Repeatable sediment associations of burrowing bivalves across six European tidal flat systems

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ABSTRACT: Burrowing bivalves are associated with particular sediment types within sedimentary systems. The degree to which bivalve sediment associations are repeatable across systems has seldom been investigated. To investigate whether such repeatability exists across tidal flats, we compared adult and juvenile distributions of 3 bivalve species (*Cerastoderma edule*, *Scrobicularia plana*, *Macoma balthica*) across 6 European tidal flats. Across systems, the adult bivalves showed fairly repeatable distributions, with *C. edule* occurring in sandy sediments and *M. balthica* and *S. plana* occurring in muddy sediments. Exceptions were observed in systems composed primarily of muddy sediments (Aiguillon Bay and Marennes-Oléron Bay) and the Dutch Wadden Sea. Interestingly, juveniles and adults of *C. edule* and *S. plana* showed similar distributions across systems. *M. balthica* juveniles and adults showed habitat separation in 3 of the 6 studied systems; in 2 of these, it has been shown previously that juvenile *M. balthica* settle in mud at high tidal levels and migrate to lower sandier flats later in life. The high occurrence of juvenile *M. balthica* towards high sandy flats in Mont Saint-Michel Bay suggests that juveniles might choose high tidal flats rather than muddy sediments per se. A repeatable association in adults and juveniles with respect to sediment could suggest that juveniles actively settle in the proximity of the adults and/or that juveniles settling away from the adults incur a higher mortality due to either predation, physiological stress, or other factors.

KEY WORDS: Habitat suitability model · Species distribution · Logistic regression · German Wadden Sea · The Wash

INTRODUCTION

In marine sediment systems, sediment grain size distributions reflect a combination of physical, e.g. hydrodynamics and biological processes such as bioturbation (Rhoads 1974, Snelgrove & Butman 1994). Because physical and biological processes affect macrobenthic communities, sediment–animal relationships are considered a convenient short-cut for examining habitat suitability (Sanders 1958, Gray 1974, Wolff 1983). For example, it has been observed that benthic species occur at their greatest densities where particular sediment grain sizes are found within local tidal flat systems (Sanders 1958, Gray 1974, Whitlatch 1980, van der Meer 1991, Ysebaert et al. 2002, Huxham & Richards 2003, Thrush et al. 2003).

The association of benthic species with certain sediments may be due to active or passive post-settlement

dispersal. In juvenile bivalves, active dispersal can be facilitated by byssus-drifting in the water column (Baggerman 1953, Butman 1987, Beukema & de Vlas 1989, Cummings et al. 1993, Norkko et al. 2001), where settlement sites can be chosen on the basis of chemical cues available within sedimentary environments (Woodin et al. 1998, Marinelli & Woodin 2002). Passive dispersal is primarily determined by hydrodynamic conditions associated with bedload transport (Commito et al. 1995, Hunt 2004), depending on the juvenile bivalve's specific density and behaviour (Hunt 2004). The spatial distributions of bivalves may also reflect post-settlement mortality due to predation, physiological stress, competition, and biological or physical disturbance (see reviews by Butman 1987, Hunt & Scheibling 1997).

Active dispersal may suggest that bivalves select their habitat to avoid the negative fitness consequences from settling in specific sediment types. For example, bivalves settling in sediment types not matched to their feeding morphology may suffer adverse fitness consequences if their feeding morphology is not matched to the specific sediment type (Drent et al. 2004). Even if sediment characteristics may not provide the active habitat selection criterion (Huxham & Richards 2003), they may give a measure of the correlated variables that influence habitat selection (Snelgrove & Butman 1994). For example, sediment type can correlate with food availability, i.e. large grain sizes and fast current flow can correlate with increased phytoplankton and small grain sizes and slow current flow can correlate with higher densities of benthic algae (Lopez & Levinton 1987).

Within tidal flat systems, bivalve distributions are known to correlate with sediment type (Ysebaert et al. 2002, Huxham & Richards 2003, Thrush et al. 2003); however, across systems few studies have demonstrated whether distributions of bivalve species are repeatable. We chose 3 benthic bivalve species (*Cerastoderma edule*, *Macoma balthica* and *Scrobicularia plana*) that are abundant in most European tidal flat systems (Tebble 1966, Beukema 1976, Bocher et al. 2007) to examine whether juvenile and adult distributions are repeatable across 6 European tidal flat systems: German Wadden Sea, The Wash, Dutch Wadden Sea, Mont Saint-Michel Bay, Marennes-Oléron Bay and Aiguillon Bay.

MATERIALS AND METHODS

Sampling sites. The German (GWS, 53° 51′ N, 08° 26′ E) and Dutch Wadden Sea (DWS, 53° 14′ N, 05° 10′ E), The Wash (Wash, 53°53′N, 00°27′E), Mont Saint-Michel Bay (MsM, 48° 48′ N, 01° 41′ E),
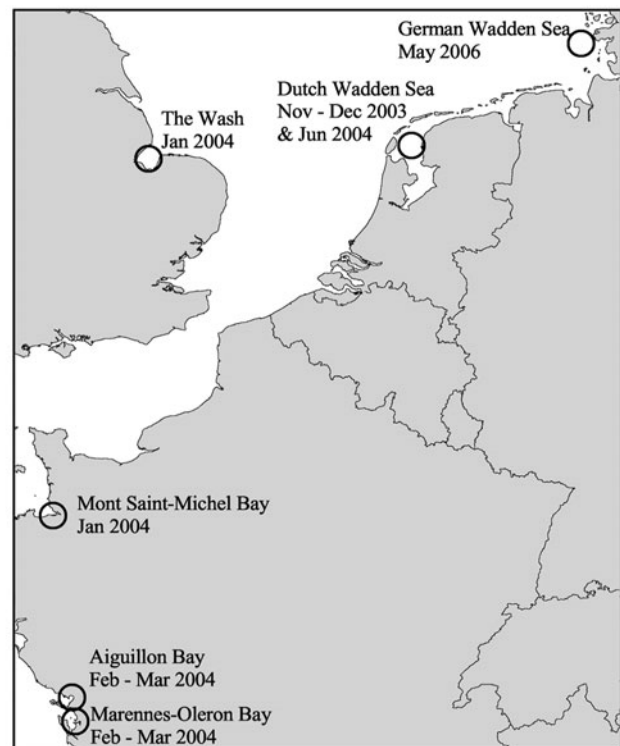

