledge of the spatial and temporal extent of direct (e.g. habitat use) and indirect (e.g. hydrodynam-



CS Community structure, ERM Extra-reef modification, HS Habitat suitability, IM Invasional meltdown, IRM Intra-reef modification, PI Population interference. Relief cast (18 x 30 cm) Pacific oyster reef *Dornumer Nacken* 2008 (approx. 6 years after initial oyster settlement). White line: Sediment surface. Top: Cluster matrix (live oysters, post-mortem oyster shells and live mussels). Bottom: Cluster anchorage (post-mortem oyster shells). Black arrow width indicates potential relevance of engineering effects on ecosystem-level.

Figure 1. Ecosystem engineering conceptual framework. Effects adapted for non-native Pacific oysters modulating resident intertidal mussel beds in the Wadden Sea of the North Sea.

ics, sediment budgets, nutrient cycling) ecological effects, and pointed out the lack of information especially at ecosystem-level. A lot of studies on engineering effects of non-native Pacific oysters have been performed in North West European Estuaries, and in particular in the UNESCO World Natural Heritage Site Wadden Sea where Pacific oysters have been successfully invading resident intertidal mussel (*Mytilus edulis*) beds (Folmer et al. 2017) (Fig. 1). Although several experimental (laboratory and on site) or in situ studies have been investigating effects of intra-reef modifications on habitat associated macrofauna (i.a. Kochmann et al. 2008, Markert et al. 2010), habitat use by birds (i.a. Markert et al. 2013, Waser et al. 2016), habitat use by fish (Dänhardt et al. in progress), habitat invasion by non-native Asian shore crabs *Hemigrapsus takanoi* (i.a. Markert et al. 2014, Waser et al. in progress), habitat invasion by non-native Japanese seaweed *Sargassum muticum* (i.a. Lang and Buschbaum 2010, Markert and Wehrmann 2013), parasite-host interactions among native and non-native species (i.a. Thieltges et al. 2009, Goedknecht et al. 2017), population dynamics (i.a. Schmidt et al. 2008; Eschweiler and Christensen 2011; Waser et al. 2015; Buschbaum et al. 2016; Reise et al. 2017a, 2017b; Folmer et al. 2017), feedback effects on the oyster itself (i.a. Troost et al. 2008, 2009) or spatially extended extra-reef modifications (i.a. Van der Zee et al. 2012, Walles et al. 2015a, Markert et al. 2016), research is far from estimating the good or the bad about the naturalization of the Pacific oyster in the Wadden Sea ecosystem. “Mussel beds” are still one of the target habitats when evaluating the good ecological status of the Wadden Sea, although most of the beds have been transformed into oyster reefs (Büttger et al. 2010, Folmer et al. 2017). The need for impacts of invasive Pacific oysters to be investigated at a range of invader density has been recognized (Green and Crowe 2014), but uniform measurements or tools that allow for comparison and extrapolation of engineering effects on a spatial scale, i.e. among tidal basins or estuaries and across nations or regions, have not yet been implemented (Folmer et al. 2017). Attempts at reaching trilateral (Netherlands, Germany and Denmark) agreements on monitoring Pacific oysters in the Wadden Sea have been made but national assessment methods had already been established independently and methodological adaption was limited by logistical and, in particular, financial effort. Likewise, the American oyster *Crassostrea virginica* has been studied comprehensively over several decades in restoration projects but universal metrics for evaluating the performance of habitat restoration were only just recently published to fulfill requests from restoration practitioners for a set of specific monitoring guidelines tiered to account for limitations in budgets and expertise (Baggett et al. 2015). Nevertheless, Kellogg et al. (2014) emphasized the need for tools that allow estimations of ecological function and related ecosystem services based on structural parameters of matured *C. virginica* reefs.

Some impacts of naturalizing oysters are considered context-dependent, e.g. provision of primary settling substrate provided at rocky shores or soft-sediments, in salt-marshes or seagrass, by *Sabellaria*-reefs or mussel beds (Padilla 2010, Herbert et al. 2016), but generalities can be deduced only from the physical presence of oysters. Engineering strength may be reflected by oyster density in clusters but the intra-reef pattern, i.e. the variability of oyster density among all intra-reef clusters in relation

to a patchy coverage of the reef area by these clusters, has important implications for a reef's structural dynamics and related biophysical properties. Biophysical interactions, i.e. feedback effects between oyster density, reef coverage, reef relief, reef height, reef areal extent and reef orientation, investigated for *C. virginica* influenced reef performance in terms of population persistence and habitat maintenance (Lenihan 1999, Schulte et al. 2009, Colden et al. 2016, Colden et al. 2017). Live oysters are commonly assessed for population studies but also post-mortem oyster shells enhance habitat heterogeneity, contribute to cluster compaction and provide settling space for spat, and thereby affect reef dynamics and biophysical properties. Mann et al. (2009) and Southworth et al. (2010) comprehensively sampled natural reefs of *C. virginica* with hydraulic patent tongs in order to assess oysters by size class and shell by volume. Shell volume referred to articulated post-mortem oyster shells (boxes), categorized as brown shell (boxes above sediment-water interface) or black shell (boxes exhumed during collection process), and seemed to include shell hash. The relationship between live *C. virginica* shell length and wet shell weight was used to estimate the amount of live shell while shell volume had to be converted to wet shell weight for comparative analyses of live proportions. This displays the complexity of structural attributes of oyster reefs in general and highlights the interplay between methodological approach and data analysis.

The present study provides the first documentation of biogenic density dynamics of Pacific oysters. Monitoring six sites over six consecutive years during post-establishment of the non-native oyster on former intertidal mussel beds in the Central Wadden Sea (Germany) compiled a comprehensive data set on shell length of live oysters and post-mortem oyster shells. Additionally, oyster individual metrics per site and year were measured to determine conversion functions from allometric scaling in order to convert the monitoring data into biomass. The two extensive datasets conditioned on interdependent analyses of the high variable oyster shape in relation to oyster size and oyster density, and interlinked estimations of areal biomass. These analyses coincidentally triggered significant interrelations between size-related population quantities and/or biomass of live oysters and/or post-mortem oyster shells. Results induced the development of a conceptual framework towards a harmonized approach to characterizing Pacific oyster reefs which will facilitate evaluations of Pacific oyster engineering strength at ecosystem-level. Analyses of this study were supplemented by mussel data as the evaluation of dominance, i.e. the determination of the keystone engineer, is one of the basic tasks when oysters invade habitats that are pre-occupied by native ecosystem engineers.

Methods

Study sites

Six sites in the intertidal of the Central Wadden Sea, German Federal State Lower Saxony, southern North Sea (Fig. 2) were monitored between 2008 and 2013 in order

to assess the density of Pacific oysters *Crassostrea (Magallana) gigas* (oyster) and blue mussels *Mytilus edulis* (mussel). The study region is characterized by muddy to sandy tidal flats with a semidiurnal tide cycle, a tidal range from 2.3 m in the west to 3.7 m in the east and a salinity range from 27 to 32. The tidal flats stretch along a 150 km coastline and cover an area of 1,380 km² (Wehrmann 2016). The study sites NL (Nordland 26.1 ha), NOR (Norderney 7.3 ha), DN (Dorumer Nacken 8.3 ha), SP (Swinplate 9.3 ha), KB (Kaiserbalje 7.0 ha) and RB (Robinsbalje 4.2 ha) are evenly distributed from the most western to the most eastern part of the study region. Tidal elevation with a mean exposure time of about 3.5 hours per tidal cycle was similar at all sites.

The oyster is non-indigenous in the Wadden Sea and has been invading the study region since 1998 (Wehrmann et al. 2000). Settlement occurred predominantly on resident intertidal mussel beds. Oysters spread rapidly (Schmidt et al. 2008) and established self-sustaining populations throughout the study region. By 2006, all of 100 recorded intertidal mussel beds were colonized by oysters (Millat 2008). Since 2008, the oyster has been considered established and all mussel beds have been transformed into oyster reefs. The intra-reef pattern is typically patchy (Fig. 3A). Oyster clusters, i.e. reef areas occupied by oysters, are irregularly interspersed by open spaces, i.e. reef areas devoid of oysters. Clusters consist of clumps of live oysters and post-mortem oyster shells (Fig. 3B). Mussels are present between oysters. Single clusters may cover large reef areas of several dozen square meters. Oyster clumps mainly cover the cluster bottom completely but may also have a scattered distribution. All clusters disconnected by a maximum of 25 m were included when confining the outline of the biogenic structure, thus the reef area (Nehls et al. 2009).

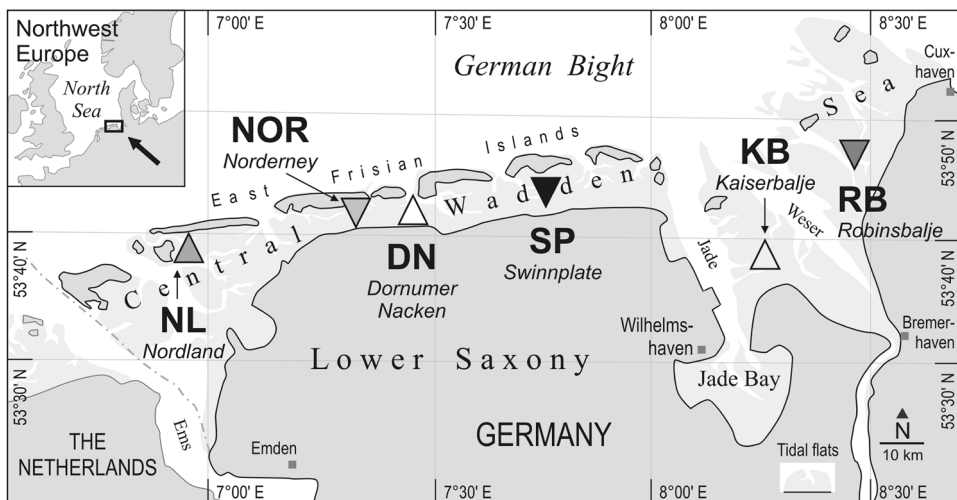


Figure 2. Location of study sites in the intertidal of the Central Wadden Sea, German Federal State Lower Saxony, southern North Sea.

Density metrics

Annual surveys and sample collections took place around low tide mainly during spring. 12 stations per site were randomly selected from a grid superimposed on a diagram of the reef area. Coordinates were recorded and stations in the field were located during each survey by using a handheld GPS. Annual re-location of a given station varied by exact position as GPS accuracy is at best a few meters. At this, re-sampling or sampling in close proximity of beforehand sampled areas was presumed to be excluded. A sample frame of 25×25 cm ($1/16$ m² or 0.0625 m²) was exclusively placed on oyster clusters, i.e. if a station was located in an open space, the closest cluster was sampled. Sample frames typically encompassed surfaces that were completely occupied by oysters. In rare cases, only single clumps, single oysters or mussels were within the frame. All material (excavation depth preferably to a maximum of 10 to 15 cm below sediment surface

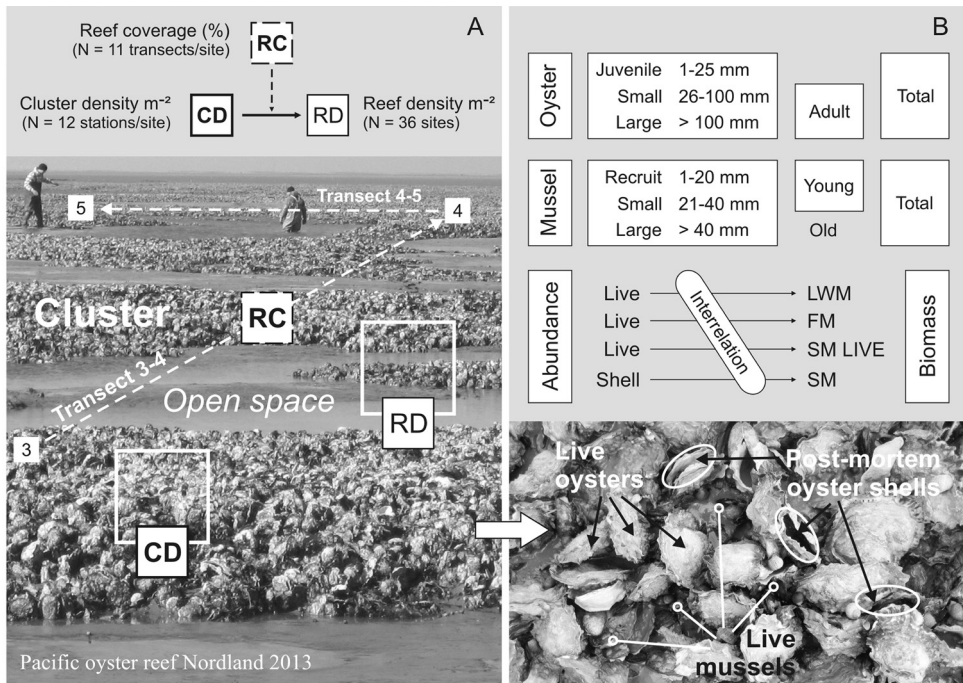


Figure 3. Density conceptual framework. **A** Areal reference. Cluster density (CD) reduced by reef coverage (RC) results in reef density (RD). Depicted are three stations (3/4/5 à 0.0625 m²), two station connecting transects (3-4/4-5) for RC and 1 m² encompassing CD/RD. **B** Density attributes. Abundance was calculated for SL-related population categories of live oysters, oyster shell and live mussels. Areal biomass was calculated from total abundance, respectively. Depicted are oysters and mussels in a cluster (top view). FM = cooked flesh mass, live = abundance of live oysters or mussels, LWM = live wet mass, shell = abundance of live oysters and post-mortem oyster shells, SM = shell mass of live oysters and post-mortem oyster shells, SM LIVE = shell mass of live oysters or mussels. See text for details.

but all live oysters included) was manually collected in buckets and stored in cooling chambers right after returning from the survey. Measurements were carried out after rinsing the samples within the next three days. Shell lengths (SL) of live oysters and post-mortem oyster shells, the latter only intact left valves and no shell fragments, and of live mussels (intact post-mortem mussel shells were extremely scarce due to rapid decay) were measured to the nearest mm. With reference to oysters, SL was recorded as the greatest distance from the hinge to the shell growth margin. This correctly is termed shell height, although commonly used to describe SL (Mann et al. 2009).

Data of each station was standardized to 1 m² cluster density (CD) (N = 432 cluster). CD of the 12 annual stations per site were averaged to CD per site and year (Fig. 3A) (N = 36 reefs). CD of the 12 annual stations per site were reduced by the annual reef coverage (RC) and averaged to reef density (RD) per site and year (N = 36 reefs). RC was assessed contemporaneously to each survey by pacing off all station connecting transects (11). Counts were made using two hand held tally counters, one for foot on cluster and one for foot on open space. RC was the proportion of steps on clusters to total steps of all transects. Total length of all transects per site was assigned to be at least 1 km and subsequently determined the order of the 12 stations. An average 167 ± 50 m per hectare was paced off and 211 ± 57 steps per hectare were made per site and year.

Individual metrics and allometric scaling

The monitoring between 2008 and 2012 was supplemented by a comprehensive biomass determination of in total 1.935 live oysters (SL 26–254 mm) and 1.553 live mussels (SL 11–70 mm). SL, live wet mass (LWM = shell, flesh and retention water), shell mass (SM LIVE) and cooked flesh mass (FM) were assessed from each individual. The determination of oyster individual metrics was based on 8 SL classes: 26–50, 51–75, 76–100, 101–125, 126–150, 151–175, 176–200, > 200 mm. Oysters up to 25 mm were excluded as the complete left valve is calcified to the attachment surface and cannot be removed without damage. The determination of mussel individual metrics was based on 6 SL classes: 11–20, 21–30, 31–40, 41–50, 51–60 and > 60 mm. Mussels up to 10 mm were excluded due to a high risk of damaging and handling efficiency. Immediately after measuring the SL of all individuals collected within the 12 stations, 10 intact and unopened individuals per species and SL class, if available, were randomly selected out of the material pool (Table 1). Fouling organisms were scraped off each shell surface. Specimen-specific SL (mm) and LWM (g), the latter to 0.001 grams accuracy, were recorded. Smaller individuals were placed in numbered tea filter bags and larger individuals numbered with a taped elastic band. Specimens were stored in a freezer and later defrosted before cooking oysters for about 10 minutes and mussels for about 5 minutes. The cooked flesh was separated from each shell, flesh and both valves were placed on paper towels before FM (g) and SM LIVE (g) were recorded to 0.001 grams accuracy.

Table 1. Number of oysters and mussels used to assess individual metrics. SP = Swinnplate, RB = Robinsbalje, NOR = Norderney, NL = Nordland, KB = Kaiserbalje, DN = Dornumer Nacken, LRD = simple reefs with low reef density, HRD = complex reefs with high reef density.

