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Temporal variability of ecological niches: a study on intertidal macrobenthic fauna

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The determination of temporal niche dynamics under field conditions is an important component of a species' ecology. Recent developments in niche mapping, and the possibility to account for spatial autocorrelation in species distributions, hold promise for the statistical approach explored here. Using species counts from a landscape-scale benthic monitoring programme in the western Dutch Wadden Sea during 1997–2005 in combination with sediment characteristics and tidal height as explanatory variables, we statistically derive realised niches for two bivalves, two crustaceans and three polychaetes, encompassing predators, suspension and bottom feeding functional groups. Unsurprisingly, realized niches varied considerably between species. Intraspecific temporal variation was assessed as overlap between the year-specific niche and the overall mean niche, and this analysis revealed considerable variation between years. The main functional groups represented by these species showed idiosyncratic and wide variability through the study period. There were no strong associations between niche characteristics and mean abundance or body size. Our assessment of intraspecific niche variability has ramifications for species distribution models in general and offers advances from previous methods. 1) By assessing species' realized niches in the multivariate environmental space, analyses are independent from the relative availability of particular environments. Predicted realized niches present differences between years, rather than annual differences in environmental conditions. 2) Using spatially explicit models to predict species habitat preferences provide more precise and unbiased estimates of species–environment relationships. 3) Current niche models assume constant niches, whereas we illustrate how much these can vary over only a few generations. This emphasizes the potentially limited scope of global change studies with forecasts based on single-time species distribution snapshots.

Understanding the distribution and abundance of organisms in space and time is at the core of ecological research (Hutchinson 1953, Begon et al. 2006); it is considered a main research frontier (Gaston 2000, Scheffer and Carpenter 2003). Yet, mechanisms driving spatial and temporal variation in abundance of many species remain poorly understood (Gaston 2000, Hughes et al. 2005) and limit our ability to predict habitat use and so help delineate conservation targets (Thrush et al. 2003, Piersma 2012). The latter seems particularly pressing in many marine ecosystems due to catastrophic global shifts, following overharvesting, pollution and the direct and indirect impacts of climate change (Hughes et al. 2005, Thrush et al. 2009).

Mapping habitat preferences and distributional overlap of marine benthic fauna, i.e. bivalves, polychaetes and crustaceans that live hidden in estuarine soft sediments, received much attention recently, particularly in the accessible intertidal (Ysebaert et al. 2002, Thrush et al. 2003, Compton et al. 2009). Most studies used logistic regressions to express habitat preferences as the probability of occurrence on the basis of presence–absence data and sediment characteristic as explanatory variable. Often data are limited to single snapshots in time for a single species, leaving us ignorant about temporal and spatial variability of the realized niche (Pearman et al. 2008, Broennimann et al. 2011).

Using species counts from a landscape-scale benthic monitoring programme in the western Dutch Wadden Sea (Piersma et al. 2001, van Gils et al. 2009) over a period of nine consecutive years (1997–2005), we statistically derive realised niches for seven common intertidal species, two bivalves, i.e. *Cerastoderma edule* and *Macoma balthica*, two crustaceans, i.e. *Corophium volutator* and *Urothoe poseidonis*, and three polychaetes, i.e. *Lanice conchilega*, *Nephtys hombergii* and *Nereis diversicolor* (Table 1). The focus of this study is to estimate intraspecific temporal and spatial variability in realised niches, taking into account

Table 1. Species-list, their abbreviation, functional traits taken from the Marine Life Information Network (<www.marlin.ac.uk>), and minimum and maximum (mean) counts per sampling station from 1997–2005. Adult and juvenile *M. balthica* (MBA and MBJ) and *C. edule* (CEA and CEJ) are treated as separate species (Material and methods).