Fig. 1. The 6 tidal flats examined in the present study are located in Germany, Britain, The Netherlands and France. The circles indicate where the tidal flats are located in these countries. The months when sampling was undertaken are given

Marennes-Oléron Bay (MOZ, 46° 55′ N, 01° 10′ W) and Aiguillon Bay (Aig, 46° 55′ N, 01° 10′ W) are located in north-western Europe (see Fig. 1). Detailed descriptions of these areas and the sampling approaches used in the present study can be found in Bocher et al. (2007) and Compton et al. (2008). All systems were sampled using a grid mapping approach in which a grid of points, distanced at 250 m intervals, was sampled over a large surface area covering the tidal range of each system (see Table 1, and maps in Bocher et al. 2007 and Compton et al. 2008). The majority of systems in the present study were sampled from 25 November 2003 to 24 March 2004, the exceptions being the Dutch Wadden Sea and German Wadden Sea, which were sampled in May 2006 and June 2204, respectively (Fig. 1, Table 1). Sample points were identified using handheld global positioning system receivers (Garmin Corporation). Descriptions of the area sampled, the local spring and neap tidal heights and the interquartile measures for the median grain size measurements are shown in Table 1. The number of benthic cores taken, and the number of individuals encountered are shown in Table 2.

In all systems, a benthic core (1/56 m^2) was taken at each sample point to a depth of 20 cm. Bivalves were

Table 1. Site descriptions including the total surface area covered by each tidal flat (total, km^2), the sampled surface area covered in the present study (sampled, km^2), the maximum neap and spring tide levels (m) and the interquartile range values (IQR) for median grain size at each system, i.e. the values at which 25, 50 and 75% of the sediment values occur (IQR 25%, median and 75%)

| Tidal flat | Area | | Tide range | | Sediment range | | |
	Total	Sampled	Neap	Spring	IQR (25%)	Median	IQR (75%)
German Wadden Sea (GWS)	570	51	2.80	3.40	148	166	172
The Wash (Wash)	270	25	3.40	6.50	94	122	165
Dutch Wadden Sea (DWS)	890	193	1.50	2.50	152	168	189
Mont Saint-Michel (MsM)	200	31.3	6.00	12.70	134	155	181
Marennes-Oléron Bay (MOZ)	13.4	13.4	2.40	5.10	12	29	67
Aiguillon (Aig)	28.7	28.7	2.40	5.10	7	8	9

separated from the sediment using a 1 mm meshed sieve and then either immediately identified or stored frozen for later measurement and identification. Juveniles are here defined as individuals with no gonad development (Cardoso 2007), i.e. *Macoma balthica* <8 mm, *Cerastoderma edule* <12 mm and *Scrobicularia plana* <8 mm (assuming the same size threshold as *M. balthica*). *S. plana* had a limited distribution, relative to the other 2 species, and was not found in the sampled area of the German Wadden Sea, and, although encountered in Mont Saint-Michel Bay (Bocher et al. 2007), the measured occurrence of juveniles was too low (n = 1) for inclusion in the model of adult and juvenile distributions (Table 2). In addition, the occurrences of adult and juvenile *S. plana* at the Dutch Wadden Sea were also low (~4%; Table 2); however, this system was included in the analysis, as both adults and juveniles were found. Low occurrences of *S. plana* in these systems could be a sampling artefact, e.g. high abundances of *S. plana* have been observed in very muddy (<63 µm) areas near the mainland coast (Zwarts 1988). In the present study, seasonal differences should be minimal across the systems sampled in the winter months, as the studied bivalve species recruit in spring across north-western Europe (*M. balthica*: Lammens 1967, Bachelet 1980, Honkoop & van der Meer 1998, *C. edule*: Guillou et al. 1990, Honkoop & van der Meer 1998, and *S. plana*: Sola 1997). Species abundance differences (probability of occurrence) mainly reflect inter-annual differences in recruitment, as recruitment is highly variable in time and space (van der Meer et al. 2001).

Sediment samples were taken regularly at 1 km intervals, at points within the overall sampling scheme, using a core of 50 mm diameter to a depth ~7 cm. Sediment grain sizes were analysed using a particle size analyser (Beckman Coulter Model LS 230), following preparation according to van den Bergh et al. (2003). Median grain size (Mdϕ) was chosen as the measure of sediment grain size, because it is correlated with the percentage of silt. In addition,

Table 2. *Macoma balthica*, *Cerastoderma edule*, *Scrobicularia plana*. The number of cores taken in each system, and the percentage occurrence of adults and the juveniles are given for the 3 bivalve species at the 6 north-western European tidal flat systems (see Table 1 for definitions)

| System | No. of cores | Age | Percent occurence | | |
			M. balthica	*C. edule*	*S. plana*
GWS	796	Adult	46	58	–
		Juvenile	2	26	–
Wash	380	Adult	86	40	12
		Juvenile	58	47	5
DWS	2733	Adult	32	15	0
		Juvenile	4	5	1
MsM	440	Adult	32	72	3
		Juvenile	11	29	0
MOZ	404	Adult	13	8	31
		Juvenile	3	5	17
Aig	462	Adult	52	10	47
		Juvenile	52	11	21

median grain size has already proven to be a useful parameter for examining animal–sediment relationships (Wolff 1973, van der Meer 1991, Ysebaert et al. 2002, Huxham & Richards 2003, Thrush et al. 2003). At the sample points where sediment samples were not taken, median grain size values were estimated with an inverse distance weighting interpolation (Fortin & Dale 2005) in ArcGIS. An inverse distance weighting interpolation calculates the missing sediment values from the surrounding measured values. Because sediment grain sizes are relatively homogenous at these systems, the interpolation procedure works well at the 250 m grid scale (see Appendix 1 in Compton et al. 2008) and does not affect the model outcomes.

The frequency of the different sediment types varies starkly between the 6 European systems (Compton et al. 2008). The 4 most northern systems are composed of sandy sediments (Mdϕ = 100 to 200 µm), albeit with different frequencies. In contrast, the 2 most southern

systems, Marennes-Oléron Bay and Aiguillon Bay, France, are composed of predominantly muddy sediments (Mdϕ < 100 µm; Bocher et al. 2007, Compton et al. 2008).