	2008	2009	2010	2011	2012	Total
Oyster						
SP (LRD)	54	57	47	58	60	276
RB (LRD)	43	51	51	62	60	267
NOR (LRD)	57	61	69	74	70	331
NL (HRD)	52	67	69	66	69	323
KB (HRD)	69	75	80	80	77	381
DN (HRD)	68	68	67	74	80	357
LRD	154	169	167	194	190	874
HRD	189	210	216	220	226	1,061
Total	343	379	383	414	416	1,935
Mussel						
SP (LRD)	50	49	60	50	57	266
RB (LRD)	50	49	55	48	55	257
NOR (LRD)	50	50	56	55	50	261
NL (HRD)	50	50	49	49	54	252
KB (HRD)	50	50	50	60	58	268
DN (HRD)	50	50	50	46	53	249
LRD	150	148	171	153	162	784
HRD	150	150	149	155	165	769
Total	300	298	320	308	327	1,553

Analyses of individual metrics were based on means per SL class. Shape was treated as a relative characteristic and was deduced from the relationship between LWM and SL. At a given SL, low LWM was interpreted to represent slender individuals and high LWM was interpreted to represent mighty individuals. The relationship between biomass (LWM, SM LIVE, FM) and SL was described by a power function $y = a(x)^b$, where y = the dependent variable for biomass (g), x = the independent variable for SL (mm), a = scalar and b = exponent (scaling parameters). Conversion functions (CF) describe allometric scaling relations of all SL classes. Oyster shape variability induced a data pooling of oyster individual metrics for allometric scaling. Individual metrics were “weighted” by reef type, i.e. pooling data of all simple reefs with low reef density (LRD) and all complex reefs with high reef density (HRD) (Figs 3, 4). Twin functions (TF) describe separate allometric scaling relations of small (SL 26–100 mm) and large (SL > 100 mm) oysters (Fig. 5). Weighted TF for oyster LWM, FM and SM LIVE and weighted CF for mussel LWM, FM and SM LIVE were determined for a general application (Figs 4, 7; Table 2). Oyster weighted TF and mussel weighted CF were applied to the SL data of the monitoring when estimating density attributes during the study period 2008–2013. SL of post-mortem oyster shells was converted by applying weighted TF for oyster SM LIVE. For additional analyses, allometric scaling relations were also determined after pooling individual metrics by site (local) or by site and year (unique).

Analyses of LWM-conversions were supplemented by the CF SH (Nehls and Büttger 2006) as the regional equation commonly used for Pacific oysters in Schleswig-Holstein (Northern Wadden Sea, Germany) with $a = 0.0032$, $b = 2.2321$, $R^2 = 0.6967$,

$N = 159$ and CF KATS (Walles 2015b) as a local equation determined from Pacific oysters at the reef KATS in the Oosterschelde estuary (The Netherlands) with $a = 0.00224$, $b = 2.13$, $R^2 = 0.97$, $N = 49$.

Density attributes

Density attribute is a generic term for the abundance of SL-related population categories of oysters or mussels, and for oyster or mussel areal biomass (Fig. 3B). Areal biomass in terms of areal LWM, FM and SM LIVE encompassed the total live population, respectively. Oyster areal SM encompassed the shell mass of all live oysters and all post-mortem oyster shells. Abundance of oysters was estimated for total, juvenile, small, large and adult individuals (Fig. 3B). This application-oriented subdivision became evident during data analyses when distinct linkages between individual metrics and oyster density were observed. Oyster spatfalls in the study region took place between late summer and early autumn (unpublished data, in prep.). These oysters had grown up to 25 mm in the following spring and were assigned as juveniles of the respective monitoring year. The remaining adult population (> 25 mm) was reasonably categorized into small (26–100 mm) and large oysters (> 100 mm). This categorization was implemented for live oysters and for oyster shell (live oysters and post-mortem oyster shells). For example, the abundance of large oysters may refer to live oysters only (large live) or to live oysters and post-mortem oyster shells (large shell). Accordingly, the proportion of large live oysters to large oyster shell was expressed as a LIVE-Factor Large. A population categorization by SL was also implemented for mussels, i.e. total, recruits, small, young and old (large) mussels (Fig. 3B). Mussels in the study area reproduced one to several times a year, between early spring and late autumn (unpublished data, in prep.). These mussels had grown up to 20 mm in the following spring and were assigned as recruits of the respective monitoring year. The remaining mature population (> 20 mm) was reasonably categorized into small (21–40 mm) and large mussels (> 40 mm). All large mussels were older than 2 years (unpublished data, in prep.). Recruits and small mussels were reasonably grouped to young mussels (1–40 mm).

Oyster and mussel density attributes were only contrasted within the same areal reference (Fig. 3). The relevance of areal reference in relation to oyster density attributes was exemplarily displayed for two reefs with similar structural density. Intra-reef variation of oyster density attributes was analyzed by determining the coefficient of variation (CV) for all sites and years. Selected CV and density attributes of oysters and mussels were interrelated. Simple linear regression analyses were performed, the coefficients of determination specified and the significance of the slope was tested (t-Test). Proportions of significant interrelations were given when the intercept was negligible, i.e. intercept not significant when $< 5\%$ of y (max). For significant interrelations between areal biomass and the abundance of large individuals, a so-called density scaling was implemented.

Oyster and mussel density attributes of all sites and years were pooled by reef type. Therefore, each site during the study period 2008–2013 was allocated by its abundance of large live oyster RD to one of the defined reef types, i.e. simple reef with low reef density (LRD) or complex reef with high reef density (HRD) (Fig. 4C). Density attributes at simple reefs (all LRD-sites) and at complex reefs (all HRD-sites) ($N = 18$ each) were averaged and the difference between reef types was tested for significance (t-Test). To display the influence of areal reference, significance was also tested between complex reef RD and simple reef CD (Table 3).

Results

Oyster shape and classification of reef types

Oyster shape was highly variable among sites (Fig. 4A). Shape differences between sites became conspicuous in large oysters (> 100 mm) and grew increasingly distinct with increasing SL. Shape of large oysters varied between wide, deep cupped mighty individuals at site SP and narrow, low cupped slender individuals at site DN. Compared to small oysters (26–100 mm), the slope of oyster shape attenuated in large oysters which emphasized a SL-related categorization of oysters into small and large oysters for allometric scaling (Fig. 5).

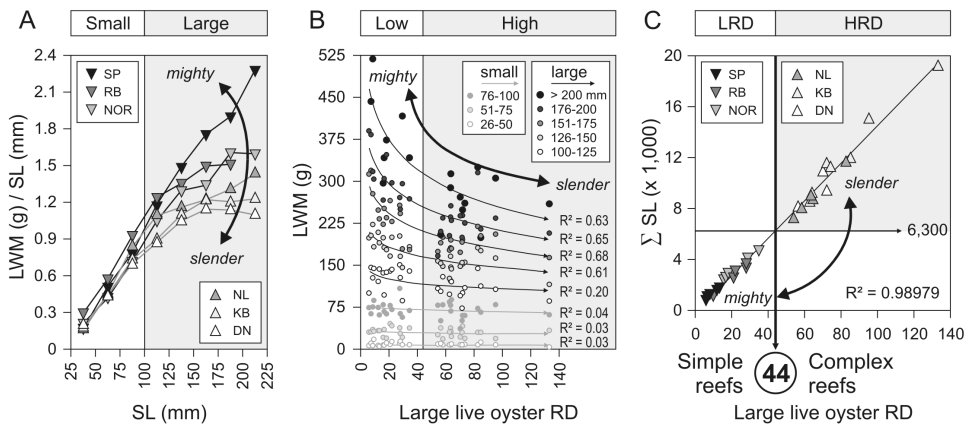


Figure 4. Oyster shape and classification of reef types. **A** Site- (SP-DN) and size-dependent (small/large) oyster shape. Plotted is individual LWM (g) per SL (mm) against SL (mm) of 8 SL classes per site. **B** Density-related (low/high) variation of oyster shape. Plotted is individual LWM (g) of 8 SL classes against large live oyster RD per site and year. Exponential trend of density-related shape difference indicated per SL class. **C** Determination of the threshold density of 44 large live oyster RD to classify sites into simple reefs with low reef density (LRD) and complex reefs with high reef density (HRD). Displayed is the linear relation of large live oyster RD to the sum of their SL. R^2 = coefficient of determination.

Observations in the field indicated that shape differences might be affected by crowding. The most reliable and comparable variable to reflect density was assumed to be biomass but abundance was the available data from monitoring while areal biomass was not yet calculated. The interlinked analyses of individual and areal data of this study eventually detected patterns and the general concept of density attributes (Fig. 3B) was accomplished. At this, large oysters were identified as intrinsic drivers of density (see paragraph on oyster density attributes). However, large oyster individual LWM (g) was exponentially related to oyster density, e.g. large live oyster RD (Fig. 4B). An increasing slender shape of large oysters with increasing RD was apparent. RD had no obvious effect on the shape of small oysters. To meet the distinctiveness of a density-related shape of large oysters for allometric scaling (Fig. 5), a classification into reef types was implemented (Fig. 4C). Therefore, large live oyster RD was related to the sum of their SL values, the latter meant to represent the SL distribution of large live oysters, respectively. A threshold density of 44 large live oyster RD was determined to separate simple reefs with low reef density (LRD) from complex reefs with high reef density (HRD). Throughout the study period of the monitoring between 2008 and 2013, sites SP, RB and NOR were assigned to simple reefs (LRD) and NL, KB and DN to complex reefs (HRD).

Oyster allometric scaling

Oyster individual biomass (LWM, SM LIVE and FM) was highly variable. The range per SL class increased with oyster size and was most considerable in the largest SL class. LWM of oysters larger than 200 mm ranged from 144.7 g (206 mm, KB 2009) to 645.2 g (239 mm, SP 2012) and the same specimens limited the range of SM LIVE (86.4 g to 427.3 g). FM of the SL class > 200 mm ranged from 7.7 g (215 mm, KB 2012) to 65.6 g (211 mm, NOR 2011).

Aiming at the determination of general biomass conversion functions with a universal application, size-dependent and density-related variability of oyster shape was considered for oyster allometric scaling. To mediate between underestimations at reefs with mighty oysters and overestimations at reefs with slender oysters, data of individual metrics was weighted by density. Therefore, individual metrics were grouped to LRD data by pooling individual metrics of all simple reefs (SP, RB, NOR 2008–2012) and to HRD data by pooling individual metrics of all complex reefs (NL, KB, DN 2008–2012) (Fig. 4C). For both reef types, power functions fitted well to the relationship between SL and biomass (LWM_{LRD} : $R^2 = 0.98563$, LWM_{HRD} : $R^2 = 0.97443$, $\text{SM LIVE}_{\text{LRD}}$: $R^2 = 0.98915$, $\text{SM LIVE}_{\text{HRD}}$: $R^2 = 0.97565$, FM_{LRD} : $R^2 = 0.95709$, FM_{HRD} : $R^2 = 0.93187$), but all slopes reflected the above mentioned size-dependent pattern (Fig. 4A). This pattern was also characteristic for all unique relationships, i.e. allometric scaling of individual metrics per site and year. Hence, the conversion of SL would underestimate the biomass of medium sized oysters and largely overestimate the biomass of oysters larger than 175 mm (Fig. 5A). Scaling relations of small oysters

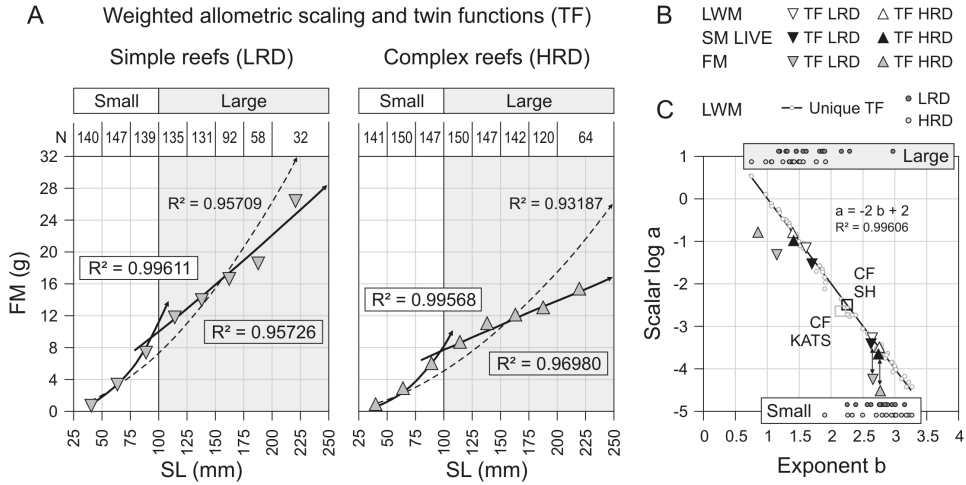


Figure 5. Oyster allometric scaling. **A** Determination of FM weighted TF. Plotted is FM (g) against SL (mm) of 8 SL classes after pooling individual metrics according to reef type (weighted). Displayed are powered relationships of all SL classes (broken line arrows), and of small and large oysters (TF) (black arrows). Given are coefficients of determination (R^2 , FM weighted TF in boxes) and number of oysters per SL class (N). **B** Plotted are scaling parameters of LWM, SM LIVE and FM weighted TF (N = 12 equations, Table 2). Note similar exponents for small oysters (arrows). **C** Plotted are scaling parameters of all LWM TF per site and year (unique) (N = 30 small, N = 30 large). Exponential relationship indicated, equation and coefficient of determination (R^2) given. Distribution of exponents at both reef type is given for small and large oysters (in boxes), respectively. Additionally plotted are scaling parameters of LWM conversion functions of two other studies (CF SH, CF KATS). Large oysters highlighted (gray area). LRD = simple reefs with low reef density, HRD = complex reefs with high reef density, TF = twin function.

attenuated in large oysters and a better fit for the relationship between biomass and SL was achieved by separating scaling relations for small and large oysters (Fig. 5A). These size-dependent power functions were termed twin functions (TF). TF were determined per reef type. The implementation of weighted TF (TF LRD, TF HRD) resulted in four equations (TF LRD/small, TF LRD/large, TF HRD/small and TF HRD/large) for LWM, SM LIVE and FM, respectively (Table 2). Compared to the calculation of oyster areal biomass by using LWM weighted TF, the regional LWM CF, i.e. determined by using the non-weighted and size-independent 5-year data set, underestimated simple reefs and overestimated complex reefs by up to 20 %.

Scaling parameters of all weighted TF (N = 12 equations) were contrasted. Small oysters scaled by similar exponents for LWM, SM LIVE and FM at LRD (b/rounded = 2.63/LWM, 2.61/SM LIVE, 2.63/FM) or at HRD (b/rounded = 2.74/LWM, 2.72/SM LIVE, 2.75/FM) (Fig. 5B). Mass differences primarily resulted from changes of the scalar. In contrast, scaling parameters for large oyster conversion did not show such a regular pattern and especially FM at both reef types scaled under other rules. While LWM and SM LIVE at HRD scaled by similar exponents (b/rounded = 1.40) and mass differences were mainly determined by different scalars, mass differences between

LWM and FM at HRD resulted from different exponents while scalars were similar. Scaling parameters for LWM, SM LIVE and FM appeared to be most heterogenic for large oysters at LRD (Fig. 5B).

Scaling parameters were also determined for small and large oyster LWM per site and year. Scaling parameters of these unique TF ($N = 60$, 30 small and 30 large) were significantly correlated (Fig. 5C). The scalar exponentially declined with increasing exponent ($\log a = -2.00 b + 1.99$, $R^2 = 0.99606$, $p < 0.001$). Exponential relations were slightly right-displaced for scaling parameters of all simple reefs ($\log a = -2.03 b + 2.09$, $R^2 = 0.99644$, $p < 0.001$) and slightly left-displaced for all complex reefs ($\log a = -1.98 b + 1.94$, $R^2 = 0.99641$, $p < 0.001$). Scaling exponents were high variable and ranged from < 1 to > 3 (Figs 4C, 5). Scaling exponents of large oysters ranged from < 1 to about 2, although one simple reef (SP 2010) had an exponent of 2.95881. Scaling exponents of small oysters ranged from about 2 to > 3 (Figs 4C, 5). Although generated by using all oyster sizes, scaling parameters of LWM conversion functions of two other studies, i.e. CF SH and CF KATS, fitted well to the exponential relationship of all unique TF of this study (Fig. 5C).

Despite the high correlation, small differences between exponents resulted in considerable different LWM (g) while an exponentially lower scalar had a strong additional effect. Considering similar exponents for small oysters ranging from $b = 2.83234$ to $b = 2.87106$ ($d = 0.03872$), the LWM of a 30 mm oyster ranged between 3.1 g and 4.2 g (+ 36 %) and of an 80 mm oyster between 49.4 g and 69.8 g (+ 41 %) (Fig. 6A). Considering small differences between exponents for large oysters ranging from $b = 1.75915$ to $b = 1.90149$ ($d = 0.14234$), the LWM of a 110 mm oyster ranged between 79.6 g and 141.1 g (+ 77 %) and of a 170 mm oyster between 171.2 to 316.6 g (+ 85 %) (Fig. 6A). Similar exponents of CF KATS and CF SH ($d = 0.1021$) resulted in extraordinarily different LWM (Figs 4C, 5A). Although the difference between scalars seemed small ($d = 0.00096$), CF SH estimated between 2 and 2.5-fold more LWM per oyster than CF KATS. The resulting LWM for a 30 mm oyster was 3.1 g and 6.2 g (+ 102 %), for a 80 mm oyster 24.3 g and 56.6 g (+ 123 %), for a 110 mm oyster 50.0 g and 115.3 g (+ 131 %) and for a 170 mm oyster 126.2 g and 304.6 g (+ 141 %) (Fig. 6A). Providing almost equal scalars of large oyster local TF RB ($a = 0.15677$) and large oyster local TF NL ($a = 0.15678$), a slightly higher exponent ($d = 0.03109$) of TF RB resulted in 17 % heavier large individuals, i.e. large oysters at the simple reef RB were mightier than at the complex reef NL (Fig. 6B).