Species	Abbr.	Life expectation and traits	Counts
Cerastoderma edule	CEA	Long-living, gregarious, suspension-feeding bivalve	0–50 (0.41)
	CEJ		0–102 (0.32)
Corophium volutator	COR	Life span < 1 year, small, burrow-dwelling Amphipod	0–609 (2.93)
Lanice conchilega	LAN	Life span ~1 year, tubicolous polychaete	0–130 (1.07)
Macoma balthica	MBA	Long-living, sub-surface living bivalve	0–129 (0.99)
	MBJ		0–293 (0.58)
Nephtys hombergii	NEP	Long-living, free-living, predatory polychaetes	0–45 (0.19)
Nereis diversicolor	NER	Long-living, omnivorous, burrow-dwelling polychaete	0–250 (2.27)
Urothoe poseidonis	URO	Short-living, small, free-living amphipod	0–220 (2.98)

spatial autocorrelation in species distributions as well as environmental variables. Spatial autocorrelation, i.e. gradients and patchiness in the distribution of species, is defined as nearby observations of species abundance being more similar than by chance alone (Legendre 1993). Spatial autocorrelation affects statistical analysis and the ecological inferences drawn from them (Lennon 2000, Wagner and Fortin 2005), since the assumption of independent errors is violated, thereby effecting estimation of standard errors, parameter estimates and model fit (Dormann et al. 2007, Kraan et al. 2010). We thus investigate temporal variation in the degree to which benthic species overlap in their multidimensional environmental niche between consecutive years, describing habitat preferences of intertidal benthic organisms at geographical scales not amenable for experimentation (Pearman et al. 2008). This so-called Hutchinsonian niche relates the occurrence of species to a subset of environmental conditions (Green 1971, Kearney 2006, Soberón 2007).

Material and methods

Study area

The studied intertidal flats comprise part of the western Dutch Wadden Sea (53°N, 4 to 5°E), a marine protected area of international importance (van Gils et al. 2006, Piersma 2009). Each late summer from 1997 to 2005 we sampled the abundance of macrozoobenthos and collected sediment samples by boat during high tide or on foot during low tide in this landscape (Piersma et al. 2001, Kraan et al. 2009a, 2010). The study area covers 225 km^2 of gullies, subtidal and intertidal mudflats bounded by the barrier islands Texel and Vlieland and the Friesland mainland coast (Fig. 1a).

Sample processing

Benthic samples, taken to a depth of 20-cm and covering 0.02 m^2, were sieved through a 1-mm mesh and all individuals were counted and identified (van Gils et al. 2006, Kraan et al. 2009a, b). These samples, 2750 per year on average, spaced in a 250 m grid, together with sediment samples, 150 per year on average at 1000 m intervals, enabled us to map the distribution of benthic fauna and sedimentary characteristics in fine detail. Sampling positions were assigned in the first year and revisited in the years following. For more details about laboratory procedures and sediment measurements see Kraan et al. (2009a, 2010) and Piersma et al. (2001).

In the Dutch Wadden Sea the surface heights of the inter- and subtidal areas are recorded at 200-m intervals and then interpolated to a 20-m grid by the National Institute for Coastal and Marine Management (RIKZ), the Netherlands, in 6-year cycles. For each year, therefore, the nearest completed height assessment was used to assign a height-measurement to sampling stations. We used inverse distance weighting to assign a median grain size value to each sampling station (Compton et al. 2009, Kraan et al. 2010).

Spatial modelling

The response variables (Table 1) were the abundances of each species, i.e. the number of individuals per species at each sampling station. In the cases of *Macoma balthica* and *Cerastoderma edule* adults and juveniles (the current year's cohort) were treated separately, because habitat preferences may differ between adults and juveniles (Beukema 1993, Compton et al. 2009, Kraan et al. 2010). Explanatory variables were median grain size (μm), tidal height relative to Dutch Ordinance Level (cm below or above DOL), their quadratic terms, as well as their interaction (Kraan et al. 2010). This approach can easily be extended by including higher order polynomials or more flexible smooth functions (Wood 2006), which allows one to capture more complex non-linear habitat preferences, such as bimodal species–environment relations.