Analysis. The number of times the bivalve species were present or absent were analysed with logistic regression for adults and juveniles. In the literature, logistic regression has also been referred to as habitat suitability modelling (Hirzel & Guisan 2002). In logistic regression, a binary response variable is related to 1 or more predictor variables through a logistic link function (McCullagh & Nelder 1989) such that:

$$\text{logit} [p(x)] = \log\{p(x)/[1 - p(x)]\} = b_0 + b_1 x + b_2 x^2 \quad (1)$$

where $p(x)$ is the probability that a species occurs as a function of an environmental variable (x) and b_0, b_1 and b_2 are estimated regression parameters. These parameters are estimated using maximum likelihood assuming binomially distributed errors. A logistic link can take a number of forms including an s-shaped function, i.e. a first-order polynomial, or a Gaussian function, i.e. a second-order polynomial. Global model significance and the significance of individual regression parameters are shown with a χ^2-test (p < 0.05), determined from the null and residual deviances and the degrees of freedom of the model. The residual deviance (D_{res}) is a measure of the deviation between the observed and fitted responses and is akin to the residual sum of squares in a linear regression (Jongman et al. 1995).

In the present study, an optimal logistic regression function was identified for each species using a model selection procedure based on the Akaike information criterion (AIC; Akaike 1974). The AIC adjusts the deviance of a given model to the number of predictor variables, i.e. a penalised log-likelihood (Quinn & Keough 2006). The model with the lowest AIC value indicates the best fit (Quinn & Keough 2006). For all species the saturated model was:

$$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x + \gamma x^2 + \gamma_i x^2 + \gamma_j x^2 + \gamma_{ij} x^2 \quad (2)$$

where y is the probability of occurrence, α is the regression intercept, β and γ are estimated regression parameters and x refers to median grain size. The index i refers to the different tidal flat systems, and j refers to age group. In each model, the baseline intercept, for comparison with the other systems, was the Dutch Wadden Sea.

Differences between adult and juvenile distributions of *Cerastoderma edule* observed in the optimal model selection procedure were later examined for significance in all systems separately using a simple Gaussian regression, instead of conducting post hoc comparisons:

$$y = \alpha + \alpha_j + \beta x + \beta_j x + \gamma x^2 \quad (3)$$

where y is the probability of occurrence, x refers to median grain size, α is the regression intercept, the index j is the age group, and β and γ are estimated regression parameters.

A common complication of the Gaussian function in Eqs. (2 & 3) is that the regression is ill-determined and will display a minimum instead of a maximum (ter Braak & Prentice 2004), which is biologically unrealistic. In such cases a first-order polynomial function was fitted:

$$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x \quad (4)$$

where y is the probability of occurrence, α is the regression intercept, β is the regression coefficient, j is the age group, i is the system and x is median grain size. In *Macoma balthica*, where a Gaussian model was ill-determined across systems, Eq. (4) was fitted as the saturated model. To further examine whether differences between adult and juvenile distributions occurred within a system, a simple polynomial regression was fitted such that:

$$y = \alpha + \alpha_j + \beta x + \beta_j x \quad (5)$$

where y is the probability of occurrence, α is the regression intercept, β is the regression coefficient, j is the age group and x is median grain size. This regression equation (Eq. 5) was used to examine whether differences were significant between juvenile and adult *M. balthica* across all systems. All analyses were done in the R programme for computing (R Development Core Team 2004).

RESULTS

The occurrences of adult and juvenile *Cerastoderma edule* displayed a significant Gaussian response to sediment, as seen by the selected quadratic terms (x^2; Table 3). However, the exact set-off and shape of the predicted Gaussian response curves differed between adults and juveniles, as seen by the terms that refer to the juvenile response curves ($\alpha_j x$, $\alpha_{ij} x$, $\beta_j x$, $\gamma_j x^2$, $\gamma_{ij} x^2$; Table 3). For the German Wadden Sea, The Wash and Mont-Saint Michel Bay, the predicted response curves of adult *C. edule* showed a repeatable and clear maximum in sandy sediments (approximate Mdϕ < 150 µm; Fig. 2). In the Dutch Wadden Sea, adult *C. edule* was predicted to occur maximally in fine-grained sediments (Mdϕ < 150 µm; Fig. 2), even though sandy sediments were available. In the 2 systems composed primarily of muddy sediments, Marennes-Oléron Bay and Aiguillon Bay, the probability of encountering adult *C. edule* was low (Fig. 2). For Aiguillon Bay, the adult

Table 3. *Cerastoderma edule*, *Scrobicularia plana*, *Macoma balthica*. Results from the model selection showing the optimal residual deviance (D_{res}) and the Akaike information criterion (AIC) in bold. Minus signs indicate terms that were deleted from the saturated model in the model selection procedure. In each equation, y is the probability of occurrence, α is the regression intercept, β and γ are the estimated regression parameters and x refers to median grain size. The index i refers to the different tidal flat systems and j refers to adult or juvenile