A higher exponent was not generally resulting in more or less LWM, i.e. in mightier or slenderer shaped oysters (Fig. 6). For small oysters, increasing exponents by exponentially declining scalars of unique TF ($R^2 = 0.98539$) (Fig. 6A) and increasing exponents of local TF (Fig. 6B) tended to estimate less LWM of 30 mm oysters ($R^2 = 0.65056$), i.e. trend to a slenderer shape ($R^2 = 0.50646$), and rather more LWM of 80 mm oysters ($R^2 = 0.23768$), i.e. trend to a mightier shape ($R^2 = 0.08260$). These trends were not reflected by weighted TF as the higher exponent of TF HRD generally estimated less LWM, i.e. trend to a more slender shape of small

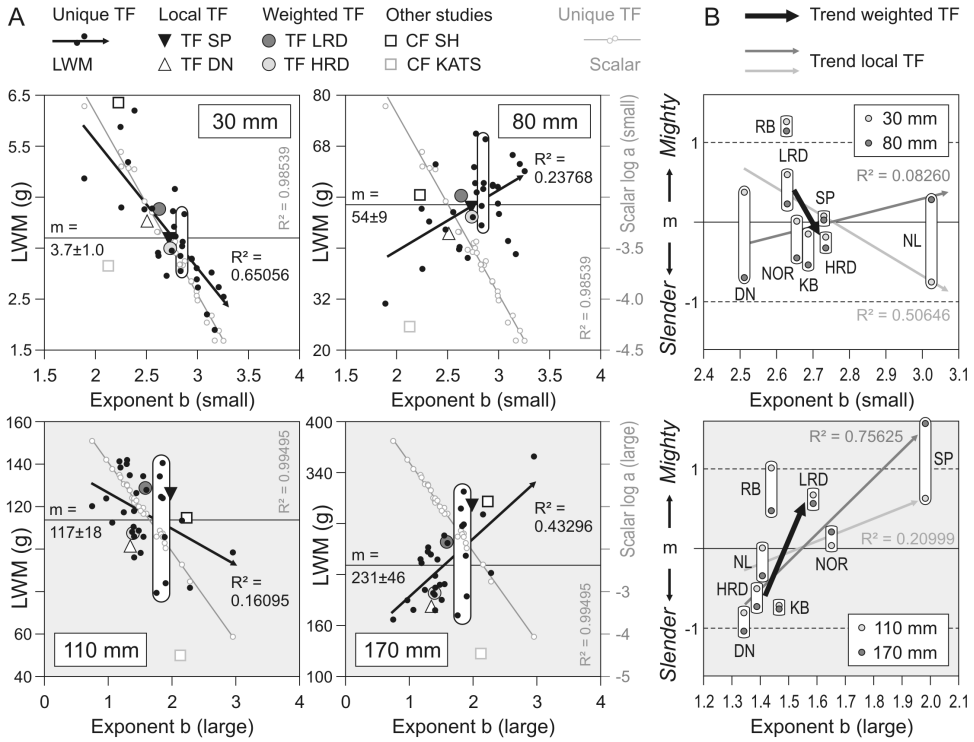


Figure 6. Relationship between scaling exponent and oyster LWM (g) of selected small (SL 30/80 mm, top) and large (SL 110/170 mm, bottom) individuals. **A** Plotted is LWM resulting from unique TF, selected local TF (SP for mighty and DN for slender shaped oysters), weighted TF (LRD, HRD) and CF of two other studies (SH, KATS) against exponent, respectively. Mean LWM (horizontal line, $m \pm SD$) and linear trend of increasing or decreasing LWM with increasing exponent of unique TF indicated (black arrow, R^2). Variability of LWM resulting from similar exponents of unique TF highlighted (rounded boxes). Additionally plotted is the exponential relationship (broken line, R^2 upend) between scalar and exponent of unique TF (gray circles). **B** Plotted is relative shape resulting from local TF (SP, RB, NOR, NL, KB, DN) and weighted TF against exponent. Relative shape = $(LWM - m) / SD$ with 0 = m and 1 = SD . Change of oyster shape with increasing exponent is displayed as a linear trend between sites (gray arrows, R^2). Trend between reef types indicated (black arrow). R^2 = coefficient of determination.

oysters (Figs 5A, B). For large oysters and analogous to small oysters, increasing exponents by exponentially declining scalars of unique TF ($R^2 = 0.99495$) (Fig. 6A) tended to estimate rather less LWM for 110 mm oysters ($R^2 = 0.16095$), i.e. trend to a slenderer shape, and more LWM for 170 mm oysters ($R^2 = 0.43296$), i.e. trend to a mightier shape. These trends were not consistently reflected by local TF or weighted TF (Fig. 6B) as higher exponents tended to or generally (as of TF LRD) estimated more LWM for 110 mm ($R^2 = 0.20999$) and 170 mm ($R^2 = 0.75625$), i.e. trend to a mightier shape of large oysters.

Variability of oyster LWM (kg) RD

The application of unique TF ($N = 60$, 30 small and 30 large) was expected to result in the most probable LWM (kg) RD per site and year during the study period 2008–2012. Respective RD were the nominal reef density (NRD, $N = 30$ local, $N = 5$ regional) when assessing deviations of areal LWM calculated by applying various CF or TF. Dynamic changes of the annual range of deviations per site, i.e. the range of the resulting LWM from the application of TF SP, TF LRD, TF HRD and TF DN, reflected site-specific temporal differences between allometric scaling relations (Fig. 7A). TF DN, representative of the slenderest shaped oysters, underestimated almost all NRD. Areal biomass was on average 23 % lower at simple reefs and 5 % lower at complex reefs which resulted in underestimations of, on average, 9 % in the study region (Fig. 7B). In contrast, TF SP, representative of the mightiest shaped oysters, overestimated most of the NRD (Fig. 7A). Deviations stayed low at the simple reefs SP and RB, but reached already up to 30 % at site NOR. TF SP resulted in distinct overestimations of up to 68 % at complex reefs, leading to an average 37 % higher areal biomass than NRD (Fig. 7A). The application of TF SP resulted in overestimations of on average 30 % in the study region (Fig. 7B). Low deviations were achieved by applying weighted TF, i.e. TF LRD to the monitoring data of simple reefs and TF HRD to the monitoring data of complex reefs. Deviations at the sites ranged from

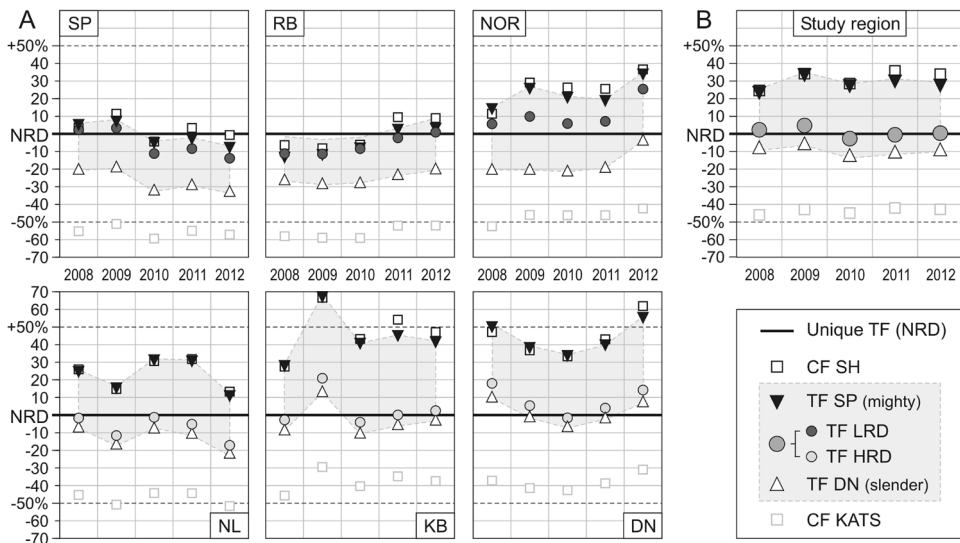


Figure 7. Variability of oyster LWM (kg) RD estimated for the study period 2008–2012. Displayed is the relative deviation (%) from nominal reef density (NRD). NRD was estimated by using unique TF. Deviations were estimated by using weighted TF (LRD, HRD), local TF (SP, DN) or CF of two other studies (SH, KATS). **A** Variability at the study sites. Sites arranged from mighty (SP) to slender (DN) oyster shape, equivalent to increasing reef density at simple (top) and complex reefs (bottom). **B** Variability in the study region. Range of deviation highlighted for TF of this study (gray area).

17 % below to 26 % above NRD, but most of the deviations stayed within ± 10 %. Deviations tended to be lower at simple reefs (mean 0.5 %) and higher at complex reefs (mean 1.4 %). The application of weighted TF resulted in an average 1 % higher biomass in the study region, ranging between 3 % below and 5 % above NRD.

The sensitivity of the interplay of an almost similar exponent and a slightly different scalar (Fig. 6B) was conspicuously reflected by resulting LWM (kg) RD that was calculated from the application of CF SH and CF KATS (Fig. 7). NRD was largely underestimated by the CF KATS (53 % at simple reefs, 41 % at complex reefs) and overestimated by the CF SH (10 % at simple reefs, 39 % at complex reefs). CF SH showed a comparable dynamic as TF SP and its application to the monitoring data resulted in biomass overestimations of on average 32 % in the study region. In contrast, the application of CF KATS resulted in an average 44 % less biomass in the study region.

Mussel allometric scaling

Mussel shape as the proportion of LWM (g) per SL varied between sites (Fig. 8A). Shape differences became obvious in old (large) mussels (> 40 mm) while the relative difference between SL classes did not change with increasing size. Shape differences seemed small but large mussels had a mightier shape (10 % more LWM) at simple reefs than at complex reefs. Thus, individual metrics of mussels from 2008 through 2012 were pooled according to reef type, i.e. weighted to simple (LRD) and complex (HRD) reefs (Fig. 8B,

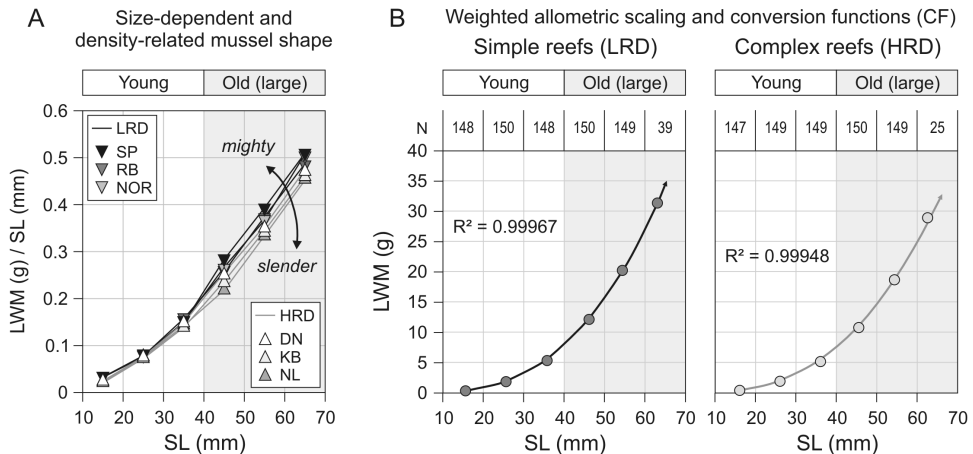


Figure 8. Mussel shape and allometric scaling. **A** Size-dependent (young/old) and density-related (LRD, HRD) mussel shape. Plotted is individual LWM (g) per SL (mm) against SL (mm) of 6 SL classes per site. **B** Determination of LWM weighted CF. Plotted is LWM (g) against SL (mm) of 6 SL classes after pooling individual metrics from 2008 through 2012 according to reef type. Given are powered relationships and coefficients of determination (R^2). Old (large) mussels highlighted (gray area). Number of mussels per SL class is given (N). Scaling parameters of all weighted CF are listed in Table 2.

Table 2). In contrast to size-dependent scaling relations of oysters and the determination of TF, powered CF perfectly described the relationship between mussel biomass and all SL classes (LWM_{LRD} : $R^2 = 0.99967$, LWM_{HRD} : $R^2 = 0.99948$, $SM\ LIVE_{LRD}$: $R^2 = 0.99927$, $SM\ LIVE_{HRD}$: $R^2 = 0.99874$, FM_{LRD} : $R^2 = 0.99845$, FM_{HRD} : $R^2 = 0.99817$).

Areal reference and oyster density attributes

The abundance of live oysters at two reefs (NL 01-04-2008, DN 29-03-2011) with similar areal LWM (kg) was contrasted (Fig. 9A). LWM at both sites was about 25 kg CD and about 12 kg RD as RC (45.9 % at NL in 2008, 46.6 % at DN in 2011) adjusted the density of clusters to the reef area. The difference between density attributes per CD and RD displayed the prominence of areal reference.

At both sites, live oysters were present in all SL classes and reached a maximum length of 230 mm (Fig. 9B). Total live abundance at the reefs differed tremendously (Figs 8A, B). DN had 4,539 total oyster CD and NL only 464. The population at DN consisted of 4,245 juvenile oyster CD and 293 adult oyster CD. Total oyster RD at DN was 2,113 consisting of 1,976 juveniles and 136 adults. Juveniles at DN dominated the total population by 93.5 %. Despite the same season, only 4.2 % were juveniles at NL and the population was dominated by adult oysters. The abundance of 205 adult oyster RD at NL was 50 % higher than at DN. The abundance of small oysters accounted for the difference between the adult populations (Figs 8A, B). A similar density at both reefs was the abundance of large oysters, i.e. 55 RD or 119 CD at NL and 56 RD or 121 CD at DN. The dynamic relation between the density attributes large live oyster and LWM was also reflected by station densities (CD) (Fig. 9C).

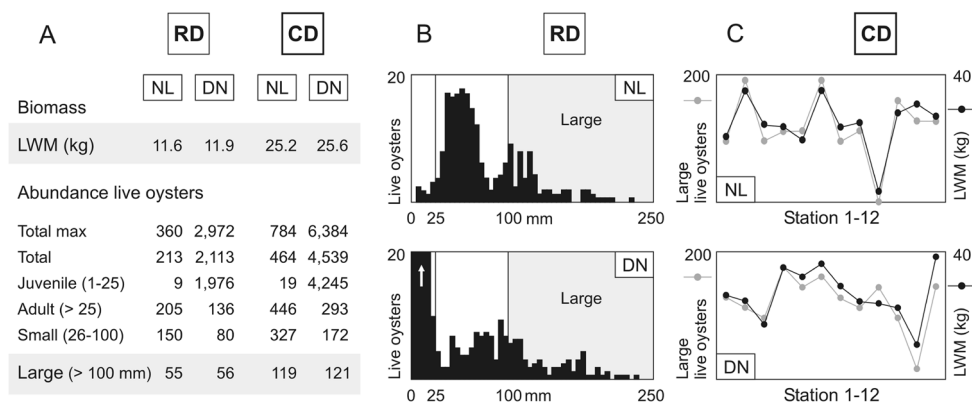


Figure 9. Density of live oysters at site NL on 01-04-2008 and site DN on 29-03-2011. **A** Density attributes LWM (kg) and abundance per areal reference RD and CD. **B** Length frequency distribution of live oyster RD. **C** Density attributes LWM (kg) and large live oyster CD at the 12 monitoring stations. Density metrics and density attributes according to Figure 3.

Intra-reef variation of oyster density attributes

A high spatial variation of oyster density attributes was present at all sites and years ($N = 36$ reefs), and generally resulted in high standard deviations. Coefficients of variation (CV) mainly ranged between 0.2 and 1.0 (Fig. 10). The variability of LWM among the 12 monitoring stations as displayed for the complex reefs NL in 2008 and DN in 2011 (Fig. 9) resulted in CV of about 0.3 which was comparably low compared to other sites (Fig. 10A). Apart from total live oyster abundance, the CV of all density attributes were moderately negative correlated with density (LWM: $R^2 = 0.62635$, $p < 0.001$, Fig. 10A; Large live: $R^2 = 0.60881$, $p < 0.001$; Adult live: $R^2 = 0.41744$, $p < 0.001$; Total live: $R^2 = 0.10091$, $p = 0.06$; SM: $R^2 = 0.58133$, $p < 0.001$, Fig. 10A; Large shell: $R^2 = 0.57057$, $p < 0.001$; Adult shell: $R^2 = 0.63452$, $p < 0.001$; Total shell: $R^2 = 0.28440$, $p < 0.001$).

CV of areal biomass (LWM or SM) and the CV of total or adult abundance (live or shell) were moderately to strongly positive correlated (LWM/total live: $R^2 = 0.51191$, $p < 0.001$; LWM/adult live: $R^2 = 0.54837$, $p < 0.001$, Fig. 10B; SM/total shell: $R^2 = 0.59549$, $p < 0.001$, Fig. 10B; SM/adult shell: $R^2 = 0.74836$, $p < 0.001$), while CV of areal biomass were higher than CV of total or adult oyster abundance (LWM: mean CV = 0.55, SM: mean CV = 0.53, Total live: mean CV = 0.49, Adult live: mean CV =

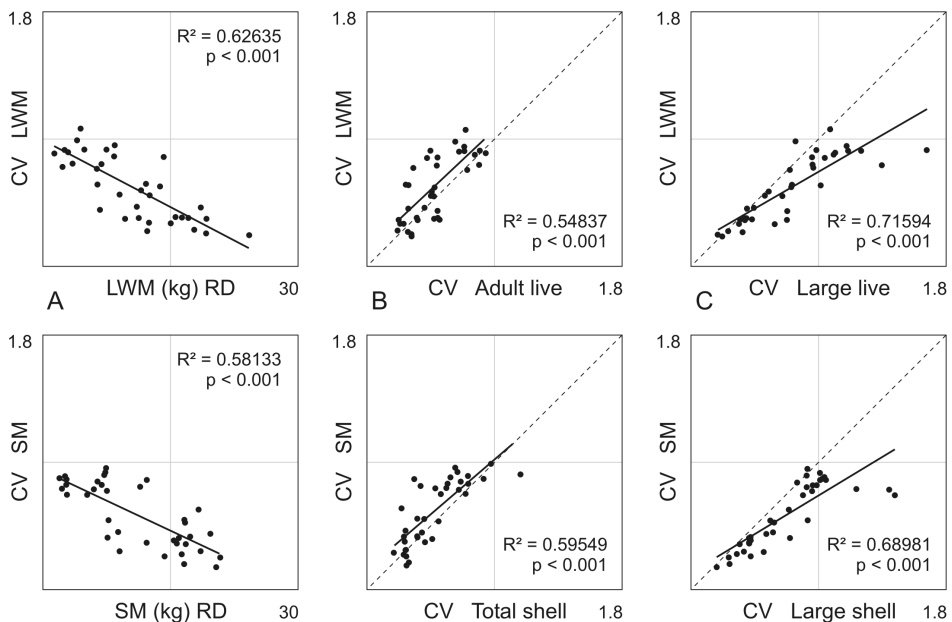


Figure 10. Coefficient of variation (CV) of selected oyster density attributes per site and year ($N = 36$ reefs). **A** Relationship between areal biomass and CV. **B, C** Interrelations between CV of abundance and areal biomass. Given are linear relationship, coefficient of determination (R^2) and significance level (p). Proportional reference line indicated (dotted). See text for all other relationships. Density metrics and density attributes according to Figure 3.