To account for spatial autocorrelation in both the distribution of species and environmental variables, we employed spatially explicit generalized estimating equations (GEE, Liang and Zeger 1986). Such regression methods are best described as cluster-models extending generalized linear models with a spatial variance–covariance matrix (Dormann et al. 2007, Kraan et al. 2010). We used a cluster size of 4×4 sampling stations, assuming a separate spatial correlation parameter for each distance-class within a cluster, while correlations between clusters are presumed absent (Carl and Kühn 2007). On a few occasions models failed to converge (Table 2). Variability of regression parameters across years was always higher than uncertainty within years (Table 2). This means that the temporal variability we describe reflects a true biological signal, beyond noise. All analyses were done in R (R Development Core

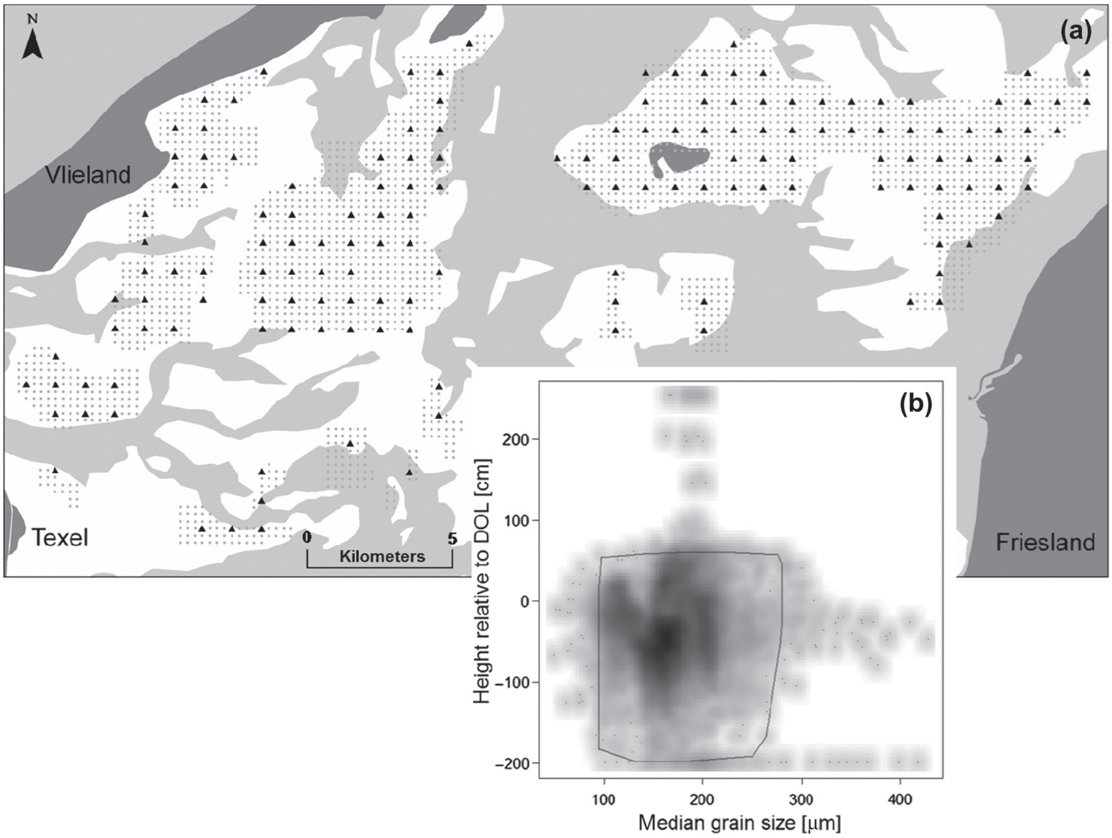

Figure 1. (a) Map of all benthic (circles) and sediment (triangles) sampling stations, on a 250 m grid and 1000 m grid, in the western Dutch Wadden Sea. White areas indicate mudflats exposed during low-water, intermediate grey areas indicate water, and land is represented by the darkest grey areas. (b) Environmental space showing all available median grain size and height relative to Dutch Ordinance Level values and the convex hull of 99% of the data points (polygon line) used for niche mapping. Darker areas, based on a smoothed scatter plot, represent sample sites with high density of sites with this combination of environmental states.