	D_{res}	AIC
C. edule optimal model:		
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \gamma x^2 + \gamma_i x^2 + \gamma_j x^2 + \gamma_{ij} x^2$		
Null	8882	8884
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x + \gamma x^2 + \gamma_i x^2 + \gamma_j x^2 + \gamma_{ij} x^2$	7720	7792
$-\gamma_{ij} x^2$	7728	7790
$-\beta_{ij} x$	**7727**	**7789**
$-\beta_{ij} x - \beta_j x$	7730	7790
$-\beta_{ij} x - \gamma_{ij} x^2$	7740	7792
$-\beta_{ij} x + \beta_i x$	7855	7907
S. plana optimal model:		
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \gamma x^2 + \gamma_i x^2$		
Null	3571	3573
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x + \gamma x^2 + \gamma_i x^2 + \gamma_j x^2 + \gamma_{ij} x^2$	2433	2481
$-\gamma_{ij} x^2$	2437	2479
$-\beta_{ij} x$	2438	2480
$-\gamma_{ij} x^2 - \gamma_i x^2$	2454	2490
$-\gamma_{ij} x^2 - \beta_{ij} x$	2443	2479
$-\gamma_{ij} x^2 - \gamma_j x^2$	2438	2478
$-\gamma_{ij} x^2 - \gamma_j x^2 - \gamma_i x^2$	2454	2489
$-\gamma_{ij} x^2 - \gamma_j x^2 - \beta_{ij} x$	2443	2477
$-\gamma_{ij} x^2 - \gamma_j x^2 - \beta_{ij} x - \gamma_i x^2$	2460	2488
$-\gamma_{ij} x^2 - \gamma_j x^2 - \beta_{ij} x - \beta_i x$	2460	2488
$-\gamma_{ij} x^2 - \gamma_j x^2 - \beta_{ij} x - \beta_j x$	**2443**	**2475**
$-\gamma_{ij} x^2 - \gamma_j x^2 - \beta_{ij} x - \beta_j x - \beta_i x$	2460	2486
M. balthica optimal model:		
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x$		
Null	9856	9858
$y = \alpha + \beta x$	**9659**	**9663**
$y = \alpha + \gamma x^2$	9682	9686
$y = \alpha + \alpha_i + \alpha_j + \alpha_{ij} + \beta x + \beta_i x + \beta_j x + \beta_{ij} x$	**8190**	**8238**
$-\beta_{ij} x$	8264	8301

response curves differed significantly from those for the Dutch Wadden Sea, whereas the response curves for the adults in the other systems did not differ relative to those for the Dutch Wadden Sea (Table 4). The predicted juvenile response curves for Mont Saint-Michel Bay differed significantly to those for the Dutch Wadden Sea, while the other systems did not differ significantly from the Dutch Wadden Sea ($\gamma_j x^2$; Table 4). Separate regressions for each system showed that the predicted response curves for adults and juveniles within the Dutch Wadden Sea were marginally, significantly different from each other (Eq. 3; DWS: D_{res} = 3092, p = 0.04), but did not differ from each other for Mont Saint-Michel Bay and the other studied systems (MsM: D_{res} = 1049, p = 0.14; MOZ: D_{res} = 357, p = 1; Aig: D_{res} = 578, p = 0.27; GWS: D_{res} = 1849, p = 0.6; Wash: D_{res} = 928, p = 0.09).

The optimal model selected for *Scrobicularia plana* showed that sediment was a significant term predicting occurrence in most systems in the present study (βx; Tables 3 & 5) and that the predicted adult and juvenile response curves did not differ from each other for most systems, as the lowest AIC value was obtained when the adult and juvenile interaction term was excluded ($-\beta_{ij} x$; Table 3). Adult *S. plana* repeatedly showed a predicted maximum occurrence in fine-grained sediments in 3 of the 4 systems (Md$\phi \approx$ 100 µm; Fig. 3), except in the Dutch Wadden Sea where overall instances of adult and juvenile occurrence were very low (Fig. 3). The predicted adult response curves for all systems differed relative to that for the Dutch Wadden Sea ($\beta_i x$; Table 5). The predicted juvenile response curve for Marennes-Oléron Bay was significantly different to that for the Dutch Wadden Sea, whereas the response curves for the other systems did not differ relative to that for the Dutch Wadden Sea ($\gamma_i x$; Table 5).

The optimal model for *Macoma balthica* included sediment as a significant term in the overall model, indicating that sediment was an important predictor for most systems (Table 3). In addition, the juvenile response curves differed significantly from the adult response curves, as the AIC value increased when this interaction term ($-\beta_{ij} x$) was removed from the linear model (Table 3). Across the 6 systems observed in the present study, adult *M. balthica* was predicted to have a repeatable and maximum occurrence in muddy sediments (Mdϕ < 150 µm; Fig. 4), with the exceptions of the Dutch Wadden Sea and Aiguillon Bay, where the predicted response curve showed a linear response with sediment (Fig. 4). The predicted response curve for adult *M. balthica* in Aiguillon Bay was not significantly different to that in the Dutch Wadden Sea, whereas the predicted response curves for the other systems differed significantly from that for the Dutch Wadden Sea (Table 6). The optimal model showed that the predicted juvenile response curves ($\beta_j x$) for Mont Saint-Michel Bay and The Wash differed significantly relative to that for the Dutch Wadden Sea, but that the juvenile response curves for the other systems did not differ relative to that for the Dutch Wadden Sea
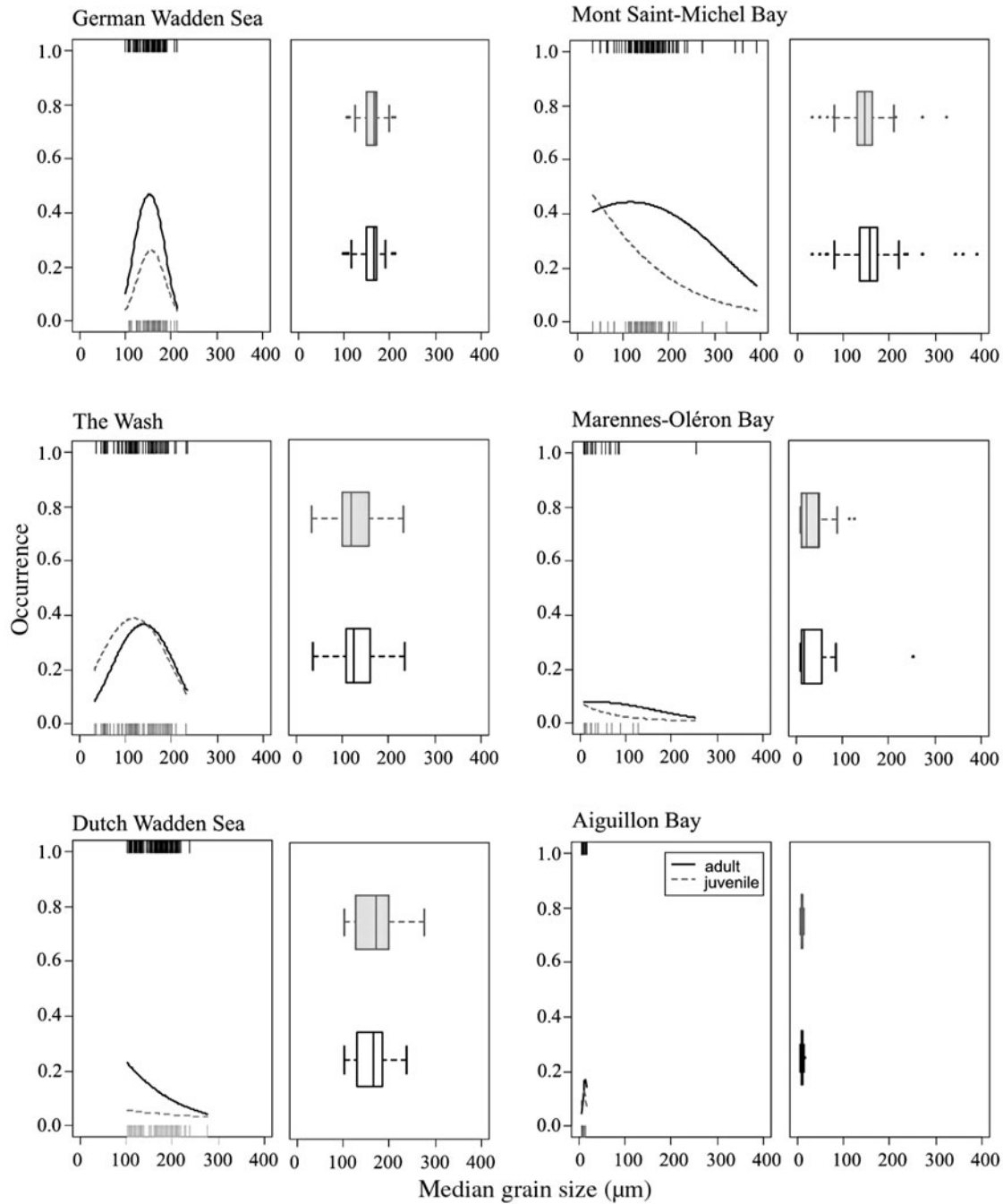
Fig. 2. *Cerastoderma edule.* Adult and juvenile distributions across the 6 European systems, shown by a logit regression fit (black lines: adults; grey dashed lines: juveniles) and a boxplot (presence only data; grey boxes: juveniles, clear boxes: adults). The raw presence data for the adults (black, top) and the juveniles (grey, bottom) are presented as a rug on the regression plots. Boxes: interquartile range of the data (first quartile, median and third quartile). Whiskers: the values that extend to 1.5 times the interquartile range. Circles: outliers