0.47, Total shell: mean CV = 0.46, Adult shell: mean CV = 0.44). CV of areal biomass (LWM or SM) and the CV of large oysters (live or shell) were strongly positive correlated (LWM/large live: $R^2 = 0.71594$, $p < 0.001$; SM/large shell: $R^2 = 0.68981$, $p < 0.001$; Fig. 10C), while CV of large oysters were higher than CV of areal biomass (Large live mean CV = 0.71, Large shell mean CV = 0.68, LWM: mean CV = 0.55, SM: mean CV = 0.53). Correlation between the CV of areal biomass and large oyster abundance was strongest at all complex reefs (LWM/large live: $R^2 = 0.84884$, $p < 0.001$, LWM: mean CV = 0.39, Large live: mean CV = 0.46; SM/large shell: $R^2 = 0.95117$, $p < 0.001$, SM: mean CV = 0.39, Large shell: mean CV = 0.46). As CV of large oysters (live or shell) at some reefs with lowest mean estimates of oyster density reached values well above 1.0, correlation between CV of areal biomass and large oyster abundance was weak at all simple reefs (LWM: $R^2 = 0.26703$, $p < 0.03$, LWM: mean CV = 0.72, Large live: mean CV = 0.95; SM: $R^2 = 0.20197$, $p < 0.06$, SM: mean CV = 0.68, Large shell: mean CV = 0.89).

Interrelations of oyster density attributes

Interrelations between oyster density attributes per site and year ($N = 36$ reefs) revealed distinct linkages, most of them showing strong linear and positive relationships (Figs 11, 12). The abundance of the total live population depended on the abundance of juvenile

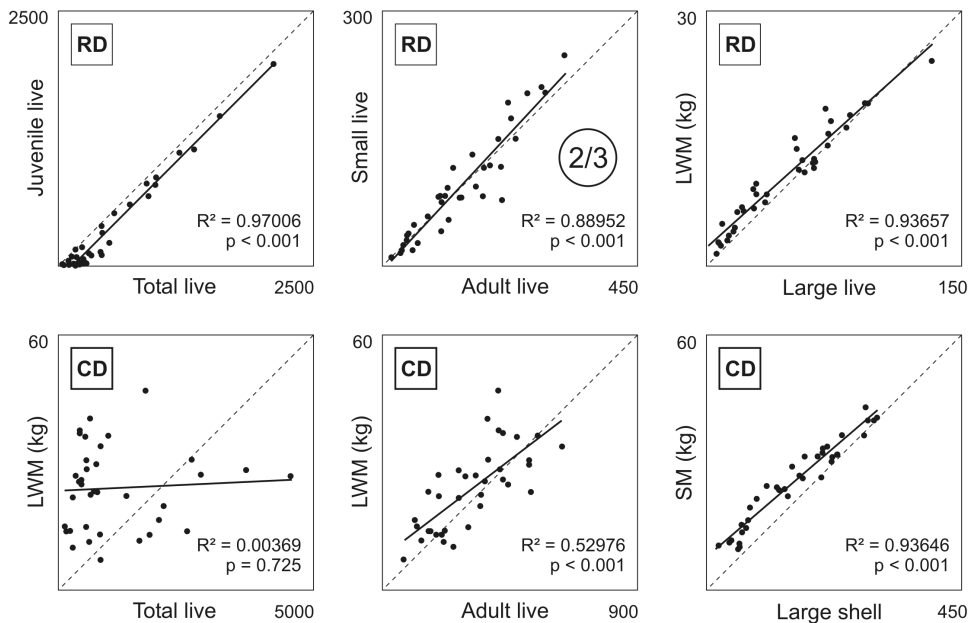


Figure 11. Interrelations between selected oyster density attributes per site and year ($N = 36$ reefs). Given are linear relationship, coefficient of determination (R^2) and significance level (p). Proportional reference line (dotted) and proportions indicated (circles). See text for all other interrelations. Density metrics and density attributes according to Figure 3.

live oysters (RD: $R^2 = 0.97006$, $p < 0.001$, Fig. 11) (CD: $R^2 = 0.98304$, $p < 0.001$). Likewise, the abundance of all shell depended on the abundance of juvenile shell (RD: $R^2 = 0.97673$, $p < 0.001$) (CD: $R^2 = 0.98404$, $p < 0.001$). Abundance of total live oysters was not explaining LWM (RD: $R^2 = 0.04935$, $p = 0.193$) (CD: $R^2 = 0.00369$, $p = 0.725$, Fig. 11). Likewise, the abundance of all shell was not explaining SM (RD: $R^2 = 0.04837$, $p = 0.197$) (CD: $R^2 = 0.00012$, $p = 0.950$). LWM increased with the abundance of adult live oysters (RD: $R^2 = 0.71402$, $p < 0.001$) (CD: $R^2 = 0.52976$, $p < 0.001$, Fig. 11) and SM with the abundance of adult shell (RD: $R^2 = 0.78733$, $p < 0.001$) (CD: $R^2 = 0.59085$, $p < 0.001$), but relationships were relatively low (RD) or even weak (CD) as the abundance of adult oysters largely depended on the abundance of small oysters (live oysters RD: $R^2 = 0.88952$, $p < 0.001$, Fig. 11) (live oysters CD: $R^2 = 0.84851$, $p < 0.001$) (oyster shell RD: $R^2 = 0.95251$, $p < 0.001$) (oyster shell CD: $R^2 = 0.91846$, $p < 0.001$). 2/3 of adult live oysters were small individuals (small adult live = 66.0 ± 15.4 %) and 3/4 of adult shell accounted for small shell (small adult shell = 75.3 ± 11.4 %). LWM was strongly related to the abundance of large live oysters (RD: $R^2 = 0.93657$, $p < 0.001$, Fig. 11) (CD: $R^2 = 0.90843$, $p < 0.001$) and SM to the abundance of large shell (RD: $R^2 = 0.95113$, $p < 0.001$) (CD: $R^2 = 0.93646$, $p < 0.001$, Fig. 11).

A linear relation existed between the abundance of large live oysters and large shell (RD: $R^2 = 0.84737$, $p < 0.001$, Fig. 12) (CD: $R^2 = 0.78122$, $p < 0.001$). Although a weak negative trend with increasing abundance of large shell was present, the propor-

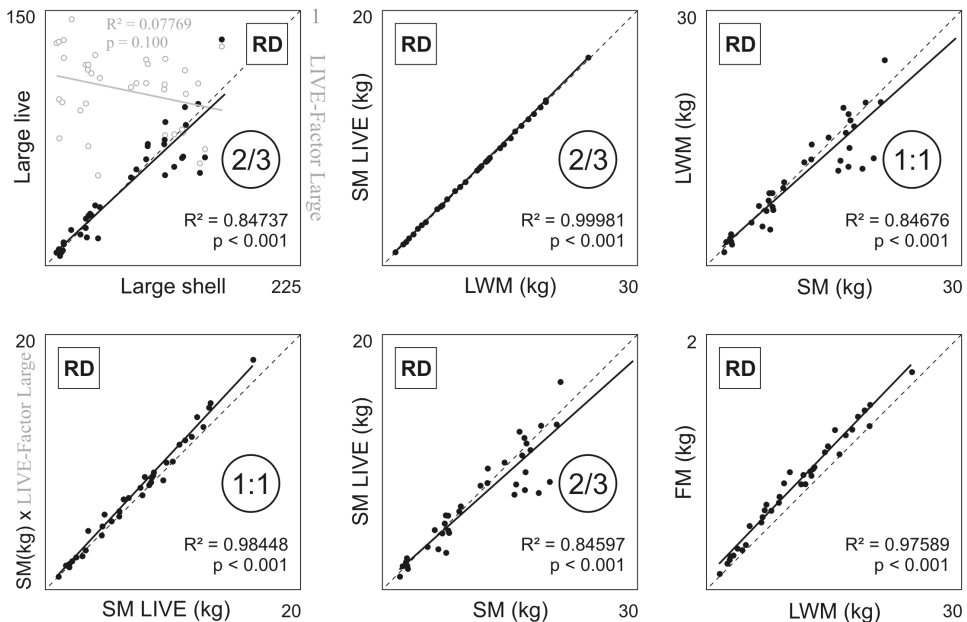


Figure 12. Interrelations between selected oyster density attributes per site and year ($N = 36$ reefs). Given are linear relationship, coefficient of determination (R^2) and significance level (p). Proportional reference line (dotted) and proportions indicated (circles). See text for all other interrelations. Density metrics and density attributes according to Figure 3.

tion of large live oysters was similar at all sites and years (RD: $R^2 = 0.07769$, $p = 0.100$, Fig. 12) (CD: $R^2 = 0.13573$, $p = 0.027$). 2/3 of all large oysters (LIVE-Factor Large = 69.0 ± 15.0 %) were alive. SM LIVE per site and year was re-calculated by multiplying SM with the respective LIVE-Factor Large. Differences to nominal SM LIVE were negligible (RD: slope = 1.07546, intercept = 0.3 %, $R^2 = 0.98448$, $p < 0.001$, Fig. 12) (CD: slope = 1.06335, intercept = 0.1 %, $R^2 = 0.97377$, $p < 0.001$).

A significant linear relation existed between the density attributes SM LIVE and LWM (RD: $R^2 = 0.99981$, $p < 0.001$, Fig. 12) (CD: $R^2 = 0.99940$, $p < 0.001$). 2/3 of the LWM accounted for SM LIVE (67.6 ± 0.8 %). As a consequence, SM LIVE correlated with the abundance of large live oysters (RD: $R^2 = 0.93833$, $p < 0.001$) (CD: $R^2 = 0.90731$, $p < 0.001$). A linear relation existed between the density attributes SM LIVE and SM (RD: $R^2 = 0.84597$, $p < 0.001$, Fig. 12) (CD: $R^2 = 0.72971$, $p < 0.001$). 2/3 of the SM accounted for SM LIVE (64.4 ± 12.3 %). As a consequence, along with the 2/3 proportions SM LIVE/LWM and SM LIVE/SM, SM equalled LWM (RD: slope = 0.89002, intercept = 2.1 %, $R^2 = 0.84676$, $p < 0.001$, Fig. 12) (CD: slope = 0.84189, intercept = 5.1 %, $R^2 = 0.73000$, $p < 0.001$). Differences between LWM and SM were noteworthy when the proportion of large live oysters was about or below 50 % which was the case in most of the study years at site NL. A strong linear relationship was relating the density attributes FM and LWM (RD: $R^2 = 0.97589$, $p < 0.001$, Fig. 12) (CD: $R^2 = 0.95781$, $p < 0.001$). Approximately 2/30 of the LWM accounted for FM but this was not significant. FM correlated with the abundance of large live oysters (RD: $R^2 = 0.86568$, $p < 0.001$) (CD: $R^2 = 0.79771$, $p < 0.001$).

Interrelations of mussel density attributes

Interrelations between density attributes of live mussels per site and year ($N = 36$ reefs) revealed distinct linkages, some of them showing strong linear and positive relationships (Fig. 13). The abundance of the total population changed in relation to the abundance of recruits (RD: $R^2 = 0.58382$, $p < 0.001$) (CD: $R^2 = 0.86588$, $p < 0.001$), but the influence of young mussels (recruits and small) on total abundance was much stronger (RD: $R^2 = 0.90472$, $p < 0.001$, Fig. 13) (CD: $R^2 = 0.97684$, $p < 0.001$). Total abundance could not explain LWM (RD: $R^2 = 0.24002$, $p = 0.002$) (CD: $R^2 = 0.00620$, $p = 0.648$). In contrast, LWM was strongly related to the abundance of old (large) mussels (RD: $R^2 = 0.93243$, $p < 0.001$, Fig. 13) (CD: $R^2 = 0.79311$, $p < 0.001$). Linear relations, but with distinct lower coefficients of determination, were also present between the abundance of mature mussels (small and large) and LWM (RD: $R^2 = 0.78340$, $p < 0.001$) (CD: $R^2 = 0.53289$, $p < 0.001$). A significant linear relation existed between the density attributes SM LIVE and LWM (RD: $R^2 = 0.98899$, $p < 0.001$, Fig. 13) (CD: $R^2 = 0.97588$, $p < 0.001$). Half of the LWM accounted for SM LIVE (49.9 ± 2.3 %). A strong linear relation existed between the density attributes FM and LWM (RD: $R^2 = 0.99237$, $p < 0.001$, Fig. 13) (CD: $R^2 = 0.97802$, $p < 0.001$). 1/7 of the LWM account-

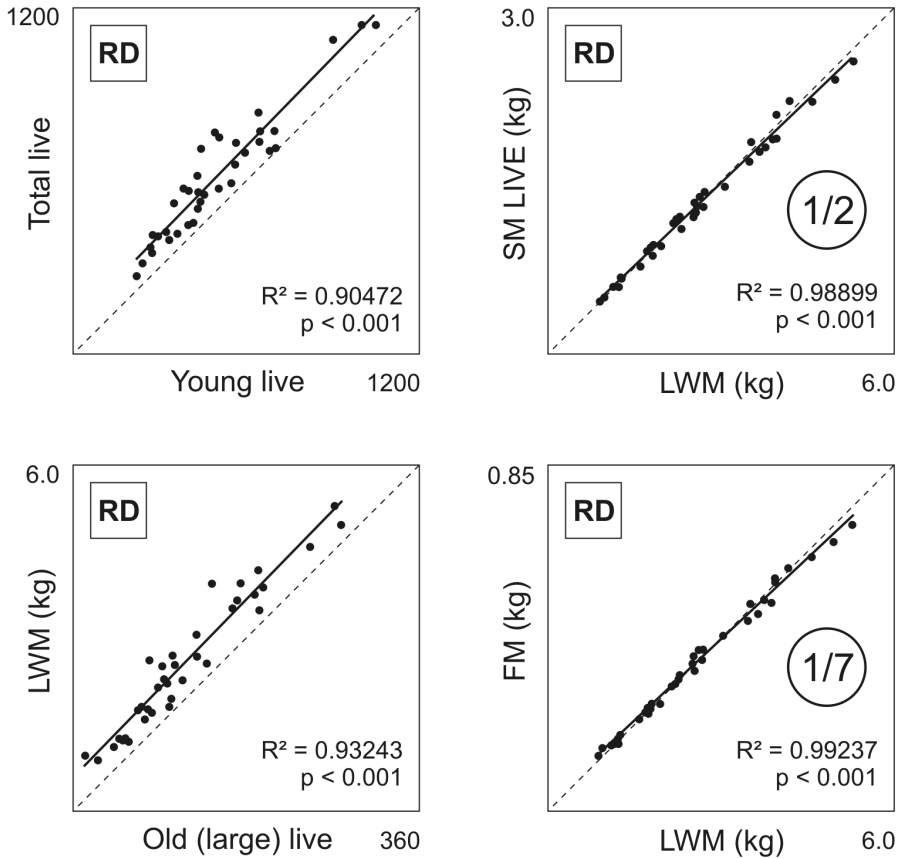


Figure 13. Interrelations between selected mussel density attributes per site and year ($N = 36$ reefs). Given are linear relationship, coefficient of determination (R^2) and significance level (p). Proportional reference line (dotted) and proportions indicated (circles). See text for all other interrelations. Density metrics and density attributes according to Figure 3.

ed for FM (14.2 ± 0.6 %). SM LIVE and FM were also related to the abundance of large mussels (SM LIVE RD: $R^2 = 0.90923$, $p < 0.001$) (SM LIVE CD: $R^2 = 0.73118$, $p < 0.001$) (FM RD: $R^2 = 0.89214$, $p < 0.001$) (FM CD: $R^2 = 0.67975$, $p < 0.001$).

Density scaling

The significant relationship between areal biomass and large individuals enabled the implementation of a density scaling for oysters and mussels. Oyster and mussel RD-scaling was performed by using RD of large individuals and biomass of all sites and years, respectively ($N = 36$ reefs). Oyster and mussel CD-scaling was performed by

Table 2. Oyster and mussel scaling parameters (a, b) of powered or linear relationships between individual metrics or density attributes. Allometric scaling (1–4) displayed in Figure 5A and (5, 6) in Figure 8B. Density scaling (7) displayed in Figure 14A and (8) in Figure 14B. R² = coefficient of determination. N = number of basic data points. Reef type determination according to Figure 4C. Density metrics and density attributes according to Figure 3.