Team) using packages *gee* (Carey 2008), *geepack* (Yan 2007) and *ncf* (Bjørnstad and Falck 2001).

Environmental niche overlap from year to year

Overlap between environmental niches relative to the mean niche of a species was calculated for each year following Dormann et al. (2009). First, we truncated the environmental space under consideration by using only data points within the convex hull of 99% of all environmental conditions across all years, i.e. the realized habitat space (Fig. 1b). Such an approach prevents extrapolation to unobserved value combinations in the environmental space (the white space in Fig. 1b). Then, based on median grain size and height combinations inside the convex hull, we used the afore-mentioned GEEs to predict species counts

Table 2. Variability of environmental parameters determining realized niches, expressed as standard deviations (σ) of the regression coefficients of the spatial GEEs between years, and as mean standard deviation within years. For abbreviations of species names see Table 1. $\sigma_{between} > \sigma_{within}$ indicates that temporal variability in niche parameters is larger than its uncertainty within years, i.e. the temporal variability is a signal, not noise.

		Regression coefficients											
		Intercept		Depth		Depth^2		Median		Median^2		Depth × Median	
	n	σ		σ		σ		σ		σ		σ	
Species	years	within	between	within	between	within	between	within	between	within	between	within	between
CEA	9	3.0845	8.7089	0.0380	0.0954	0.0235	0.0302	0.0001	0.0003	0.0001	0.0001	0.0001	0.0003
CEJ	9	2.2102	3.7578	0.0295	0.0454	0.0251	0.0430	0.0001	0.0001	0.0001	0.0002	0.0002	0.0002
COR	8	9.4191	20.5841	0.1141	0.2017	0.0286	0.0519	0.0003	0.0006	0.0001	0.0003	0.0002	0.0003
LAN	8	4.3793	12.8313	0.0515	0.1712	0.0235	0.0509	0.0002	0.0006	0.0001	0.0001	0.0001	0.0003
MBA	9	0.8847	2.7019	0.0111	0.0193	0.0065	0.0181	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001
MBJ	8	1.6300	14.0597	0.0192	0.1583	0.0195	0.0321	0.0001	0.0004	0.0000	0.0001	0.0001	0.0001
NEP	9	1.9056	3.3331	0.0248	0.0339	0.0174	0.0317	0.0001	0.0001	0.0000	0.0001	0.0001	0.0002
NER	8	1.4047	3.5036	0.0171	0.0343	0.0096	0.0265	0.0001	0.0001	0.0000	0.0001	0.0001	0.0001
URO	8	5.1489	7.3520	0.0559	0.0764	0.0211	0.0431	0.0002	0.0002	0.0001	0.0001	0.0001	0.0003

to this habitat space for each year (for graphical representation see Kraan et al. 2010). GEEs were employed year- and species-specific, but all contained the same set of explanatory variables (Table 2). The range of environmental data was divided in 100 equidistant steps, yielding 9316 points per year inside the convex hull. Predicted species counts were divided by the sum of predicted values for each year, yielding relative abundance values between 0 and 1, thereby correcting for differences in abundance due to, for example, very successful recruitment events between years. Moreover, predicted relative abundances are now similarly scaled, thus allowing direct comparisons across species. Niche overlap was calculated on the basis of overlap in parameter, not geographical, space, as