(Table 6). Separate regression analyses showed that the adult and juvenile response curves did not differ within the Wash (Eq. 5; D_{res} = 874, p = 0.7). Instead, the predicted juvenile response curves for the Wash differed from those for the other systems because of higher occurrence probabilities over sediment type

(Fig. 4). Separate regression analyses for the German Wadden Sea, the Dutch Wadden Sea and Mont Saint-Michel Bay showed significant differences between adult and juvenile response curves (Eq. 5; GWS: D_{res} = 1108, p = 0.01; DWS: D_{res} = 3933, p < 0.001; MsM: D_{res} = 737, p < 0.001). The predicted response curves for

Table 4. *Cerastoderma edule*. Model results for *C. edule* (see Table 3) where the Dutch Wadden Sea is the intercept system relative to the other systems. See Table 1 for tidal flat systems. Juv: juveniles; Mdφ: median grain size

	Coefficient	Estimate	SE	z-value	Pr(>|z|)
Intercept	α	3.521	0.9182	3.834	<0.001
Aig	α	−9.79	1.625	−6.024	<0.001
GWS	α	−20.9	2.488	−8.399	<0.001
MOZ	α_i	−5.989	0.9483	−6.316	<0.001
MsM	α	−4.036	1.05	−3.843	<0.001
Wash	α	−7.19	1.068	−6.733	<0.001
Juv	α_j	−0.5227	0.6989	−0.748	0.45
Aig × Juv	α_{ij}	1.329	0.7982	1.665	0.1
GWS × Juv	α_{ij}	0.3267	0.6067	0.539	0.59
MOZ × Juv	α_{ij}	0.4774	0.6185	0.772	0.44
MsM × Juv	α_{ij}	1.249	0.3971	3.145	<0.001
Wash × Juv	α_{ij}	1.979	0.448	4.417	<0.001
Mdφ		−0.0568	0.0112	−5.055	<0.001
Juv × Mdφ	β_j	−0.015	0.0078	−1.928	0.05
Aig × Mdφ	β_i	0.7631	0.2561	2.98	<0.001
GWS × Mdφ	β_i	0.2834	0.0328	8.638	<0.001
MOZ × Mdφ	β_i	0.0582	0.0134	4.355	<0.001
MsM × Mdφ	β_i	0.0618	0.0123	5.021	<0.001
Wash × Mdφ	β_i	0.1015	0.0142	7.145	<0.001
Mdφ^2		0.0001	0	4.129	<0.001
Aig × Mdφ^2	γ_i	−0.0267	0.0116	−2.307	0.02
GWS × Mdφ^2	γ_i	−0.0009	0.0001	−8.204	<0.001
MOZ × Mdφ^2	γ_i	−0.0002	0	−3.44	<0.001
MsM × Mdφ^2	γ_i	−0.0002	0	−4.479	<0.001
Wash × Mdφ^2	γ_i	−0.0003	0	−6.211	<0.001
Juv × Mdφ^2	γ	0.0001	0	2.645	<0.001
Aig × Juv × Mdφ^2	γ_j	−0.0065	0.0047	−1.372	0.17
GWS × Juv × Mdφ^2	γ_j	0	0	0.109	0.91
MOZ × Juv × Mdφ^2	γ_j	0	0	−0.588	0.56
MsM × Juv × Mdφ^2	γ_j	0	0	−2.979	<0.001
Wash × Juv × Mdφ^2	γ_j	0	0	−1.687	0.09

these systems showed that juveniles at Mont Saint-Michel Bay occurred towards sandier sediments than the adults did, whereas the juveniles in the German Wadden Sea and Dutch Wadden Sea occurred towards muddier sediments than the adults did (see Fig. 4). Differences between the juveniles and adults were not significant for the other systems (Eq. 5; MOZ: D_{res} = 347, p = 0.41; Aig: D_{res} = 1189, p = 0.59).