A.							
Oyster							
Individual biomass							
Power $y = a(x)^b$	Reef type	y (g)	a	x (mm)	b	R²	N (individuals)
(1)	LRD	LWM	0.00056	SL Small	2.62918	0.99922	426
	LRD	LWM	0.07430	SL Large	1.58733	0.99339	448
	HRD	LWM	0.00032	SL Small	2.73533	0.99977	438
	HRD	LWM	0.15631	SL Large	1.39051	0.98933	623
	LRD	SM LIVE	0.00041	SL Small	2.60492	0.99932	426
	LRD	SM LIVE	0.03139	SL Large	1.68592	0.99632	448
	HRD	SM LIVE	0.00022	SL Small	2.72139	0.99991	438
	HRD	SM LIVE	0.10021	SL Large	1.40173	0.98607	623
	LRD	FM	0.00006	SL Small	2.63358	0.99611	426
	LRD	FM	0.05292	SL Large	1.13888	0.95726	448
	HRD	FM	0.00003	SL Small	2.75259	0.99568	438
	HRD	FM	0.15576	SL Large	0.84818	0.96980	623
Areal biomass							
Power $y = a(x)^b$	Areal reference	y (kg)	a	x (individuals)	b	R²	N (reefs/clusters)
(7)	RD	LWM	0.53024	Large live	0.78807	0.94308	36
	RD	SM LIVE	0.36776	Large live	0.78075	0.94425	36
	RD	SM	0.46366	Large shell	0.75970	0.93298	36
	RD	FM	0.05763	Large live	0.70352	0.88740	36
	CD	LWM	0.87434	Large live	0.73150	0.98488	432
(8)	CD	SM LIVE	0.58360	Large live	0.73395	0.98364	432
	CD	SM	0.87596	Large shell	0.68669	0.98203	432
	CD	FM	0.10784	Large live	0.63904	0.95734	432
Linear $y = a(x)+b$	Areal reference	y (kg)	a	x (kg)	b	R²	N (reefs/clusters)
	RD	SM LIVE	0.67	LWM		0.99981	36
	RD	FM	0.07	LWM	0.09	0.97589	36
	CD	SM LIVE	0.67	LWM		0.99966	432
	CD	FM	0.07	LWM	0.15	0.98363	432
B.							
Mussel							
Individual biomass							
Power $y = a(x)^b$	Reef type	y (g)	a	x (mm)	b	R²	N (individuals)
(5)	LRD	LWM	0.00013	SL	3.00001	0.99967	784
(6)	HRD	LWM	0.00016	SL	2.92377	0.99948	769
	LRD	SM LIVE	0.00005	SL	3.08179	0.99927	784
	HRD	SM LIVE	0.00006	SL	2.98792	0.99874	769
	LRD	FM	0.00006	SL	2.69075	0.99845	784
	HRD	FM	0.00010	SL	2.51770	0.99817	769
Areal biomass							
Linear $y = a(x)+b$	Areal reference	y (kg)	a	x (individuals)	b	R²	N (reefs/clusters)
	RD	LWM	0.01723	Large	0.54972	0.93423	36
	RD	SM LIVE	0.00819	Large	0.31445	0.90923	36
	RD	FM	0.00225	Large	0.09810	0.89214	36
	CD	LWM	0.01532	Large	2.05974	0.97846	432
	CD	SM LIVE	0.00752	Large	1.07499	0.97139	432
	CD	FM	0.00200	Large	0.33956	0.97029	432
Linear $y = a(x)+b$	Areal reference	y (kg)	a	x (kg)	b	R²	N (reefs/clusters)
	RD	FM	0.13	LWM	0.02	0.99237	36
	CD	FM	0.13	LWM	0.07	0.99612	432

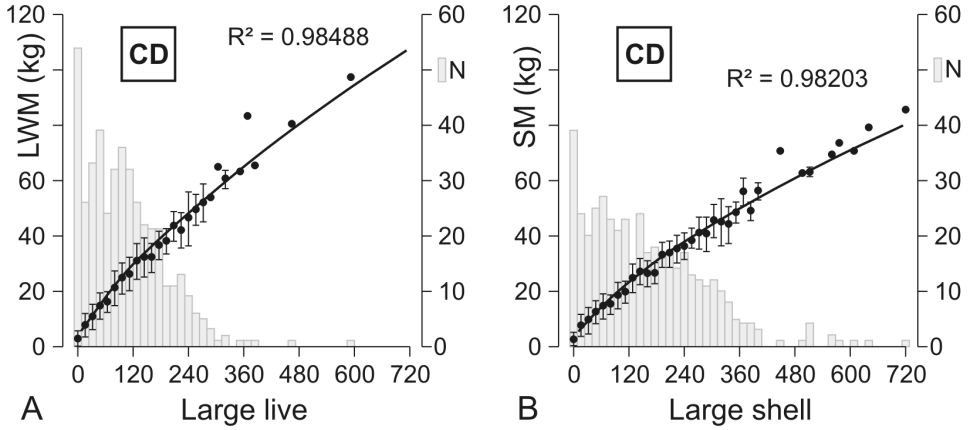


Figure 14. CD-density scaling of large oysters. **A** Plotted is LWM (kg) \pm SD against large live oysters per abundance class. **B** Plotted is SM (kg) \pm SD against large oyster shell per abundance class. Abundance classes derived from pooling 432 stations to intervals of 16 large oyster CD, respectively. N = Number of stations per abundance class (bars). Powered relationship indicated and coefficient of determination (R^2) given. Scaling parameters listed in Table 2 (7, 8). Density metrics and density attributes according to Figure 3.

using the CD of large individuals and biomass at all stations, respectively ($N = 432$ cluster). Therefore, stations were pooled by the abundance of large individuals into abundance classes and mean biomass \pm standard deviation was determined from all stations within each class. As frame size was 1/16 of a square meter, 16 individuals was the minimal interval per abundance class.

37 abundance classes resulted from the maximum abundance of 592 large live oyster CD to scale oyster LWM (Fig. 14A), SM LIVE and FM. 54 of the 432 stations were without large live oysters and had a mean of 3.9 ± 3.4 kg LWM, 2.6 ± 2.2 kg SM LIVE and 421 ± 366 g FM. 45 abundance classes resulted from the maximum abundance of 720 large oyster shell CD to scale oyster SM (Fig. 14B). 39 of the 432 stations were without large oyster shell and had a mean of 3.5 ± 3.2 kg SM. 78 abundance classes resulted from the maximum abundance of 1,248 large live mussel CD to scale mussel LWM, SM LIVE and FM. One of the 432 stations was without large live mussels and had 1.0 kg LWM, 0.5 kg SM LIVE and 187 g FM. Best fit for oyster density scaling per areal reference was a power function $y = a(x)^b$ with y = biomass (kg), a = scalar, x = abundance of large oysters and b = exponent. Best fit for mussel density scaling per areal reference was a linear equation $y = a(x) + b$ with y = biomass (kg), a = scalar, x = abundance of large mussels and b = intercept. Scaling parameters of all equations are given in Table 2.

Simple vs. Complex reefs

Irrespective of areal reference, all oyster density attributes but total or juvenile abundance were significantly different among reef types. Simple reefs with LRD were sig-

Table 3. Oyster and mussel density attributes (mean \pm SD) per areal reference (RD, CD) at simple and complex reefs during the study period 2008–2013 (N = 18 reefs per reef type). IND = individuals. Additionally given are proportions of live oysters (LIVE-Factor) and mean oyster SL. Dominance by biomass is given for oysters and dominance by abundance of large individuals is given for mussels. Significant difference between reef types per areal reference and between RD at complex reefs vs. CD at simple reefs is indicated (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Density metrics and density attributes according to Figure 3.

Areal reference		RD		p	RD		p	CD		p	CD	
Reef type		Simple			Complex			Simple			Complex	
Density attribute	Unit	mean	SD		mean	SD		mean	SD		mean	SD
A.												
Oyster												
Reef coverage	%	33.5	11.9	***	48.9	4.1						
Total live	IND	384.9	368.1		570.5	560.2		1,053.9	844.6		1,183.9	1,217.5
Total shell	IND	1,038.2	1,272.7		1,345.7	798.8	*	2,659.0	2,545.3		2,756.1	1,669.4
Juv live	IND	306.0	358.2		369.6	585.5		827.0	868.0		774.3	1,267.9
Juv shell	IND	870.5	1,213.2		929.8	833.5	*	2,188.0	2,482.7		1,910.7	1,754.5
Adult live	IND	78.9	52.4	***	200.9	59.9		226.9	109.6	***	409.6	109.1
Adult shell	IND	167.7	110.7	***	415.9	98.4		471.0	213.2	***	845.4	170.1
Small live	IND	59.9	48.4	***	128.5	59.4		170.1	107.9	*	261.0	112.5
Small shell	IND	140.5	107.5	***	305.2	92.8		387.3	216.5	**	618.3	166.4
Large live	IND	19.0	9.8	***	72.4	20.0	*	56.8	25.4	***	148.6	39.3
Large shell	IND	27.2	13.5	***	110.7	22.1	*	83.7	40.5	***	227.1	44.4
FM	kg	0.5	0.2	***	1.1	0.2	*	1.4	0.5	***	2.3	0.5
LWM	kg	5.5	2.6	***	15.2	3.6		16.4	5.9	***	31.2	6.8
LWM Small	kg	1.8	1.3	***	3.6	1.5		5.1	2.8	*	7.4	3.1
LWM Large	kg	3.6	1.8	***	11.5	3.5		11.1	5.3	***	23.6	6.7
SM live	kg	3.8	1.7	***	10.2	2.4		11.2	4.0	***	20.9	4.6
SM	kg	5.7	2.5	***	16.5	2.7		17.2	6.0	***	33.7	4.8
LIVE-Factor Total	%	46.1	24.4		37.6	15.8						
LIVE-Factor Juv	%	38.3	31.2		23.3	24.6						
LIVE-Factor Adult	%	50.0	14.2		48.7	9.4						
LIVE-Factor Small	%	44.9	14.6		41.7	11.6						
LIVE-Factor Large	%	71.8	16.2		66.2	13.6						
SL total live	mm	38.3	26.2		59.1	26.6						
SL Total shell	mm	27.3	15.6	*	38.0	15.5						
SL Juv live	mm	9.8	4.5		11.1	3.1						
SL Juv shell	mm	10.2	3.5		11.1	2.2						
SL Adult live	mm	82.9	17.6		91.7	13.1						
SL Adult shell	mm	69.5	15.4	*	78.0	7.9						
SL Small live	mm	59.1	9.1		59.6	8.8						
SL Small shell	mm	51.1	7.2		53.9	5.3						
SL Large live	mm	139.9	12.1		143.8	8.2						
SL Large shell	mm	137.3	9.0		142.0	7.4						
B.												
Mussel												
Total	IND	529.7	149.3	*	696.2	243.2	***	1,744.8	825.2		1,434.9	529.4
Recruits	IND	270.9	138.8		316.1	177.7	**	957.1	743.1		660.8	401.6
Small	IND	168.7	80.7	*	234.1	104.0	***	530.6	262.0		479.2	215.7
Young	IND	439.6	156.8		550.2	229.2	***	1,487.7	889.8		1,140.0	510.2
Large/Old	IND	90.0	49.2	**	146.0	71.5	***	257.1	87.7		294.9	137.3
FM	kg	0.3	0.1	*	0.4	0.2	***	0.9	0.2		0.8	0.3
LWM	kg	2.1	1.0	*	3.0	1.2	***	6.3	1.4		6.1	2.4
SM LIVE	kg	1.1	0.5		1.4	0.6	***	3.3	0.7		2.9	1.2
C.												
Dominance												
Oyster FM	%	59.6	9.0	***	73.9	6.8						
Oyster LWM	%	70.9	7.8	***	83.8	4.6						
Oyster SM LIVE	%	75.9	7.0	***	87.9	3.6						
Oyster SM	%	82.8	5.4	***	92.0	3.0						
Mussel Large LIVE	%	81.0	7.9	***	64.2	10.0						
Mussel Large SHELL	%	74.8	10.1	***	54.1	13.0						

nificantly less covered by clusters than complex reefs with HRD (Table 3). The difference of RC did not alter general characteristic differences between reef types but increased the significance level of small oyster occurrence between reef types. Irrespective of areal reference, juvenile oyster abundance (live or shell) was not significantly higher at complex reefs. Likewise, total oyster abundance (live or shell) did not differ between reef types, although slightly higher at complex reefs, but mean oyster size was on average significantly larger at complex reefs than at simple reefs. The size difference resulted from a significantly higher abundance of small and large oysters (live or shell) at complex reefs. The mean size of small or large oysters was similar at both reef types, although slightly larger at complex reefs. The proportion of live oysters per density attribute was similar at both reef types, although slightly lower at complex reefs. Irrespective of areal reference, the structural density attributes large oyster (live or shell) and biomass (FM, LWM, SM LIVE and SM) were significantly higher at complex reefs than at simple reefs. Oyster station density (CD) at simple vs. complex reefs reached maximum values of 17,504 vs. 9,088 juvenile shell, 1,648 vs. 1,776 adult shell, 1,456 vs. 1,536 small shell, 448 vs. 720 large shell or 70 vs. 86 kg SM, 5,104 vs. 6,016 juvenile live oyster, 880 vs. 1,232 adult live oysters, 816 vs. 1,008 small live oysters, 368 vs. 592 large live oysters or 83 vs. 97 kg LWM, respectively. This shows that single clusters at simple reefs can be built by exceptional high oyster density.

CD of mussel abundance and biomass was similar at both reef types, although slightly higher at simple reefs, but the difference of RC altered these relationships. When abundance was calculated across the reef area, mussel recruit RD was still similar between reef types, but significantly more small and especially more large mussels were colonizing complex reefs which also resulted in significantly higher biomass than at simple reefs.

Both reef types were dominated by oyster biomass. Dominance of oyster biomass increased from FM over LWM, SM LIVE to SM but was always significantly higher at complex reefs than at simple reefs. Oyster SM dominated the total SM, i.e. SM of oysters plus SM LIVE of mussels, to 83 % at simple reefs and 92 % at complex reefs. In contrast, both reef types were dominated by mussel abundance when large individuals of both species were taken into account. Dominance of large mussels was significantly higher at simple reefs than at complex reefs but declined from 81 % to 75 % at simple reefs and from 64 % to only 54 % at complex reefs when large post-mortem oyster shells were included in the total abundance of large individuals.

Discussion

Pacific oyster reefs in the study area constitute undisturbed systems without external larval supply from oyster culture, addition of oysters by transplanting or extraction of oysters by harvesting. Results of this study are assumed to comply with naturally matured Pacific oyster reefs worldwide. The prominent status of large oysters for both allometric scaling and density induced the development of a conceptual framework towards a harmonized approach to characterizing Pacific oyster reefs (Box 1). The con-

cept applies to the proposed density attributes of this study (Fig. 3), where biotic density (abundance or biomass of live oysters) is a function of ecological structure and biogenic density (abundance or biomass of oyster shell) is a function of biophysical structure. The concept applies to cluster density (CD) as a function of vertical structure and to reef coverage (RC) as a function of horizontal structure, both resulting in reef density (RD) as a function of reef texture. Reef texture can be equated with reef complexity. Hence, engineering strength as a function of reef complexity or reef performance is assumed to be reflected by RD.

Oyster shape and allometric scaling

Oyster allometric scaling should be rated far more complex than previously considered. Large oysters had an exceptional scaling behavior which considerably affected scaling relations. Length versus weight data indicating a size-dependent scaling behavior was also displayed in earlier studies on Pacific oysters (Nehls and Büttger 2006, Walles et al. 2015b) but was not noticed or not considered relevant. Results of this study conditioned on the implementation of a novel size-dependent concept of twin functions (TF) for the estimation of oyster individual biomass by SL (Fig. 5). This study demonstrated that the interplay of scaling parameters is highly sensitive to the estimation of oyster individual biomass and that conclusions on oyster shape should not be drawn from scaling exponent only (Fig. 6). Shape variability of especially large oysters was remarkably and fundamentally affected the estimation of areal biomass (Fig. 7). Results of this study showed that the shape variation of especially large oysters was related to oyster density which conditioned on the implementation of weighted TF by classifying reefs by oyster density, i.e. the abundance of large live oyster RD. Powell et al. (2016) mentioned that variation in oyster shape has not yet been predictably associated with oyster density. Results of this study imply that this may have been related to the lack of comparable measurements for density.

In accordance with the spatial and temporal variation in the length-biomass relationship for American oysters *C. virginica* (Powell et al. 2016), a negative relationship between scalar and scaling exponent described shape differences of Pacific oysters. Powell et al. (2016) found the scalar of *C. virginica* declining by the cube root. In contrast, the scalar of Pacific oysters declined exponentially. As scaling exponents of both species had the same exceedingly large range from < 1 to > 3 , a higher shape variability of Pacific oysters than of *C. virginica* can be assumed. The variability of Pacific oyster scaling exponents mainly resulted from the separate conversion of small and large oysters but variability per site (spatial) and year (temporal) added to the size-related range (Fig. 5). Powell et al. (2016) suggested that their high variability of scaling exponents was a result of anisodiametric growth and mentioned the contribution of many cohorts over a long period of years. While their analyses were based on individuals representing the size ranges in the samples and size distributions or maximum sizes were not analyzed, the authors discussed the high variability of scaling exponents with respect

to lower condition disproportionately directed at larger *C. virginica*. Given that size-dependent allometric scaling of small and large oysters is characteristic of all oyster species, especially at increasing SL, the maximum shell length class used for allometric scaling, and due to a high variable oyster shape also the number of individuals per SL class, has important implications for the determination of scaling parameters.