$$NO_{ij} = \frac{1}{N}\sum_{k=1}^{N}\frac{\min(\hat{y}_{ik},\hat{y}_{jk})}{\max(\hat{y}_{ik},\hat{y}_{jk})}$$

where $\hat{y}_{.k}$ is the predicted relative abundance probability for the kth of N habitat hypercube combinations in year i or year j (Dormann et al. 2009, Broennimann et al. 2011). Therefore, niche overlap represents the proportion of the niche space occupied in two successive years relative to the total niche space occupied in the two years combined. As niche overlap calculations are bounded within the matrix of original environmental data and each environmental combination occurs only once (Dormann et al. 2009), this approach is an improvement of the so-called 'niche-equivalency' methods (Warren et al. 2008).

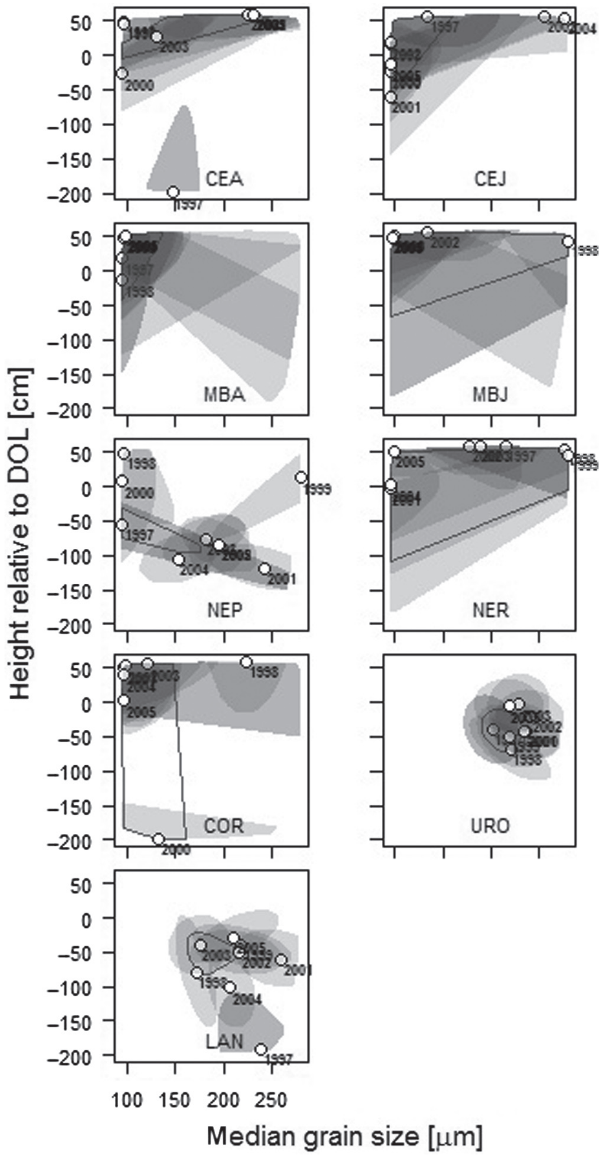

Figure 2. Habitat preferences of intertidal macrobenthic species in the western Dutch Wadden Sea. The area inside the polygon line depicts the mean overall top 5% preferred niche from 1997 to 2005; white dots indicate the maximum value per year (note that some years overlap); grey areas surrounding the maximum annual values show the 10% most suitable areas. For abbreviations of species names see Table 1.

