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Burrow distribution of three sandeel species relates to beam trawl fishing, sediment composition and water velocity, in Dutch coastal waters

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ABSTRACT

Sandeel partly spend their life buried in the sediment, without a permanent burrow opening or an inhalant opening in the sediment. We linked the presence of three sandeel species (*Ammodytes tobianus*, *A. marinus* and *Hyperoplus lanceolatus*) off the southern Dutch coast of the North Sea to sediment related environmental variables; (1) sediment composition, with a hypothesized preference for low silt content and high medium-coarse sand content, (2) water velocity near the seabed, with a hypothesized preference for high water velocity and (3) fishing effort of the beam trawl fleet targeting flatfish and shrimp, with a hypothesized negative impact of fishing on sandeel presence. Data originated from an intensive benthic sampling scheme, VMS and logbook databases and a hydrodynamic model. Statistical models were run including these environmental variables plus year, depth, water temperature and salinity. Sandeel presence was negatively correlated with flatfish and shrimp fisheries – both *Ammodytes* species with flatfish fisheries and *H. lanceolatus* with shrimp fisheries. Water velocity and silt content were correlated as hypothesized with the presence of all species, and sand content was positively correlated with both *Ammodytes* species. The remaining environmental variables also showed a significant relation with at least two sandeel species. These findings agree with and greatly expand on previous studies on the relation between sandeel and its environment.

1. Introduction

Sandeel contribute markedly to the total fish biomass in the North Sea (Sparholt, 1990). The oil-rich, highly energetic fish are a part of the diet of many top predators and the most important prey species for many seabirds (e.g. Engelhard et al., 2014; ICES, 2014; Rindorf et al., 2000). The most common and best studied species of sandeel in the North Sea is *Ammodytes marinus* (Raitt). In the North Sea it co-occurs with *A. tobianus* (Linnaeus) and *Hyperoplus lanceolatus* (Le Sauvage). Sandeel live semi-pelagic: most of the year the fish live predominantly burrowed in sandy substrates, except during a brief spawning period in winter (Hoines and Bergstad, 2001; Winslade, 1974b, both regarding *A. marinus*) and an extended period in spring and early-summer, when they spend part of the daytime foraging in the water column (Rindorf et al., 2000; Winslade, 1974a, 1974b, 1974c, regarding *A. marinus*, van Deurs et al., 2011, regarding *A. tobianus* and Reay, 1970, regarding all three species).

Sandeel are believed to exhibit high sand bank fidelity. Larvae can be transported over large distances but once juveniles settle on a sand bank, sandeel abstain from large-scale dispersion (Engelhard et al., 2008; Gauld, 1990; Jensen et al., 2011; Robinson et al., 2013). Also when foraging, sandeel tend to remain near their burrow sites (Kuhlmann and Karst, 1967; Reay, 1970; Robinson et al., 2013; van der Kooij et al., 2008). This small home range makes sandeel an ideal fish to study its relation with the environment.

Because of the semi-burrowed lifestyle it is likely that sediment related characteristics of the environment are important in explaining the distribution of sandeel. Besides being burrowed for the largest part of their lives, sandeel do not have permanent burrow openings or an inhalant opening in the substrate (Reay, 1970). Both easy penetration of the sediment and sufficient supply of oxygen in the sediment will thus play a role in the habitat choice of sandeel (Reay, 1970; Wright et al., 2000). Studies have shown that sandeel exhibit a preference for sediment with a high content of large-sized particles ('sand') and avoidance of sediment with high content of small-sized particles ('silt') (Holland et al., 2005; Reay, 1970, regarding sandeel in general; Wright et al., 2000, regarding *A. marinus*). The absence of an inhalant opening in the substrate is hypothesized to lead to a preference for locations with high water flow at the seabed, for oxygen supply (Meyer et al., 1979; Reay, 1970; Wright et al., 2000). Another sediment related

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characteristic that may affect the occurrence of sandeel is the fishing intensity of beam trawl fisheries. Beam trawl ships tow their net over the sea floor, with a steel beam keeping the net open. Ships targeting flatfish also use tickler chains, which plough through the top layer of sediment. Beam trawl fisheries physically disturb the seabed up to at least the first 6 cm (Bergman and Hup, 1992; Watling and Norse, 1998). This type of fisheries extract many non-target benthic organisms from the seabed and can also kill, damage or deter the benthic organisms which are not fished up in numerous ways (Alverson et al., 1994; Broadhurst et al., 2006; Kaiser et al., 2006; Kelleher, 2005). Sandeel species residing in the upper layer of the sediment may thus be sensitive to the presence of such fisheries.

Thus, sediment composition, water velocity and fishing intensity of beam trawl ships are expected to have an influence on the burrow distribution of the three sandeel species. Only the relation of sediment and *A. marinus* has actually been studied in the past. Here, the influence of the three environmental characteristics on sandeel burrow distribution is examined in the Voordelta, an area off the southern Dutch coast, with the following hypothesized relations: (1) a negative relation of sandeel with the fishing effort of the beam trawl fleet, (2) a negative relation with silt content of the sediment and a positive relation with sand content, (3) a positive relation with water velocity at the seabed.