DISCUSSION

In the present study, 3 burrowing bivalve species *Cerastoderma edule*, *Scrobicularia plana* and *Macoma balthica* showed repeatable distributions with respect to sediment grain size. Specifically, the adults of all 3 species occurred predominantly in specific sediment types, and the juveniles of 2 species, *C. edule* and *S. plana*, had distributions that did not differ from that of the adults. In *M. balthica* the juveniles occurred away from the adults in 3 of 6 tidal flat systems, consistent

with their known active migration away from the area of first settlement (Beukema & de Vlas 1989, Bouma et al. 2001). These results suggest that the individual species models can be applied to the same species on other tidal flats, as long as the systems are open offshore tidal flats and are not heavily influenced by anthropogenic factors, e.g. fisheries and pollution.

In all 3 species, the adults showed a repeatable association with particular sediment types across the studied systems. The suspension feeder *Cerastoderma edule* occurred mostly in sandy sediments (Mdφ ≈ 150 µm), similar to results for other studied systems (optimum at Mdφ = 62.5 to 125 µm in Wolff 1973 and at Mdφ ≈ 125 µm in Ysebaert et al. 2002 and Huxham & Richards 2003). Where sandy sediments were not available, *C. edule* occurred in soft mud (Marennes-Oléron Bay and Aiguillon Bay). In the Dutch Wadden Sea, *C. edule* occurred in greatest abundance towards fine-grained sediments, even though sandy sediments were available. Here, *C. edule* has been undergoing a shift in its distribution from predominantly sandy to higher and muddier nearshore sediments (Piersma et al. 2001, Zwarts et al. 2004, Beukema & Dekker 2006).

Table 5. *Scrobicularia plana*. Model results for *S. plana* (see Table 3) where the Dutch Wadden Sea is the intercept system relative to the other systems. Abbreviations are the same as in Table 4

|	Coefficient	Estimate	SE	z-value	Pr(>|z|)
Intercept	α	−60.04	21.1	−2.85	<0.001
Aig	α_i	59.53	21.11	2.82	<0.001
MOZ	α_i	58.77	21.1	2.79	<0.001
Wash	α_i	59.33	21.12	2.81	<0.001
Juv	α_j	0.225	0.389	0.58	0.56
Aig × Juv	α_{ij}	−1.012	0.42	−2.41	<0.01
MOZ × Juv	α_{ij}	−0.797	0.43	−1.85	0.06
Wash × Juv	α_{ij}	−1.219	0.493	−2.47	<0.01
Mdφ	β	0.613	0.236	2.59	<0.001
Aig × Mdφ	β_i	−0.665	0.246	−2.71	<0.001
MOZ × Mdφ	β_i	−0.607	0.236	−2.57	<0.01
Wash × Mdφ	β_i	−0.607	0.237	−2.56	<0.01
Mdφ^2	γ	−0.002	0.001	−2.58	<0.01
Aig × Mdφ^2	γ_i	0.004	0.002	1.72	0.09
MOZ × Mdφ^2	γ_i	0.002	0.001	2.52	<0.01
Wash × Mdφ^2	γ_i	0.002	0.001	2.3	0.02
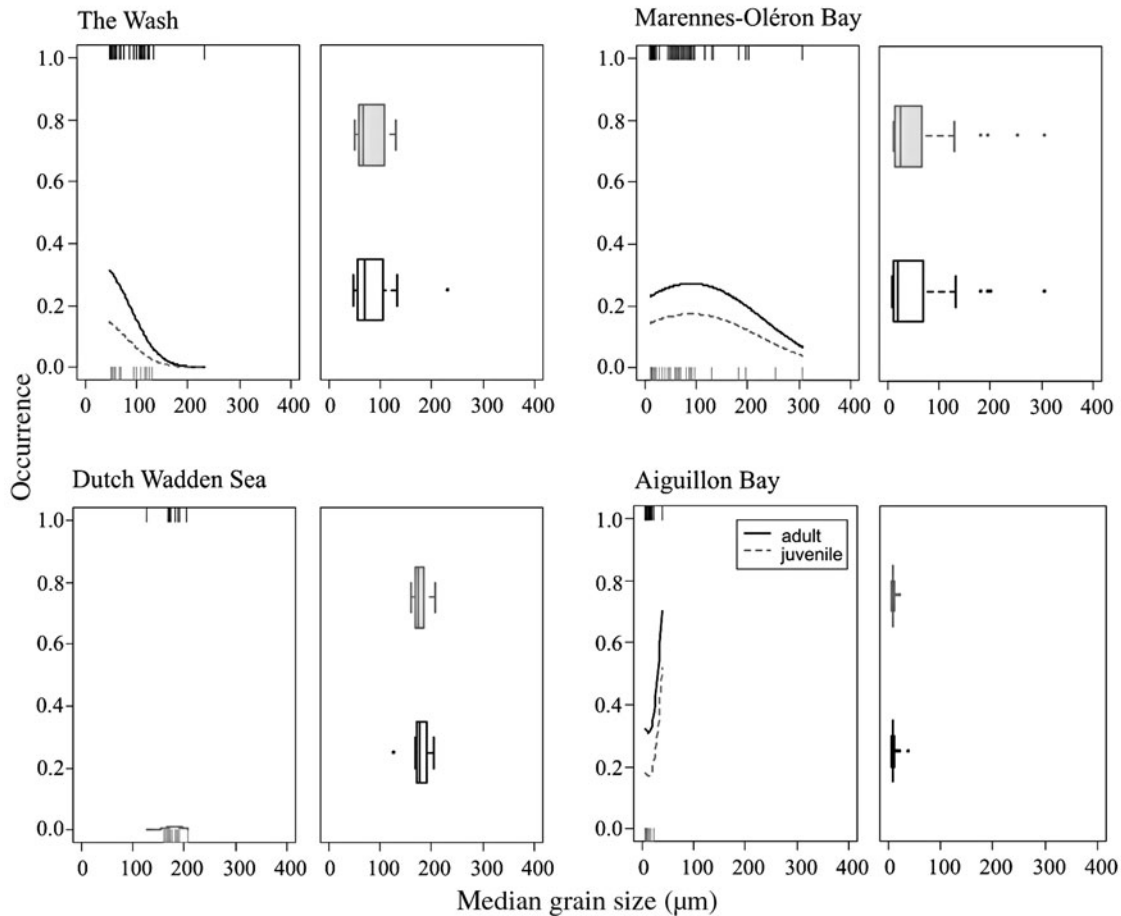
Fig. 3. *Scrobicularia plana*. Adult and juvenile distributions, with respect to median grain size, for each of the 4 European systems; shown by a logit regression fit (black lines: adults; grey dashed lines: juveniles) and a boxplot (presence only data; grey boxes: juveniles, clear boxes: adults). The raw presence data for the adults (black, top) and the juveniles (grey, bottom) are presented as a rug on the regression plots. Box definitions as in Fig. 2