Results

Habitat preferences varied considerably between species (Fig. 2). In *Cerastoderma edule*, adults and juveniles both preferred areas high in the intertidal zone, but the preference for sediment grain size was much less specific, with predicted maximum values of habitat suitability ranging between muddy sediments (e.g. 100 µm in 1998 for adults) to coarse grained mudflats (e.g. 270 µm in 2004 for juveniles). Adult *Macoma balthica* clearly favoured muddy sediments with short inundation times, although the positioning of the 10% best habitats per year varied substantially. Similarly, juvenile *M. balthica* preferred areas located high in the intertidal zone, but, based on the annual 10% best areas, with a wide range of acceptable grain sizes. Habitat suitability for *Lanice conchilega* was highest in the more sandy areas at intermediate depth. *Nephtys hombergii* favoured no particular habitat, although the best 5% overall hint at a preference for more muddy areas not too high in the intertidal. *Nereis diversicolor* preferred high intertidal areas, but there was a noticeable shift in preferred median grain size from sandy sediments (e.g. 1997 and 1998) to more muddy sediments (e.g. 2004 and 2005). *Corophium volutator*, with the exception of 1998 and 2000, favoured muddy areas with short inundation times. *Urothoe poseidonis* was remarkably consistent in its habitat preferences, i.e. coarse sediments at intermediate depth.

The temporal variation in realised niches, assessed as overlap between the year-specific intraspecific niche and the overall intraspecific mean niche (Fig. 3), illustrates the reproducibility in the response of organisms within the same functional group. Suspension-feeding bivalves, such as adult and juvenile *C. edule*, occupied a flexible niche between years, leading to zigzag pattern in niche overlap between 30% and 70%. Adults of the deposit-feeding bivalve *M. balthica* reached maximum niche overlap of 80% in 2000 and 2002; otherwise niche overlap was ~60%. Mean niche overlap of juvenile *M. balthica* was 30% on average (Fig. 3), thereby reflecting their wide range of preferred habitats (Fig. 2). The sedentary polychaete, *L. conchilega* overlapped with the mean niche at 40%, respectively. *Nereis diversicolor* and *Nepthys hombergii*, both mobile polychaetes, showed a steady increase in niche overlap with the mean niche. The opposite was seen in

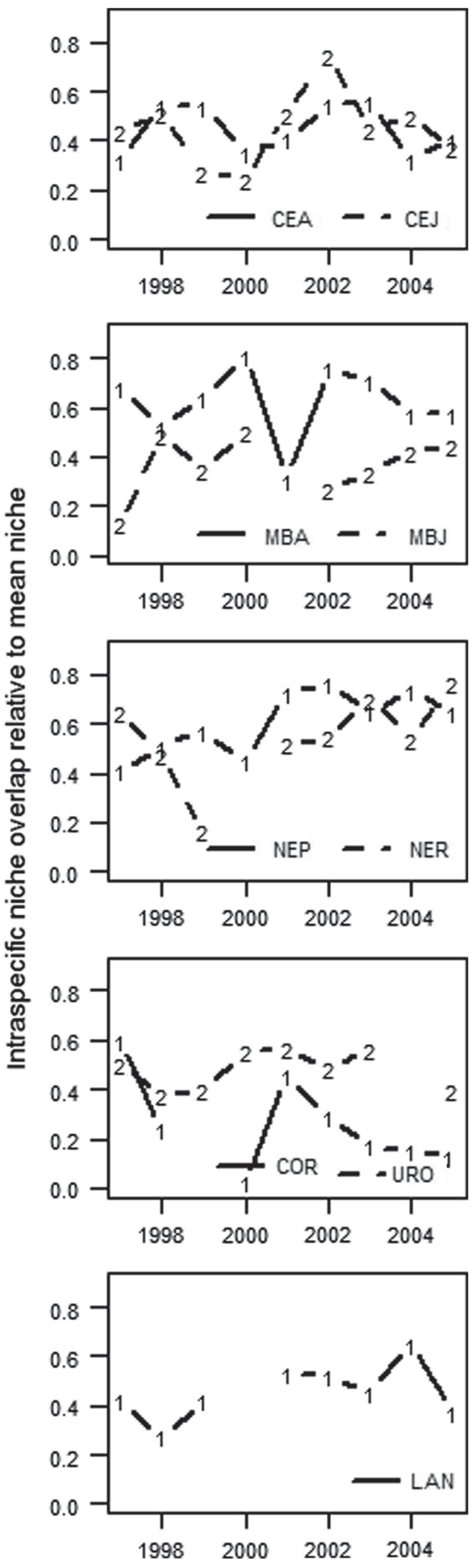

Figure 3. Intraspecific niche overlap relative to the mean niche in the period 1997–2005 with species paired by their functional group. No significant correlations between species could be detected. Missing years are due to non-convergent GEEs. For abbreviations of species names see Table 1.