Higher scaling exponents of *C. virginica* were characterized by narrower shells (slender shape) and Powell et al. (2016) discussed lower scaling exponents as a mechanism to maximize shell production. As the average value of *C. virginica* scaling exponents was 2, the authors proposed that scaling near the square rather than the cube is a constraint imposed by exigency of carbonate production for reef maintenance and accretion in the face of high rates of taphonomic degradation. In contrast, although this study showed that ad hoc conclusions on oyster shape by scaling exponent only is questionable (Fig. 6), higher scaling exponents of Pacific oysters tended to result in higher biomass, i.e. wider and deeper cupped oysters or a mighty shape (this study, Walles et al. 2015b). Although there was a density-related component, this trend was mainly size-dependent. Small oysters, less space limited at simple reefs and by settling on con-specifics at the upper end of the cluster matrix also at complex reefs, tended to scale near the cube as typically found in other bivalves (Powell et al. 2016). Large oysters, especially when forced by crowding at complex reefs, tended to scale below the square (Fig. 5). The only way to optimize food intake at increasing structural density, i.e. decreasing available space in an increasing 3-dimensional complex matrix, is a high variability of growth form, i.e. oysters are able to grow increasingly slender and long (narrow and low cupped). Density-related shape was also considered for Pacific oysters in the Northern Wadden Sea when determining the CF SH (Nehls and Büttger 2006). To compensate observed shape differences due to crowding, roundish individuals from one low density site, and long and narrow individuals from one high density site were used for allometric scaling, but values for low or high density were not given. Oysters at the reef KATS in the Oosterschelde Estuary were long and narrow (CF KATS) compared to short and wide shaped oysters at other sites in the area (Walles et al. 2015b, 2015c), but densities given in total abundance cannot explain shape differences. CF SH and CF KATS differed by only 0.1 between scaling exponents and 0.001 between scalars, but estimated conspicuous biomass differences, e.g. 230.4 g LWM (CF SH) versus 96.7 g LWM (CF KATS) for a 150 mm oyster. As a consequence, density estimates at complex reefs with high reef density (this study) resulted in about 40 % more (CF SH) versus 40 % less (CF KATS) areal biomass (Fig. 7). Besides examples given for the variability of oyster shape by similar scaling exponents (Fig. 6), this clearly demonstrates that the interplay of the two scaling variables is highly sensitive to the biomass calculation. Underestimating the relevance of the applied conversion function can have fundamental effects on further analyses like potential relationships between abundance and areal biomass. This study considered the observed size-dependent and density-related oyster allometry by implementing weighted TF (Fig. 5, Table 2) which most likely supported the detection of significant interrelations between abundance and areal biomass.

Areal reference and density attributes

Reise et al. (2017a) pointed out that Pacific oyster density comparisons are hampered by different methods of quantification, i.e. coverage, abundance or biomass, and that densities are not convertible. This study is first in documenting the crucial relevance of areal reference, i.e. CD and RD, when comparing densities. Densities per areal reference differed significantly and were clearly not convertible or comparable (Table 3). Naturally matured oyster reefs comprise a multitude of clusters with varying density. Oysters typically cover the occupied bottom of clusters completely. RC results from the patchy distribution of all clusters across the reef area. Such morphology has also been described for reefs of *C. virginica* (i.a. Allen et al. 2011). Coverage was also recognized as an important metric in reef restoration. On the other hand, abundance data of *C. virginica* studies seem to preferably refer to CD. Albeit not always explicitly clarified in the method section, most studies documenting Pacific oyster abundance also seem to refer to CD (i.a. Fey et al. 2010; Büttger et al. 2011; Walles et al. 2015b, 2015c; Holm et al. 2015; Reise et al. 2017a, 2017b). Reise et al. (2017a) stated that abundance of 100 oysters m^{-2} usually amounts to about 25% cover, > 400 m^{-2} to 100 % cover and > 1000 m^{-2} comprise large oysters. Here, cover describes the small-scale distribution within a certain area of a reef but still refers to CD. At this, stations of this study occasionally included only one oyster clump, single oysters or even just mussels and resulted in very low or no oyster CD, i.e. three stations without live oysters, two even without oyster shells, but all three with mussels. A scattered distribution of oysters in certain parts of a reef was reflected by RD, i.e. depending on RC. The method to assess RC that was applied within this monitoring registers steps with “foot on cluster” that may also be only one clump or even a single oyster or mussel, and “foot on open space” that included all unoccupied surfaces of the reef, i.e. also open spaces between scattered distributed oysters. About 1700 steps from pacing off 11 transects between stations determined RC, i.e. the proportion of occupied surface to open space. Transect coverage was highly variable and ranged from 0–78% at simple reefs and from 6–86% at complex reefs. Published data on Pacific oyster RD is scarce (Schmidt et al. 2008) although data potentially exist in all Wadden Sea regions as Folmer et al. (2017) displayed standing stock dynamics between 2000 and 2013 for the regional tidal flat systems (unoccupied areas are included). Uncertainty of areal reference hampers comparability and especially leads to biased interpretation of habitat structure at ecosystem-level. Density attributes per RD or per CD that reflected structure at simple and compact reefs of this study differed significantly, but were similar when areal reference was ignored (Table 3).

Density assessments of introduced Pacific oysters prior to establishment or at low invasive potential mainly focus on maximum abundance of live oysters (i.a. Escapa et al. 2004, Schmidt et al. 2008, Fey et al. 2010, Wrange et al. 2010). Successful establishment and increasing oyster density disproportionately increase the number of spat and total abundance significantly depends on dynamic changes of spatfall intensity. This study showed that juveniles can account for over 90 % of the total live population

after years of good spatfall (Figs 8, 9). Hence, smallest oysters are often omitted for comparable analyses (Büttger et al. 2011) or are even excluded from assessment due to their difficult detection (Reise et al. 2017a). Inconsistency of the smallest size used to quantify the adult population hamper comparability between studies. Especially the smallest size classes experience exceedingly high fluctuations of oyster occurrence due to sampling season, spatfall intensity or methodological effort. As a consequence, comparison of adult oyster abundance referring to oysters > 20 mm (Reise et al. 2017a), > 25 mm (this study), > 30 mm (Büttger et al. 2011) or even > 58 mm (Holm et al. 2015) is difficult or not even reasonable.

Under the assumption that biomass is an appropriate variable to reflect habitat structure, interrelations presented within this study revealed a rather weak correlation between the abundance of adult oysters and biomass (Fig. 11). Therefore, the adult population category, most likely irrespective of the smallest size class used, does not verifiably qualify for conclusions on habitat structure or cluster matrix which makes comparisons of density by abundance of adult oysters even more questionable. Reise et al. (2017a) investigated the invasion trajectory of Pacific oysters in the northern Wadden Sea and recorded oyster densities by CD. The authors concluded that abundances of about 1,000 adult live oysters (> 20 mm) with a weight of about 30 kg LWM were common features in the Wadden Sea. In contrast, the mean CD of 432 stations over a 6-year period during post-establishment in the Central Wadden Sea (this study) was only 318 adult live oysters (> 25 mm), but this putative low abundance accounted for 24 kg LWM. Only one of the 432 stations of this study consisted of > 1,000 and only 17 % of the stations consisted of > 500 adult live oysters (> 25 mm). In contrast to these comparably low abundances, 33 % of the stations had > 30 kg LWM. The one station with 1,232 adult live oysters (> 25 mm) accounted for 49 kg LWM while the highest biomass of 97 kg LWM corresponded to only 800 adult live oysters (> 25 mm). Fey et al. 2010 reported that “dense reefs” in the western Wadden Sea may contain > 500 adult oysters (CD) and adult was only mentioned in the abstract while not defined or used otherwise throughout the paper), weighing more than 100 kg fresh weight (LWM). Biomass may have been largely overestimated as Fey et al. 2010 applied the CF SH to their high-density reefs. The CF SH estimated about 40 % more biomass at compact reefs of this study. Total abundance assessed at three steady and undisturbed Pacific oyster reefs in the Oosterschelde Estuary was 782, 536 and 396 live oyster CD, accounting for 20, 17 and 11 kg live oyster shell (Wallès et al. 2015c). Densities by biomass ranged between characteristic densities at simple and complex reefs of this study (Table 3), but data provided by Wallès et al. (2015c) did not allow for comparison of adult live oyster abundance. Nevertheless, this exemplary data compilation displays a high uncertainty when comparing density by total abundance or by abundance of adult oysters especially when conclusions on habitat structure should be drawn.

Increasing oyster density, establishment and maturation of oyster reefs also increase the number of biogenic density variables that can or even should be assessed when population dynamics or especially ecosystem engineering effects are investigated. Additionally to live oysters, also shell of post-mortem oysters contribute to the complexity

of the biogenic structure which influences population dynamics and habitat biophysical properties by feedback effects, especially at ecosystem-level (i.a. Schulte et al. 2009). Besides difficulties of comparing abundance data, also the available biomass data is highly variable. Oyster biomass has been measured as volume in liter (i.a. Mann et al. 2009, Lejart and Hily 2011) or mass/weight in kg of shell, flesh and retention water (LWM, i.a. this study, Büttger et al. 2010, Walles et al. 2015c), shell of live oysters (SM live, i.a. this study, Walles et al. 2015c), wet or dry shell of live and post-mortem oysters (SM, i.a. this study, Walles et al. 2015c), live oysters (LWM) and post-mortem shell (fresh mass, i.a. Lejart and Hily 2011), and also tissue fresh, wet, dry or ash free dry weight (i.a. Mann et al. 2009, Lipcius et al. 2015) was used to describe oyster biomass. Enhanced logistical and especially financial efforts often lead to limited data assessments, e.g. only live oysters, abundance, biomass or simplified biomass assessments due to handling efficiency of clumps that include live oysters with tissue and (at best sediment-free) post-mortem shell (Cognie et al. 2006, Lejart and Hily 2011). Conversions between mass and volume are possible and have been applied in some studies (i.a. Mann et al. 2009). The assessment of LWM for Pacific oysters in the Wadden Sea was adapted to the regional common practice to estimate mussel density and to evaluate the ecological status of mussels (Büttger et al. 2010, Folmer et al. 2017). This study complementarily assessed SM LIVE, SM and FM of live oysters and contemporaneously recorded the density of post-mortem shell. Results revealed significant interrelations which qualified the proposed density attributes for a general application.

The repeated occurrence of 2/3 proportions for a variety of density attributes was striking and may reflect relationships typically found at naturally matured and healthy Pacific oyster reefs. Providing a 2/3 proportion of large live oysters to large shell or SM LIVE to SM, LWM and SM reached the same values because the shell of live oysters (SM LIVE) accounted for 2/3 of the LWM (Fig. 12). A 2:1 relationship between live and post-mortem large oysters was present at almost all reefs investigated. In some years at reef NL, only half of all large oysters were alive. Effects of reef size or reef shape were not investigated within this study but the frequent lower proportion of live oysters at NL may be related to reef density dependent effects with differential feedbacks of ecosystem engineering due to the exceptional size of this reef. NL stretches over 26 ha which is much larger than the average 7 ha of all other reefs investigated. The characteristic 2:1 relationship between live and post-mortem Pacific oysters shell mass was also found at reefs in the Oosterschelde Estuary, The Netherlands (Walles et al. 2015c). In contrast, Mann et al. (2009) stated that good habitats of *C. virginica* are characterized by a 1:2 relationship between live and brown (equivalent to post-mortem shell) shell weight while much lower proportions of live individuals were present in poor habitats.

The use of several population categories to compare oyster density by abundance has also been implemented for *C. virginica*. Similar to juvenile Pacific oysters, *C. virginica* recruits comprise individuals < 25 or < 30 mm (i.a. Peters et al. 2017, Theuerkauf et al. 2017). In contrast, the common practice to subdivide adult *C. virginica* into small and large individuals is not based on demographic or ecological characteristics

but mediated by human interest at the legally harvestable oyster size of ≥ 75 mm (i.a. Chai et al. 1992, Southworth et al. 2004, Peters et al. 2017, Theuerkauf et al. 2017). Interestingly, older studies on the growth rate of small *C. virginica* used size classes < 100 mm (Rothschild et al. 1994). This study found a substantiate subdivision of adult Pacific oysters by the prominent status of large individuals that are > 100 mm. Adult oyster abundance depended on the presence of small oysters, while biomass depended on the number of large oysters (Fig. 11). Large oyster abundance was not subjected to strong short-term fluctuations and reflected areal biomass largely independent of the presence of smaller size classes. The correlation between large oyster abundance and areal biomass was significant for large live oysters and LWM, SM LIVE or FM, respectively, and for large oyster shell and SM. Hence, with respect of areal reference, large oyster abundance can be converted into areal biomass (Figs 9, 11; Table 2).

Reef types

The classification of reef types has also been implemented in other studies to investigate ecosystem engineering impacts of oyster reefs. Different approaches were applied to measure or construct reef types by abundance (i.a. Blomberg et al. 2017), shell layers (i.a. Schulte et al. 2009, Lipcius et al. 2015), cover (i.a. Wagner et al. 2012), weight (i.a. Mann et al. 2009) or liter (i.a. Grabowski 2004, Grabowski and Powers 2004). Two to three reef types were commonly defined. Accordingly, this study classified two reef types, i.e. simple and complex reefs, as more reef types would have led to fuzzy transitions, increasingly unclear delimitations and non-significant differences for the high variability of oyster density at naturally grown reefs. Significant effects of engineering strength may only be detected at significant different structural complexity.

Blomberg et al. (2017) described reef types by abundance of spat (≤ 25 mm) and adult *C. virginica* (> 25 mm) and revealed that differences in oyster reef structure were not affecting the composition of food resources. Providing that representative extracts of the adult *C. virginica* populations were used for their analyses, the size range from 25.4 to 76.8 mm (mean 47 mm) was suitable for comparison with small Pacific oysters (CD) in this study (mean 59 mm) (Table 3). 196 adult (small live) *C. virginica* at natural and 280 at restored reefs were within the range of 170 small live Pacific oysters at simple and 261 at complex reefs. Although small Pacific oyster abundance and their corresponding LWM of 5.1 kg at simple reefs vs. 7.4 kg at complex reefs were significantly different between reef types, the significant structural difference between simple and complex reefs manifested only at 16.4 vs. 31.2 kg LWM. High numbers of small oysters may not have the potential to build high complex 3-dimensional structures. Even the maximum abundance of 1,008 small live Pacific oysters (mean 49 mm) reached only 17.5 kg LWM which would comply with a typical CD at simple reefs. Hence, structural differences revealed by Blomberg et al. (2017) were significant on a local, small-scale consideration but, de facto, most probably too weak to detect ecosystem engineering effects as the described reef types would assign to simple reefs.

Studies investigating *C. virginica* restoration success assessed oyster abundance as a function of reef height (Schulte et al. 2009, Lipcius et al. 2015). Reef height was pre-constructed by placing shell layers at different vertical reliefs. A key mechanism underlying *C. virginica* recovery after 3 years was vertical relief as oyster (total live) abundance was 4-fold higher on high-relief reefs (HRR) than on low-relief reefs (LRR) (Schulte et al. 2009). Abundance comprised mainly small oysters of up to 100 mm while a distinct 3-dimensional matrix built by large individuals was proposed to develop only in the future. This is in contrast to naturally matured Pacific oyster reefs in the Wadden Sea but the approach to define two reef types, beside un-restored bottom (*C. virginica* reefs) vs. open spaces (Pacific oyster reefs), is the same. Complex reefs with high reef density (HRD) and simple reefs with low reef density (LRD) comply with HRR and LRR in terms of differential ecosystem engineering due to vertical structure.

To simulate low or high density, Wagner et al. (2012) constructed reef density on a small-scale pseudo-cluster by spreading clumps of about 10 Pacific oysters between 100 and 150 mm to 2 m² plots of 30 and 70 % cover (number of clumps not given). Although this cover approach is hardly reproducible or comparable to other studies, this investigation (unintentionally?) implemented the prominent status of large oyster abundance by their experimental design. Most likely, this has been supportive in detecting significant differences between target variables meant to reflect engineering strength on a small-scale experimental approach.

Another approach to describe reef types was implemented by Mann et al. 2009. The authors plotted live shell weight against total shell weight and revealed that 92 % of 166 data points were equally distributed between the associations low total shell weight + low live shell weight and high total shell weight + high live shell weight. Although no significant relationship between measurements was found, the observation underpins a classification of two reef types.

Grabowski (2004) and Grabowski and Powers (2004) constructed low habitat complexity or low vertical relief by a layer of unaggregated oyster shell and high habitat complexity or high vertical relief by substituting upward orientated oyster cluster. Comparable liters of shell and cluster were used within studies but varied between studies. Both approaches could detect significant different engineering effects. Grabowski (2004) and Grabowski and Powers (2004) used the terms simple and complex reef for their reef types. The coincidence of terms was only detected at the time of discussing the findings of this study. The intention to express structural differences by the terms simple and complex reef is shared in the two studies but the implementation differs. The terms simple and complex reefs were most suitable for the concept of this study and were retained as the constructed “reefs” rather represented simple or complex clusters and not entire reefs.

This study initially implemented the classification of reef types as a tool for oyster allometric scaling due to the observed density-related variation of oyster shape (see subsection “oyster shape and allometric scaling”). However, pooling the monitoring data by reef type qualified for a delimitation of threshold or target densities to evaluate the status of (naturally matured) Pacific oyster reefs by reef type characteristic density attributes. The need for targeted research of Pacific oyster reefs was emphasized by

Folmer et al. (2017) but the authors stated that natural or targeted levels are hard to answer because these levels are impossible to define for naturally fluctuating populations. Allen et al. (2011) recognized the lack of a clear empirical or theoretical basis for setting operational targets of *C. virginica* population size and structure to evaluate reef-level restoration success. Nevertheless, the authors explicitly recommended a combination of density variables and established threshold and target abundance, biomass and coverage as performance metrics of *C. virginica* restored reefs. This study found a significant relationship between the abundance of large Pacific oysters and areal biomass which enabled the determination of one density variable for the classification of the reef types (Fig. 4C).

The implementation of a threshold density aimed at a general application, i.e. applicable also to data sets of other studies, and the decision was made in favor of large live oyster RD. The areal reference RD considers the variable density of clusters and their spatial distribution across the reef area. At this, RD reflects reef texture or reef complexity. Reef texture or reef complexity has implications for engineering strength at ecosystem-level. High density cluster, i.e. clusters with high vertical structure and a complex matrix, may also develop in restricted parts of simple reefs but on a large-scale perspective, the entity of all clusters and their distribution across the reef area will trigger reef type characteristic engineering effects. RD was also chosen to comply with a variety of monitoring methods, i.e. field studies where coverage was assessed or could possibly be estimated in retrospect, dredging, tong or grab sampling.