This upward shift appears to be associated with large-scale mechanical cockle dredging of the previously preferred lower lying sandy areas (Piersma et al. 2001).

Consistent with previous studies (Hughes 1969, 1970, Sola 1997), *Scrobicularia plana* was predicted to occur in muddy sediments in 3 of the 4 systems. In the present study, *Macoma balthica* was predicted to have maximum and repeatable occurrences in fine-grained sediments (<100 μm), similar to those seen in other systems (~75 μm; Ysebaert et al. 2002). Although *M. balthica* did not show a clear distributional response to sediment in Aiguillon Bay and the Dutch Wadden Sea, the high probability of occurrence in Aiguillon Bay suggests that muddy sediments are suitable for this species to survive at high densities. In the Dutch Wadden Sea, *M. balthica* showed no sediment preference, suggesting either this species occurs broadly across all sediments or that the distribution of this species has been modified by human disturbance (Piersma et al. 2001, Beukema & Dekker 2006, van Gils et al. 2006).

The latter option seems plausible, as high densities have previously been recorded in fine-grained sediments (Beukema 1976, Wolff 1983) and the probability of encountering *M. balthica* is currently very low (J. Drent pers. obs.). It seems that the population densities and spatial distributions of *M. balthica* and *C. edule* have changed in the Dutch Wadden Sea, suggesting that a common factor might have negatively affected these species (Zwarts et al. 2004).

The predicted optimal occurrence of the suspension feeder *Cerastoderma edule* in sandy sediments and the deposit feeders *Scrobicularia plana* and *Macoma balthica* in muddy sediments appears to be consistent with the notion that feeding mode is associated with sediment type (Sanders 1958, Levinton 1972). For example, fine-grained muddy sediments are expected to be associated with a higher organic material content than sandy sediments, and as such provide a higher quality feeding habitat for deposit feeders (Sanders 1958, Levinton 1972). However, as feeding mode vari-
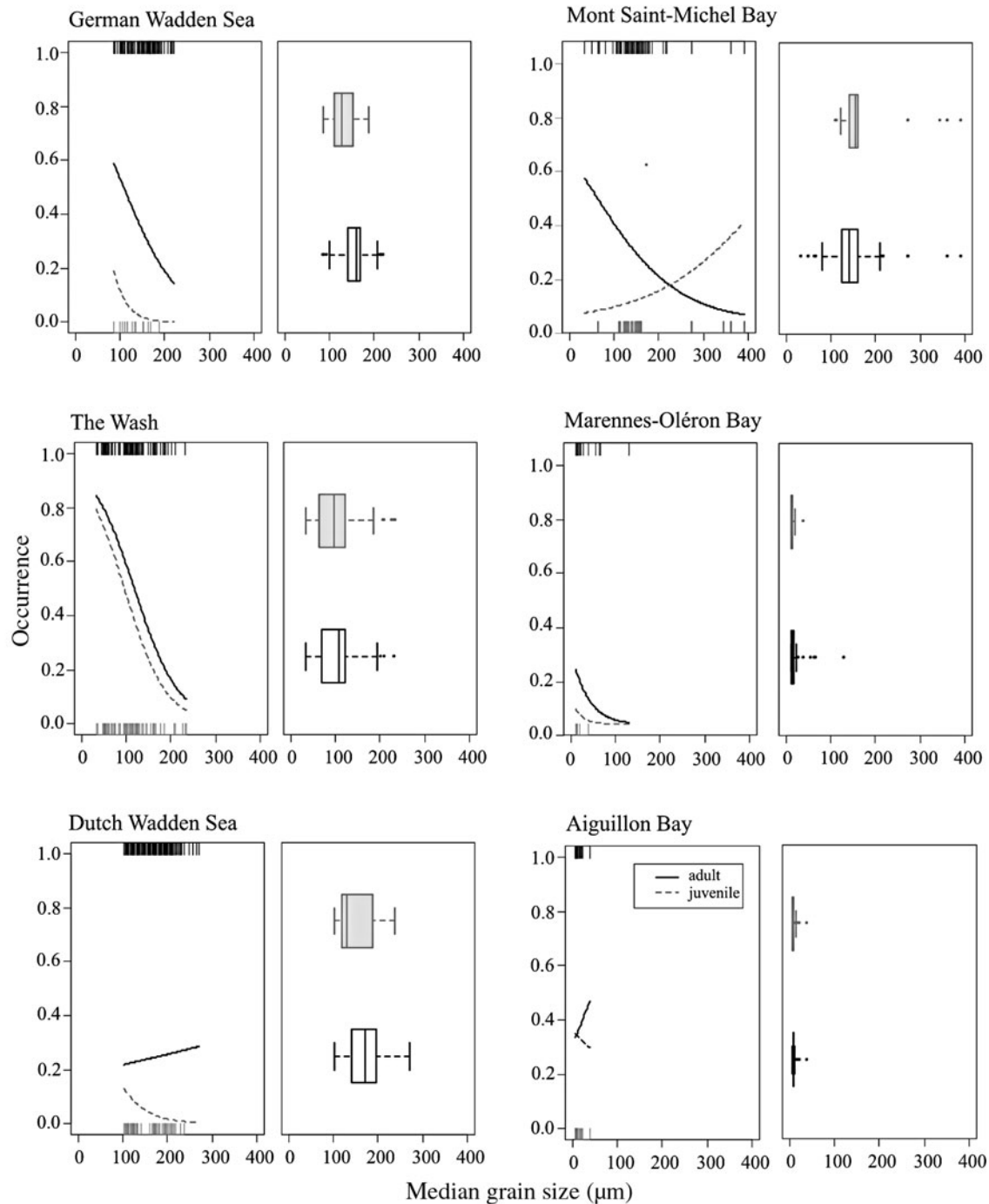
Fig. 4. *Macoma balthica*. Adult and juvenile distributions across the 6 European systems, shown by a logit regression fit (black lines: adults; grey dashed lines: juveniles) and a boxplot (presence only data; grey boxes: juveniles, clear boxes: adults). The raw presence data for the adults (black, top) and the juveniles (grey, bottom) are presented as a rug on the regression plots. Box definitions as in Fig. 2