the amphipod *C. volutator*, which decreased its overlap with the mean niche in the period 1997–2005. The amphipod *U. poseidonis* overlapped the mean niche with ~50%, corroborating its small range of preferred habitats (Fig. 2).

We tried to correlate niche overlap with mean annual abundance and body size. None of these revealed a statistical relationship with niche overlap (results not shown, p-value paired *t*-test > 0.1).

Discussion

Inquiries into the distributions of marine benthic fauna hold promise for a better understanding of their habitat preferences in space and time, as well as offering empirical verification of the largely theoretical 'niche machinery' (Pulliam 2000), which thus far is strongly biased towards terrestrial species (Hirzel and Le Lay 2008, but see Green 1971). Previous studies in intertidal ecosystems mostly considered species distributions along a one-dimensional environmental gradient (e.g. median grain size, Compton et al. 2009, or relative height/inundation times, Beukema 1993, but see Kraan et al. 2010); still, they allow for qualitative comparisons. For example, adult *M. balthica*, in the period of study, no longer occupied the deeper and sandier parts of the Wadden Sea as found previously by Beukema (1993) and others. At least since 1997, the lower parts no longer seem to be favourable habitat (Fig. 2). With a rapid decline in the western Dutch Wadden Sea (van Gils et al. 2009), the habitat preferences of *M. balthica* seem to have shifted as well. Whether this is best explained by changes in predation, parasite loads, survival, growth, reproductive output (Beukema 1993, Philippart et al. 2003) or anthropogenic pressures (Piersma et al. 2001, Kraan et al. 2007), warrants further study. In any case, the impact on life-history dynamics of the recent shifts must be considerable, since changes in sediment composition influence the feeding performance of bivalves (Drent et al. 2004).

Cerastoderma edule, adults and juveniles, are shown here to generally favour muddy areas (Fig. 2), consistent with previous assessments (Compton et al. 2009), but our current analysis also suggest that they avoid the low intertidal. However, the large year-to-year variation in preferred sediments of adults and juveniles is puzzling given the longevity and sedentary behaviour of cockles. Perhaps such variation may be attributed to selective mechanical harvesting of large cockles (> 19 mm), which affected large parts of the Dutch Wadden Sea during our study period (Piersma et al. 2001, Kraan et al. 2007), and consistently dredged out parts of the adult population and redistributed juveniles after discarding. It remains to be seen whether this variable habitat preferences can be confirmed in future years, now that this type of fisheries has been banned.

The modelled shift in realized niche of *N. diversicolor* towards muddier sites matches a geographical shift in increasing abundance from the western to the eastern Dutch Wadden Sea (Kraan et al. 2009a), which comprises more muddy sediments. *Urothoe poseidonis* is a species that occupies the burrows of sedentary lugworms (*Arenicola marina*), which is likely reflected by their rather low flexibility in habitat suitability (Fig. 2). In summary, our statistically derived realized niches of benthic macrozoobenthos illustrate large intraspecific variation in habitat preferences between years, which disagrees with what is currently known about their distributions and demands on habitat features.