By being the counterparts of the areal biomass variables LWM, SM LIVE, FM or SM, the abundance of large live oysters or large oyster shell would have qualified to differentiate simple from complex reefs. The use of abundance over areal biomass as a threshold density was imperative for the interdependent relationship of density-related oyster shape and areal biomass. The threshold density of large live oyster abundance enables its application also to data sets from reduced monitoring effort, e.g. already existing studies where post-mortem shell was not assessed. Irrespective of reef type, the 2:1 relationship between live and post-mortem large oysters resulted in comparable values for areal LWM and SM (Fig. 12). Providing that naturally matured Pacific oyster reefs predominately consist of 2/3 live large oysters, main structural differences between reef types are reflected by the abundance of live large oysters only. Studies that only assessed biomass may use a converted threshold density. For example, using the equation “Oyster/Areal biomass/RD/LWM/Large live” (Table 2), the threshold abundance of 44 large live oyster RD equates to 10.5 kg LWM RD. With respect to areal reference, simple and complex reefs significantly differed by all but juvenile density attributes, including RC (Table 3). Mean oyster size and the proportion of live oysters per density attribute were similar between reef types.

Ruesink et al. (2005) mentioned that *C. virginica* reefs are stronger than those of *C. gigas*. Pacific oyster reefs of this study comprise naturally matured 10 to 15 year old unexploited reefs with live oysters and post-mortem shell up to 268 mm. Vertical structure is built by some large and increasingly slender oysters while small oysters condense the matrix by covering large individuals. Vertical structure at most reefs increased with time by accumulation of sediment, burial of post-mortem oysters and

shell accretion of old and young generations. A similar architecture was described for historic, natural *C. virginica* pre-exploitation reefs (DeAlteris 1988). Irrespective of areal reference, density attributes presented within this study suggest that Pacific oyster reefs in the Central Wadden Sea are stronger in terms of biogenic structure than those of recent *C. virginica*. Biogenic density at natural *C. virginica* reefs in the James River ($N = 166$) reached 17 kg total shell wet weight m^{-2} (live and post-mortem brown shell) while the majority of all “high shell reefs” ($N = 76$) ranged between 8 and 13 kg (Mann et al. 2009). In comparison, Pacific oyster reefs ($N = 36$) reached a maximum of 43 kg SM CD (live and post-mortem shell) and complex reefs had on average 34 kg SM CD ($N = 18$) (Table 3). On the other hand, the assessment of *C. virginica* density by patent tongs may also reflect RD. With a maximum of 21 kg SM RD ($N = 36$) and an average 16.5 kg SM RD at complex reefs ($N = 18$) (Table 3), biogenic density at Pacific oyster reefs was still higher than at natural *C. virginica* reefs in the James River. The median of all natural *C. virginica* reefs was 4.8 kg SM which was less than the average 5.7 kg SM RD at simple Pacific oyster reefs. Furthermore, *C. virginica* reefs seem to be characterized by a 1:2 relationship between live and post-mortem brown shell (Mann et al. 2009) while a 2:1 relationship between live and post-mortem shell was characterizing Pacific oyster reefs. Additionally, recruitment of Pacific oysters seems to be more successful than that of *C. virginica*. Irrespective of reef type, juvenile (live or shell) Pacific oysters comprised about 70 % or more of the population (live or shell) (Table 3) while juvenile *C. virginica* seem to hold 30 % or less (Mann et al. 2009, Schulte et al. 2009). Sousa et al. (2009) stated that ecosystem effects of *C. virginica* are similar to Pacific oysters but that *C. virginica*, by forming larger reefs, sustainably affect large-scale hydrodynamics, estuarine water circulation and sedimentation. Reef size of natural *C. virginica* reefs in the James River varied from 1.3 ha to 500 ha subtidal reef area (Mann et al. 2009). The largest reefs, encompassing an immense area of about 2000 ha by bordering on each other, had consistently less than 3 kg total shell wet weight m^{-2} (live and post-mortem brown shell). This density was comparable to SM per RD at the simple reef SP of this study. Site SP had the lowest Pacific oyster densities and the lowest coverage throughout the study period. Reef texture had almost no relief and was dominated by strongly scattered distributions of oyster clumps. Ecosystem engineering was observed to be very weak and may not be stronger at potentially larger reef size. In contrast, although density distribution at the complex reef NL was highly variable across the reef area, 35 kg SM CD (870 adult or 240 large shell) covered about 50 % of the reef area. According to its density but also to its exceptional size (26 ha) compared to other study sites (about 8 ha), the complex reef NL experiences accentuated ecosystem engineering and features a pronounced relief with several large tidal pools reaching some dozen square meters which stay inundated to depths of over 1 m during low tide. Independent of reef size, complex reefs are assumed to experience feedback processes that facilitate reef performance, population persistence and reef stability (Markert in prep.).

Population interference and dominance

The distinction of reef types and the implementation of density attributes enabled a first estimate of ecosystem-level impact of oysters on mussels. Analogous to large oysters, oyster density at complex reefs also forced large mussels to grow slenderer than at simple reefs (Fig. 8). Eschweiler and Christensen (2011) found that large mussels tend to move to the bottom of the cluster matrix in the presence of shore crabs. Although large mussels at the bottom are more protected against detrimental barnacle overgrowth (Buschbaum et al. 2016), mussels suffer from reduced food supply and increased sedimentation (Eschweiler and Christensen 2011). A slenderer shape of mussels within densely packed oysters may facilitate a facultative migration to optimize the trade-off by immediate response, e.g. presence/absence of crabs or birds according to inundation or season.

One would expect that the available space is limiting mussel occurrence at complex reefs but mussel CD was not significantly different between reef types (Table 3). This implies that oyster density, i.e. engineering strength, had no effect on mussel density. In contrast, due to a higher RC, RD at complex reefs supported significantly higher mussel biomass, higher abundance of small and especially large mussels. Although proportions of oyster and mussel densities were not affected, this demonstrates the vital importance of areal reference when evaluating engineering effects at ecosystem-level.

Analogous to oysters, abundance of large mussels determined dynamic changes of mussel biomass (Fig. 13). At this, the relationship between large oysters and large mussels was a reliable counterpart of a biomass comparison. At both reef types, more large mussels than large oysters were present but oysters were dominating all biomass variables, i.e. LWM, SM LIVE, SM and FM (pictured in Folmer et al. 2017, Fig. 4). At complex reefs, oyster dominance by biomass was significantly higher and large mussel dominance significantly lower than at simple reefs. Although the proportion of FM to LWM was twice as high in mussels as in oysters, oysters were dominating both reef types by all biomass variables. Considering also the shell of post-mortem oysters to reflect reef biogenic structure, the dominance of large mussels decreased at both reef types and oyster SM largely dominated with over 80 % at simple reefs and over 90 % at complex reefs. This demonstrates the relevance of density attributes that are chosen for the evaluation of dominance.

In the trilateral Wadden Sea, where non-native Pacific oysters have been invading native mussel beds in the intertidal of the Netherlands, Germany and Denmark, a visually appraised “coverage” of the two species, i.e. proportions, is recommended to evaluate dominance (Folmer et al. 2017). To date it is not clear if or under what uniform metrics these oyster/mussel mixed biogenic structures should be called beds or reefs - notwithstanding that these terms relate to differential ecosystem engineering. Most recently, Reise et al. (2017b) suggested the term “oyssel reef” which nicely refers to a coexistence of oysters and mussels but, after all, disrespects the main ecosystem engi-

neering species which is playing the key role in structuring and modulating biophysical properties and habitat characteristics. At this, Reise et al. (2017b) discussed the hostile takeover in terms of ecosystem engineering effects that are characteristic for oysters or complex reefs while mussels were discussed as associated species that live within the cluster matrix. Reise et al. (2017b) contrasted the abundance of adult oysters (> 20 mm) and adult mussels (> 10 mm) at one site in the Northern Wadden Sea but, as adult abundance cannot be reliably compared, data could not reflect the observed oyster dominance in the field. In contrast, the comparison of biomass, abundance of large individuals or the inclusion of post-mortem oyster shell could have led to similar results on dominance that was found within this study. This study will hopefully impel scientists and decision-makers to implement an adapted strategy for the evaluation of the keystone engineering species by uniform metrics, e.g. the proposed density attributes of this study, which will also provide clarification to the denomination of oyster/mussel mixed biogenic structures in the Wadden Sea.

Implications for monitoring

Oyster density assessments are time-consuming and costly. Monitoring reef density dynamics on a large-scale regular basis is a special task that requires even more logistical and financial effort. Monitoring programs implemented after the bioinvasion of Pacific oysters in the trilateral Wadden Sea regions, respectively Western, Central and Northern Wadden Sea, have been reduced or even stopped completely although the need to evaluate long-term ecosystem engineering effects by intensified monitoring was postulated (Folmer et al. 2017). Folmer et al. (2017) also pointed out the lack of systematic measurements and recommended harmonization on density variables and applied method to improve comparability between regions while at the same time maintaining comparability within existing series.

The concept of large oyster abundance as intrinsic drivers of biotic and biogenic Pacific oyster density turned out to be an easy tool that will allow trans-regional comparisons of reef structural complexity independent of methodological approach (hand, dredge, grab, corer or tong), sampling season (spatfall intensity) or ecosystem (rocky shores or soft sediment, different primary settling substrate, intertidal or subtidal, invaded, naturalized or native environment). The concept of large oyster abundance maintains density comparisons within series and also retrospective comparisons of old data sets will be possible. The density attribute large oyster (live or shell) as an equivalent measurement to areal biomass (LWM, SM LIVE, FM or SM), will substantially reduce the logistical and financial effort of future monitoring as only large oysters have to be counted for an empirical characterization of Pacific oyster reefs, i.e. using a 10 cm reference object while exact shell length measurements are not required.

Although this study revealed that the abundance of large oysters (live or shell) can be converted into areal biomass (LWM, SM LIVE, FM or SM), data with different areal references (CD or RD) remain non-convertible and non-comparable. A variety of monitoring methods exist while the nature of the applied method basically determines

areal reference. For example, the deployment of an oyster dredge always results in RD as a haul samples clusters and open spaces between clusters while conclusions on CD cannot be drawn. Field investigations in the intertidal commonly assess oyster density exclusively in clusters (CD) and the coverage of a reef by clusters (RC) has to be assessed separately to estimate RD. This study first displays the crucial relevance of areal reference for comparative analyses of oyster density (see subsection “areal reference and density attributes” and “reef type”) and the respective applied monitoring method should be thoroughly scrutinized with respect to areal reference. Besides raising awareness of the relevance of areal reference, the scope of this study is not to recommend the “best” or “one-fits-all” monitoring method. On the contrary, results of this study indicate that the large oyster concept is independent of monitoring method (if areal reference is considered) and applicable without a significant loss of existing precision levels, especially when the focus of the data analyses concerns the determination of reef type or the empirical characterization of reefs by structural complexity.

The CV is an index of dispersion but also a measure of the SE relative to the mean, i.e. $RSE = CV \times 29 [100/\sqrt{n} \text{ (} n = 12 \text{ stations of this study)}]$. The uncertainty of the mean estimate at the sites of this study mainly ranged between 6 and 29 % for all density attributes while the uncertainty increased with decreasing oyster density. Relative precision of the present monitoring may overall be rated unacceptable and indicate increasing the number of samples, especially at simple reefs. On the other hand, the CV should rather be interpreted as a measure of characteristic intra-reef variability of oyster density distribution than the determination of monitoring precision. Each site of this study has a characteristic intra-reef pattern. Simple reefs can have high oyster densities in some parts of the reef although most parts have very low structural complexity or even a scattered distribution of single oyster clumps. Such a characteristic intra-reef pattern will always lead to high standard deviations and high CV, especially at simple reefs. A higher number of stations would increase the RSE of the mean estimate, but the mean estimate and the natural variability of cluster density distribution across a reef’s area will basically not change. Simple reefs will remain classified as simple reefs no matter whether the number of samples will be increased. At this, the CV at complex reefs with a rather homogenous distribution of oyster density across the reef area was 0.2 which signifies an acceptable “precision level” of 6 %. Nevertheless, the range of CV of all density attributes and CV of all density attributes per site were comparable. In particular, CV of the structural density attributes areal biomass (LWM or SM) and large oyster abundance (live or shell) were strongly correlated and “precision level” of the estimates of mean density at the sites was similar. The similarity between CV of all density attributes, in particular structural, will most likely also apply to other sampling strategies. The reliability of a comparative analysis of large oyster abundance among studies with different sampling designs is presumed to equal otherwise implemented comparisons of areal biomass or adult oysters. At this, the large oyster concept allows monitoring programs/sampling strategies that were established due to local survey resources to be maintained.

Although the choice of monitoring method depends on local logistical and financial feasibility, only RD qualifies for evaluations of the relationship between oyster density and engineering effects on ecosystem-level. Long-term intrinsic processes of a reef (e.g. popu-

lation dynamics, biophysical properties) and direct (e.g. habitat provision) or indirect (e.g. hydrodynamics, sediment budgets, nutrient cycling) engineering effects at ecosystem-level depend on oyster density of the total reef area where the entity of all clusters and their patchy distribution across the reef area perform as a bio-geo-morphological unit.

Conclusion

This study contributes to remedy the state of uncertainties when comparing the density of Pacific oysters and their reefs. The division of oyster populations into size-related abundance categories has been implemented in other studies but interrelations of abundance and biomass have not yet been investigated on an empirical basis. Large Pacific oysters were intrinsic drivers for dynamic changes of density by biomass which offered the opportunity to formulate potential strategies for characterizing Pacific oyster reefs (Box 1). Findings from this study may encourage researchers to detect similar patterns in other oyster species.

Results of this study advocate a harmonization of the developed density attributes with a clear specification of areal reference. This study is the first to provide a comprehensive set of characteristic density attributes per areal references (RD and CD) at two different reef types (simple and complex reefs). The classification of reef types meets the need for targeted research. The compilation of density attributes at simple and complex reefs shall serve as a density guide which enables a context-integrated evaluation of how dense a given reef actually is. By assessing its status, preliminary conclusions on expected low or high impact probability can be drawn.

Focusing on large oyster abundance will reduce monitoring efforts, will enable trans-regional comparisons of reef structure and will facilitate evaluations of engineering strength, reef performance and invasional impacts at ecosystem-level. Complemen-

<div><div><div>Box 1.</div><div>Conceptual framework toward a harmonized approach to characterizing Pacific oyster reefs</div></div><div><div>1 Areal references (cluster density or reef density)</div><div><div>- CD = function of vertical structure</div><div>- RC = function of horizontal structure</div><div>- RD = CD x RC = function of reef texture</div><div>- RD reflects reef complexity and reef performance</div><div>• RD = function of engineering strength on ecosystem-level</div></div><div><div>2 Density attributes (abundance or biomass)</div><div><div>- Live oysters or LWM, FM, SM LIVE = biotic density</div><div>- Shell of live and post-mortem oysters or SM = biogenic density</div><div>• Abundance = juv < 26 mm, small 26-100 mm, large > 100 mm</div></div><div><div>3 Weighted (LRD or HRD) twin functions (small or large)</div><div><div>- Comply with density-related and size-dependent oyster shape</div><div>- Improve estimations of individual biomass by SL</div><div>- Qualify for standard conversion of SL into biomass:</div><div>• TF LRD or TF HRD</div></div></div></div></div></div>	<div><div>4 Abundance of large oysters (live or shell)</div><div><div>- Intrinsic density attribute of oyster reefs</div><div>• conversion into biotic and biogenic structure (biomass)</div><div>- Independent of sampling season</div><div>- Independent of assessment method (e.g. field/dredge)</div><div>- Independent of (invaded) ecosystem (e.g. rock/soft)</div><div>- Reduces logistical and financial effort of future monitoring</div><div>• counts of large oysters (SL measurements not necessary)</div><div>- Applicable to old data sets</div><div>- Allows trans-regional comparability of oyster density</div><div>- Allows classification of reef types</div><div>- Facilitates characterization of oyster reefs</div><div>- Promotes evaluation of engineering strength</div></div><div><div>5 Classification of reef types (simple or complex reef)</div><div><div>- Complies with density-related oyster shape</div><div>• improves estimations of individual biomass by SL (application of TF LRD or TF HRD)</div><div>- Provides reference density attributes</div><div>• characterization of oyster reefs</div><div>- Promotes evaluation of engineering strength</div></div></div></div>
--	--

Box 1.

tary investigations are needed to relate engineering strength in terms of large oyster density to specific ecological effects. Furthermore, the integration of reef areal extent, reef morphology in terms of reef shape or reef orientation, and also a long-term temporal component should be considered.

Acknowledgements

Sincere thanks and great respect to Achim Wehrmann, Abteilung Meeresforschung, Senckenberg am Meer Wilhelmshaven, who managed with utter conviction a continuation of the monitoring over so many years. Appreciation is due to the many people who contributed to the collection of the data. Special thanks to technical assistant Torsten Janßen, Abteilung Meeresforschung, Senckenberg am Meer Wilhelmshaven, who smoothed logistical processes during monitoring. Monitoring was carried out within the framework of the projects (i) “Management der Bioinvasion der Pazifischen Auster”, financially supported from 11/2006 to 12/2008 by the Niedersächsische Wattenmeer Stiftung and the Senckenberg Gesellschaft für Naturforschung, (ii) “SafeGuard. Ausbreitung der Pazifischen Auster”, financially supported from 05/2009 to 10/2012 by the European Regional Development Fund INTERREG IVa and SGN (Senckenberg Gesellschaft für Naturforschung), and (iii) “Klimaveränderung und Bioinvasionen als Steuerungsfaktoren von ecosystem engineering”, financially supported from 05/2012 to 06/2014 by LOEWE (Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomische Exzellenz of the Hessisches Ministerium für Wissenschaft und Kunst), BiK-F (Biodiversität und Klima-Forschungszentrum) and SGN (Senckenberg Gesellschaft für Naturforschung). With kind support from Gabriele Gerlach, IBU (Institut für Biologie und Umweltwissenschaften), Carl von Ossietzky Universität Oldenburg, data was mainly analyzed during a scholarship within the framework of the IBR-project “Interdisciplinary approach to functional biodiversity research”, funded from 08/2015 to 07/2018 by the MWK (Ministerium für Wissenschaft und Kultur) Niedersachsen. Special thanks are due to NLPV (Nationalparkverwaltung Niedersächsisches Wattenmeer) for appropriate authorizations during field work. I am grateful to Ana-Maria Krapal and Philippe Gouletquer for valuable remarks and constructive comments which improved an earlier version of the manuscript.