ations of benthic bivalves are multi-dimensional and gradual (Brafield & Newell 1961, Hughes 1969, Thompson & Nichols 1988, Compton et al. 2007), bivalve distributions reflect not only sediment type, but also the associated organic content and a flow regime

that optimizes feeding efficiency (see review by Snelgrove & Butman 1994).

Even though *Cerastoderma edule* spat (<1 mm) can actively migrate under calm hydrodynamic conditions (Baggerman 1953, de Montaudouin & Bachelet 1996),

Table 6. *Macoma balthica*. Model results for *M. balthica* (see Table 3) where the Dutch Wadden Sea is the intercept system relative to the other systems. Abbreviations are the same as in Table 4

	Coefficient	Estimate	SE	*z*-value	Pr(>|z|)
Intercept	α	−1.491	0.255	−5.86	<0.001
Aig	α_i	0.697	0.383	1.82	0.07
GWS	α_i	3.204	0.557	5.76	<0.001
MOZ	α_i	0.431	0.351	1.23	0.22
MsM	α_i	1.972	0.491	4.02	<0.001
Wash	α_i	3.828	0.425	9.01	<0.001
Juv	α_j	1.819	0.572	3.18	<0.001
Aig × Juv	α_{ij}	−1.609	0.704	−2.29	0.02
GWS × Juv	α_{ij}	−1.598	1.451	−1.1	0.27
MOZ × Juv	α_{ij}	−3.046	0.804	−3.79	<0.001
MsM × Juv	α_{ij}	−5.914	0.852	−6.94	<0.001
Wash × Juv	α_{ij}	−2.117	0.747	−2.83	<0.001
Mdφ	βx	0.002	0.001	1.43	0.15
Aig × Mdφ	β_i	0.015	0.032	0.49	0.63
GWS × Mdφ	β_i	−0.018	0.003	−5.19	<0.001
MOZ × Mdφ	β_i	−0.033	0.009	−3.91	<0.001
MsM × Mdφ	β_i	−0.013	0.003	−4.06	<0.001
Wash × Mdφ	β_i	−0.022	0.003	−7.34	<0.001
Juv × Mdφ	β_j	−0.024	0.004	−6.53	<0.001
Aig × Juv × Mdφ	β_{ij}	−0.001	0.046	−0.02	0.98
GWS × Juv × Mdφ	β_{ij}	0	0.01	0.03	0.98
MOZ × Juv × Mdφ	β_{ij}	0.004	0.028	0.14	0.89
MsM × Juv × Mdφ	β_{ij}	0.042	0.005	8.19	<0.001
Wash × Juv × Mdφ	β_{ij}	0.022	0.005	4.24	<0.001

juvenile and adult *C. edule* showed similar distributions. The overlapping distributions of the juveniles and adults could suggest that juveniles actively settle in the proximity of the adults and/or that juveniles settling in the proximity of adults are more likely to survive; however, this would seem surprising as adult *C. edule* can negatively affect larval settlement (André & Rosenberg 1991, de Montaudouin & Bachelet 1996). Alternatively, these results could suggest that predation is higher on juveniles settling outside of the adult cockle beds. However, if this were the case, it would be surprising to find that distributions are repeatable across systems, as we would expect variable predation to lead to juvenile distributions that would differ across systems. The matching distributions of juvenile and adult *Scrobicularia plana* could suggest that either juvenile bivalves actively settle in the proximity of the adults or that mortality is higher away from the adults.

Macoma balthica juveniles occurred in muddier sediment types than the adults in the German Wadden Sea and Dutch Wadden Sea, whereas, in Mont Saint-Michel Bay, the juveniles occurred in sandier sediments than the adults did. Habitat separation, with respect to sediment, is probably associated with post-settlement dispersal. *M. balthica* is known to migrate, via byssus thread drifting, to high on the intertidal during post-settlement to avoid predation before later

migrating to lower tidal flat areas (Beukema & de Vlas 1989, Bouma et al. 2001). At the 2 Wadden Sea study sites, muddy areas occur high in the intertidal (Zwarts et al. 2004), but, in Mont Saint-Michel Bay, the highest tidal flat areas are sandy (see Appendix 1 in Compton et al. 2008). In the 3 systems where differences between juveniles and adults were not apparent, it could either suggest that stronger hydrodynamics prevent habitat separation (Bouma et al. 2001), that sediment is not a good measure of tidal height at these systems, or that juvenile migration occurred prior to sampling, e.g. *M. balthica* in the Dutch Wadden Sea migrate during winter, whereas *M. balthica* at Westerschelde migrate in summer (Bouma et al. 2001, Hiddink & Wolff 2002, Beukema & Dekker 2003).

In the present study, we showed that (1) adults have repeatable distributions across tidal flats and (2) that juveniles can occur either in the same sediments as the adults, in the case of *Cerastoderma edule* and *Scrobicularia plana*, or in different sediment types when there is post-settlement migration as in *Macoma balthica*. Unfortunately, however, we cannot infer which habitat selection mechanisms might lead to these repeatable distributions. In fact, the observed repeatable distributions could even reflect processes that vary from system to system (Thrush et al. 2005). Alternatively, the repeatable associations in adults and juveniles, with respect to sediment, could suggest that juveniles actively settle in the proximity of the adults and/or that juveniles settling away from the adults incur a higher mortality due to either predation, physiological stress, or other factors. More experimental work and system comparisons using distribution models are needed if we are to understand what factors determine sediment associations in bivalves and other benthic species.

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