Our rigorous determination of temporal niche dynamics under field conditions, regarded as highly relevant from an ecological as well as evolutionary point of view (Wiens and Graham 2005, Pearman et al. 2008), show that niches are not related to mean annual abundance (Fig. 3). Two complementary explanations exist. 1) Mass effects, such as spill-over from source to sink habitats (Marshall et al. 2010), do not seem to be a structuring mechanism in the distribution of benthic species in coastal areas, leading to benthic species often being absent from suitable habitat and therefore having limited distributions (Pulliam 2000, Armonies and Reise 2003). 2) Our sampling took place in late summer and autumn; therefore many processes regulating distributional patterns might have already taken place. Recruitment and succeeding settlement occur in summer and are considered important factors determining benthic species distributions (van der Meer et al. 2001, Armonies and Reise 2003). Thus, prior to our sampling of the mudflats, recruits may indeed have migrated to less benign areas and died.

The approach to statistical niche modelling employed here handles autocorrelation in response and explanatory variables, as well as non-Gaussian distributions, assesses niches and deducts habitat preferences of species in fine detail, as illustrated for seven common macrozoobenthic species inhabiting intertidal sandflats in the western Dutch Wadden Sea (Fig. 2–3). Such spatially explicit models have proven their merits in marine environments (Aarts et al. 2008, Kraan et al. 2010) and elsewhere (Legendre and Fortin 1989, Keitt et al. 2002, Beale et al. 2010). Our explanatory variables, sediment grain size and depth, commonly used as typical environmental variables that structure spatial distributions of marine benthic species (Beukema 1993, Compton et al. 2009), have shown to be of critical importance in spatially structuring benthic species distributions at the landscape scale addressed in this study (Ysebaert et al. 2002, Kraan et al. 2010).

Our assessment of niche variability has ramifications for species distribution models in general and offers advances from previous methods. Firstly, by assessing species' realized niches in the multivariate environmental space, niche overlap is independent from the relative availability of particular environments (Dormann et al. 2009, Broennimann et al. 2011). Each combination of environmental characteristics occurs exactly once. Therefore, the differences we observed in environmental associations within species can be interpreted as differences in selected habitats between years, rather than differences in environmental conditions between years. Second, application of GEEs to predict species habitat preferences provides more precise and unbiased estimates of species–environment relationships (Dormann et al. 2007, Kraan et al. 2010). Thirdly, niche models assume constant niches (Pearman et al. 2008), whereas we illustrate how much these can vary over short time scales (Table 2, Fig. 2–3). This emphasizes the limitations of single-time descriptions of species niches (van der Meer 1999), but also illustrates the potentially limited scope of global change studies with forecasts based on single-time species distributions. Similarly, the typical collection of data over many years will lead to an apparent occupancy of a wide niche space, while we here show that at any given point only a fraction of the potential niche space is actually occupied. We interpret this finding as evidence for high variability in limiting factors: species will evolve to be adapted to the smallest common denominator of environmental constraints but their population dynamics will remain strongly affected by varying limitations. Our approach allows, in principle, the identification of a core niche, which represents the minimum requirements of the species. While current approaches of modelling the realised niche will overestimate habitat suitability for any given year, the core niche will underestimate it. These two extremes could form uncertainty bounds for predictions of changes of species distributions under environmental change.

Our correlative approach reflects species' realized niches, since competitive interactions between species or causal links with chosen predictor variables are only implicit in these analyses (Colwell and Rangel 2009, Kearney and Porter 2009). The advantage of this correlative approach is that little knowledge is required on the exact causal relationship between species and their environment. Mechanistic habitat suitability models, however, might outperform correlative models when forecasting species distributions under environmental change (Davis et al. 1998, Kearney and Porter 2009, Dormann et al. 2012). The correlative approach should give valuable information to mechanistic models, such as which processes seem to be acting and how they vary through time. Moreover, this framework can be extended to *n* environmental dimensions (Dormann et al. 2009). As such, mapping species' habitat suitability is in principle useful for evaluating management options (Thrush et al. 2003, Sorte et al. 2010) and can underpin the integrated management of coastal ecosystems (Foley et al. 2010).

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