This article is dedicated to the fond memory of Gerald Millat.

References

- Allen S, Carpenter AC, Luckenbach M, Paynter K, Sowers A, Weissberger E, Wesson J, Westby S (2011) Restoration goals, quantitative metrics and assessment protocols for evaluating success on restored oyster reef sanctuaries. Report of the oyster metrics workgroup Sustainable Fisheries Goal Implementation Team of the Chesapeake Bay Program. <http://www.chesapeakebay.net>

- Baggett LP, Powers SP, Brumbaugh RD, Coen LD, DeAngelis BM, Greene JK, Hancock BT, Morlock SM, Allen BL, Breitburg DL, Bushek D1, Grabowski JH, Grizzle RE, Grosholz ED, La Peyre MK, Luckenbach MW, McGraw KA, Piehler MF, Westby SR, zu Ermgassen PSE (2015) Guidelines for evaluating performance of oyster habitat restoration. *Restoration Ecology* 23: 737–745. <https://doi.org/10.1111/rec.12262>
- Blomberg BN, Lebreton B, Palmer TA, Guillou G, Pollack JB, Montagna PA (2017) Does reef structure affect oyster food resources? A stable isotope assessment. *Marine Environmental Research* 127: 32–40. <https://doi.org/10.1016/j.marenvres.2017.03.003>
- Buschbaum C, Cornelius A, Goedknecht MA (2016) Deeply hidden inside introduced biogenic structures – Pacific oyster reefs reduce detrimental barnacle overgrowth on native blue mussels. *Journal of Sea Research* 117: 20–26. <https://doi.org/10.1016/j.seares.2016.09.002>
- Büttger H, Berg T, Nehls G (2010) Evaluation of mussel beds in the North-Frisian Wadden Sea – according to the EU Water Framework Directive and EU Habitats Directive. In: Marencic et al. (Eds) *Science for Nature Conservation and Management: The Wadden Sea Ecosystem and EU Directives. Proceedings of the 12th International Scientific Wadden Sea Symposium in Wilhelmshaven, Germany. Waddens Sea Ecosystem No. 26. Common Wadden Sea Secretariat, (Wilhelmshaven).* <https://bioconsult-sh.de/de/referenzen/publikationen/>
- Büttger H, Nehls G, Witte S (2011) High mortality of Pacific oysters in a cold winter in the North-Frisian Wadden Sea. *Helgoland Marine Research* 65: 525–532. <https://doi.org/10.1007/s10152-011-0272-1>
- Chai AL, Homer M, Tsai C-F, Gouletquer P (1992) Evaluation of oyster sampling efficiency of patent tongs and an oyster dredge. *North American Journal of Fisheries Management* 12: 825–832. [https://doi.org/10.1577/1548-8675\(1992\)012<0825:EOOSEO>2.3.CO;2](https://doi.org/10.1577/1548-8675(1992)012<0825:EOOSEO>2.3.CO;2)
- Cognie B, Haure J, Barillé L (2006) Spatial distribution in a temperate coastal ecosystem of the wild stock of the farmed oyster *Crassostrea gigas* (Thunberg). *Aquaculture* 259: 249–259. <https://doi.org/10.1016/j.aquaculture.2006.05.037>
- Colden AM, Fall KA, Cartwright GM, Friedrichs CT (2016) Sediment suspension and deposition across restored oyster reefs of varying orientation to flow: implications for restoration. *Estuaries and Coasts* 39: 1435–1448. <https://doi.org/10.1007/s12237-016-0096-y>
- Colden AM, Latour RJ, Lipcius RN (2017) Reef height drives threshold dynamics of restored oyster reefs. *Marine Ecology Progress Series* 582: 1–13. <https://doi.org/10.3354/meps12362>
- DeAlteris JT (1988) The geomorphic development of wreck shoal, a subtidal oyster reef of the James River, Virginia. *Estuaries* 11: 240–249. <https://doi.org/10.2307/1352010>
- Escapa M, Isacch JP, Daleo P, Alberti J, Iribarne O, Borges M, Dos Santos EP, Gagliardini DA, Lasta M (2004) The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in Northern Patagonia. *Journal of Shellfish Research* 23: 765–772.
- Eschweiler N, Christensen HT (2011) Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *Journal of Experimental Marine Biology and Ecology* 403: 90–95. <https://doi.org/10.1016/j.jembe.2011.04.010>
- Fey F, Dankers N, Steenbergen J, Goudswaard K (2010) Development and distribution of the non-indigenous Pacific oyster (*Crassostrea gigas*) in the Dutch Wadden Sea. *Aquaculture* 18: 45–59. <https://doi.org/10.1007/s10499-009-9268-0>

- Folmer E, Büttger H, Herlyn M, Markert A, Millat G, Troost K, Wehrmann A (2017) Beds of blue mussels and Pacific oysters. In: Kloepper S et al. (Eds) Wadden Sea Quality Status Report 2017. Common Wadden Sea Secretariat (Wilhelmshaven). <https://qsr.waddensea-worldheritage.org/reports/beds-blue-mussels-and-pacific-oysters>
- Goedknecht A, Schuster A-K, Buschbaum C, Gergs R, Jung AS, Luttikhuisen PC, van der Meer J, Troost K, Wegner KM, Thielges DW (2017) Spillover but no spillback of two invasive parasitic copepods from invasive Pacific oysters (*Crassostrea gigas*) to native bivalve hosts. *Biological Invasions* 19: 365–379. <https://doi.org/10.1007/s10530-016-1285-0>
- Grabowski JH (2004) Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85: 995–1004. <https://doi.org/10.1890/03-0067>
- Grabowski JH, Powers SP (2004) Habitat complexity mitigates trophic transfer on *Crassostrea*-reefs. *Marine Ecology Progress Series* 277: 291–295. <https://doi.org/10.3354/meps277291>
- Green DS, Crowe TP (2014) Context- and density-dependent effects of introduced oysters on biodiversity. *Biological Invasions* 16: 1145–1163. <https://doi.org/10.1007/s10530-013-0569-x>
- Herbert RJH, Humphreys J, Davies CJ, Roberts C, Fletcher S, Crowe TP (2016) Ecological impacts of non-native Pacific oysters (*Crassostrea gigas*) and management measures for protected areas in Europe. *Biodiversity and Conservation* 25: 2835–2865. <https://doi.org/10.1007/s10531-016-1209-4>
- Holm MW, Davids JK, Dolmer P, Vismann B, Hansen BW (2015) Moderate establishment success of Pacific oyster, *Crassostrea gigas*, on a sheltered intertidal mussel bed. *Journal of Sea Research* 104: 1–8. <https://doi.org/10.1016/j.seares.2015.07.009>
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386. <https://doi.org/10.2307/3545850>
- Kellogg LM, Cornwell JC, Owens MS, Luckenbach MW, Ross PG, Leggett TA (2014) Scaling ecosystem services to reef development: effects of oyster density on nitrogen removal and reef community structure. Virginia Institute of Marine Science. College of William and Mary.
- Kochmann J, Buschbaum C, Volkenborn N, Reise K (2008) Shift from native mussels to alien oysters: differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology* 364: 1–10. <https://doi.org/10.1016/j.jembe.2008.05.015>
- Lang AC, Buschbaum C (2010) Facilitative effects of introduced Pacific oysters on native macroalgae are limited by a secondary invader, the seaweed *Sargassum muticum*. *Journal of Sea Research* 63: 119–128. <https://doi.org/10.1016/j.seares.2009.11.002>
- Lenihan HS (1999) Physical-biological coupling on oyster reefs: habitat structure influences individuals performance. *Ecological Monographs* 69: 251–275. [https://doi.org/10.1890/0012-9615\(1999\)069\[0251:PBCOOR\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0251:PBCOOR]2.0.CO;2)
- Lejart M, Hily C (2011) Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. *Journal of Sea Research* 65: 84–93. <https://doi.org/10.1016/j.seares.2010.07.004>
- Lipcius RN, Burke RP, McCulloch DN, Schreiber SJ, Schulte DM, Seitz RD, Shen J (2015) Overcoming restoration paradigms: value of the historical record and metapopulation

- dynamics in native oyster restoration. *Frontiers in Marine Science* 2: 65. <https://doi.org/10.3389/fmars.2015.00065>
- Mann R, Southworth M, Harding LM, Wesson JA (2009) Population studies of the native Eastern oyster, *Crassostrea virginica*, (Gmelin, 1791) in the James River, Virginia, USA. *Journal of Shellfish Research* 28: 193–220. <https://doi.org/10.2983/035.028.0203>
- Markert A, Wehrmann A, Kroencke I (2010) Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* 12: 15–32. <https://doi.org/10.1007/s10530-009-9425-4>
- Markert A, Esser W, Frank D, Wehrmann A, Exo KM (2013) Habitat change by the formation of alien *Crassostrea*-reefs in the Wadden Sea and its role as feeding sites for waterbirds. *Estuarine, Coastal and Shelf Science* 131: 41–51. <https://doi.org/10.1016/j.ecss.2013.08.003>
- Markert A, Wehrmann A (2013) Bestandserfassung von *Sargassum muticum* auf dem Nordland im Rahmen einer Bioinvasionsphase. Reports Juni and November 2013. Forschungsauftrag im Rahmen einer Pilotstudie der Nationalparkverwaltung Niedersächsisches Wattenmeer (Wilhelmshaven).
- Markert A, Raupach MJ, Segelken-Voigt A, Wehrmann A (2014) Molecular identification and morphological characteristics of native and invasive Asian brush-clawed crabs from Japanese and German coasts: *Hemigrapsus penicillatus* (De Haan, 1835) versus *Hemigrapsus takanoi* Asakura & Watanabe 2005 (Crustacea: Brachyura). *Organisms, Diversity and Evolution* 14: 369–382. <https://doi.org/10.1007/s13127-014-0176-4>
- Markert A, Matsuyama K, Rohde S, Schupp P, Wehrmann A (2016) First record of the non-native Pacific bryozoan *Smittoidea prolifica* Osburn, 1952 at the German North Sea coast. *Marine Biodiversity* 46: 717–723. <https://doi.org/10.1007/s12526-015-0415-8>
- Millat G (2008) Gesamtbestandserfassung der eulitoralischen Miesmuschelbänke bis 2007 im Rahmen des Monitorings zum Miesmuschelbewirtschaftungsplan. Nationalparkverwaltung Niedersächsisches Wattenmeer (Wilhelmshaven).
- Nehls G, Büttger H (2006) Ausbreitung und Nutzung der Pazifischen Auster *Crassostrea gigas* im Nationalpark Schleswig-Holsteinisches Wattenmeer. Austernbericht 2006. BioConsult SH (Husum).
- Nehls G, Witte S, Büttger H, Dankers N, Jansen J, Millat G, Herlyn M, Markert A, Kristensen PS, Ruth M, Buschbaum C, Wehrmann A (2009) Beds of blue mussels and Pacific oysters. Thematic Report No. 11. In: Marencic H and de Vlas J (Eds) *Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group* (Wilhelmshaven). <https://www.waddensea-worldheritage.org/resources/ecosystem-25-wadden-sea-quality-status-report-2009>
- Padilla DK (2010) Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. *Integrative and Comparative Biology* 50: 213–225. <https://doi.org/10.1093/icb/icq080>
- Peters JW, Eggleston DB, Puckett BJ, Theuerkauf SJ (2017) Oyster demographics in harvested reefs vs. no-take reserves: implications for larval spillover and restoration success. *Frontiers in Marine Science* 4: 326. <https://doi.org/10.3389/fmars.2017.00326>

- Powell EN, Mann R, Ashton-Alcox KA, Kim Y, Bushek D (2016) The allometry of oysters: spatial and temporal variation in the length-biomass relationships for *Crassostrea virginica*. *Journal of the Marine Biological Association of the United Kingdom* 96: 1127–1144. <https://doi.org/10.1017/S0025315415000703>
- Reise K, Buschbaum C, Büttger H, Rick J, Wegner MK (2017a) Invasion trajectory of Pacific oysters in the northern Wadden Sea. *Marine Biology* 164: 68. <https://doi.org/10.1007/s00227-017-3104-2>
- Reise K, Buschbaum C, Büttger H, Wegner MK (2017b) Invading oysters and native mussels: from hostile takeover to compatible bedfellows. *Ecosphere* 8: e01949. <https://doi.org/10.1002/ecs2.1949>
- Rothschild BJ, Ault JS, Gouletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Marine Ecology Progress Series* 11: 29–39. <https://doi.org/10.3354/meps111029>
- Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters. Ecosystem effects and restoration implications. *Annual Review of Ecology, Evolution, and Systematics* 36: 643–689. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152638>
- Schmidt A, Wehrmann A, Dittmann S (2008) Population dynamics of the invasive Pacific oyster *Crassostrea gigas* during the early stages of an outbreak in the Wadden Sea (Germany). *Helgoland Marine Research* 62: 367–376. <https://doi.org/10.1007/s10152-008-0125-8>
- Schulte DM, Burke RP, Lipsius RN (2009) Unprecedented restoration of a native oyster meta-population. *Science* 325: 1124–1128. <https://doi.org/10.1126/science.1176516>
- Southworth M, Harding J, Mann R (2005) The status of Virginia's Public Oyster Resource 2004. Virginia Institute of Marine Science, College of William and Mary.
- Sousa R, Jorge L, Gutiérrez JL, Aldridge DC (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* 11: 2367–2385. <https://doi.org/10.1007/s10530-009-9422-7>
- Southworth M, Harding JM, Wesson LA, Mann R (2010) Oyster (*Crassostrea virginica*, Gmelin 1791) population dynamics on public reefs in the Great Wicomico River, Virginia, USA. *Journal of Shellfish Research* 29: 271–290. <https://doi.org/10.2983/035.029.0202>
- Theuerkauf SJ, Eggleston DB, Theuerkauf KW, Puckett BJ (2017) Oyster density and demographic rates on natural intertidal reefs and hardened shoreline structures. *Journal of Shellfish Research* 36: 87–100. <https://doi.org/10.2983/035.036.0111>
- Thieltges DW, Reise K, Prinz K, Jensen KT (2009) Invaders interfere with native parasite-host interactions. *Biological Invasions* 11: 1421–1429. <https://doi.org/10.1007/s10530-008-9350-y>
- Troost K, Kamermans P, Wolff WJ (2008) Larviphagy in native bivalves and an introduced oyster. *Journal of Sea Research* 60: 157–163. <https://doi.org/10.1016/j.seares.2008.04.006>
- 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). *Journal of Sea Research* 61: 153–164. <https://doi.org/10.1016/j.seares.2008.11.006>
- Van der Zee E, van der Heide T, Donadi S, Eklöf J, Eriksson B, Olf H, van der Veer H, Piersma T (2012) Spatially extended habitat modification by intertidal reef-building bivalves has

- implications for consumer-resource interactions. *Ecosystems* 15: 664–673. <https://doi.org/10.1007/s10021-012-9538-y>
- Wagner E, Dumbauld BR, Hacker SD, Trimble AC, Wisheart LM, Ruesink JL (2012) Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. *Marine Ecology Progress Series* 468: 149–160. <https://doi.org/10.3354/meps09952>
- Walles B (2015a) The ecosystem engineer *Crassostrea gigas* affects tidal flat morphology beyond the boundary of their reef structure. *Estuaries and Coasts* 38: 941–950. <https://doi.org/10.1007/s12237-014-9860-z>
- Walles B (2015b) The role of ecosystem engineers in the ecomorphological development of intertidal habitats. PhD Thesis. Wageningen University (Wageningen).
- Walles B, Mann R, Ysebaert T, Troost K, Herman PMJ, Smaal AC (2015c) Demography of the ecosystem engineer *Crassostrea gigas*, related to vertical reef accretion and reef persistence. *Estuarine, Coastal and Shelf Science* 154: 224–233. <https://doi.org/10.1016/j.ecss.2015.01.006>
- Waser AM, Splinter W, van der Meer J (2015) Indirect effects of invasive species affecting the population structure of an ecosystem engineer. *Ecosphere* 6: 109. <https://doi.org/10.1890/ES14-00437.1>
- Waser AM, Deuzeman S, van Kangeri AK, van Winden E, Postma J, de Boer P, van der Meer J, Ens B (2016) Impact on bird fauna of a non-native oyster expanding into blue mussel beds in the Dutch Wadden Sea. *Biological Conservation* 202: 39–49. <https://doi.org/10.1016/j.biocon.2016.08.007>
- Wehrmann A, Herlyn M, Bungenstock F, Hertweck G, Millat G (2000) The distribution gap is closed – first record of naturally settled Pacific oysters *Crassostrea gigas* in the East Frisian Wadden Sea, North Sea. *Senckenbergiana maritima* 30: 153–160. <https://doi.org/10.1007/BF03042964>
- Wehrmann A (2016) Wadden Sea. In: Harff J, Meschede M, Petersen S, Thiede J (Eds) *Encyclopedia of Marine Geosciences*. Springer (Dordrecht). https://doi.org/10.1007/978-94-007-6238-1_143
- Wrange AL, Valero J, Hakestad LS, Strand O, Lindegarth S, Christensen HT, Dolmer P, Kristensen PS, Mortensen S (2010) Massive settlements of the Pacific oyster, *Crassostrea gigas*, in Scandinavia. *Biological Invasions* 12: 1453–1458. <https://doi.org/10.1007/s10530-009-9565-6>