2. Materials and methods

2.1. Dredge survey

The Voordelta is a shallow and dynamic coastal area. The fresh water outlet of the river Waal through the former sea inlet, but now dammed, Haringvliet (Fig. 1) causes high local gradients in salinity. There are several shallow sand banks, interspersed with deeper canals and open water areas. In the autumn of the years 2009–2012 an extensive fine-scaled grab survey was performed. The distribution of the 406 planned stations over the Voordelta is stratified according to the importance of areas for the benthic community (Fig. 1). Sampling was carried out on a regular grid, varying in cell size between 64 and 225 ha depending on the stratum, with one randomly chosen sampling point per grid cell. Aspects of habitat structure and benthic composition were taken into account in the survey design.

The sampling campaign took ca. 6 weeks, in September (43% of the samples), October (48%) and November (9%). Some locations were sampled but removed from the analyses due to missing sediment data or because no estimation could be made for the fishing effort in the vicinity. Of the planned stations, the majority was sampled adequately every year; 404 in 2009 and 2010, 402 in 2011 and 401 in 2012. In total the survey thus yielded 1611 samples. The stations were sampled with a trawled dredge. The blade of the dredge has a width of 10 cm and sampling depth is 9 cm. The dredge is trawled over a distance of 100 to 150 m. While towed, a strip of sediment with its biotic content is excavated and transported into the cage. The stainless steel cage has a mesh size of 0.5 cm. Depth of each sampling location was determined at approximately the midpoint of the transect, during the sediment sampling (see Section 2.1.2).

2.1.1. Sandeel identification

Sandeel were individually frozen and brought to the lab for identification to the species level, following Hureau and Monod (1979) and Wheeler (1969). Only fish that were intact (from tail to head) could be identified, because identification requires characteristics set over the whole length of the fish. This resulted in a large fraction of the caught sandeel not being identified. For every complete sandeel there were roughly 1.5 incomplete sandeel. The assumptions were made that (a) the species of sandeel and (b) geomorphological differences between stations do not influence the chance of being damaged by the dredge. We thus assumed that the identified sandeel are representative for the overall distribution of the species and can be used to investigate their relationship with the environment and fishing disturbance.

2.1.2. Sediment analysis

Sediment grain analyses were performed on sediment samples collected with a boxcorer approximately at the midpoint of the survey transects. The technical details of the sediment analyses are described in the Appendix. The following sediment classes were defined: “silt” (≤ 63 μm diameter) and sand identified as “very fine” (> 63 to ≤ 125 μm), “fine” (> 125 to ≤ 250 μm), “medium” (> 250 to ≤ 500 μm) and “coarse” (> 500 to ≤ 1000 μm). These five classes add up to 100%. The sediment in the samples consisted mostly of intermediate grains sizes (medium and fine sand), with mostly low concentrations of coarse and very fine sand and silt. The sediment traits are highly correlated among each other. The relationship between the five sediment classes in the field is described in the Appendix. Following the findings of previous studies (Holland et al., 2005; Reay, 1970; Wright et al., 2000), two sediment characteristics that show the strongest relation with the distribution of sandeel were used in the statistical models: the medium-coarse sand (250–1000 μm) content and the silt (0–63 μm) content. Sand is usually defined as having a median particle size of up to 2000 μm, but sand of 1000–2000 μm was removed from the samples before analysis.

2.2. Estimated abiotic variables

2.2.1. Estimated fishing effort

The most common fisheries in the Voordelta are the beam trawl fisheries with 260–300 horse power targeting flatfish (with a mesh size of 70–99 mm and using tickler chains) and shrimp (with a mesh size of 16–31 mm). Taking the site fidelity of sandeel into account, the effect of fishing is assumed to be long term: mortality by trawling over the past year (September–August) is expected to affect the distribution of sandeel in the subsequent autumn period. Fishing intensity of these fleets was estimated based on the VMS (Vessel Monitoring by Satellite) data of the Dutch beam trawl fleet, as collected for the Dutch Ministry of Economic Affairs. This information was linked to information in the ship's log book on gear, horse power and landings (Hintzen et al., 2012). For the technical details of this analysis, see the Appendix. The subsequent estimate of local fishing effort is expressed as fraction area trawled within a 50 m radius of a sampling location. For example, a fishing effort of 2.0 can be interpreted as the complete vicinity of a location having been trawled twice in the prior year - or half the area having been trawled four times.

2.2.2. Estimated environmental variables

A hydrodynamic model (see the Appendix for a technical description) was used to estimate the spatial and temporal dynamics of water velocity, temperature and salinity. Based on a set of standard model schematizations, hind cast simulations of the Voordelta area were run. As input for the model, empirical datasets were added for astronomical tidal constituents, fresh water river discharges, atmospheric forcing such as wind and pressure fields and atmospheric heating, and sea water and river temperature. Water level, temperature and salinity were calibrated with real-time measurements carried out during the dredge survey and collected by governmental surveys. The accuracy of the model results turned out to be appropriate (see the Appendix).

Per sampling location, the local values for water salinity at the bottom (‘salinity’), water temperature at the bottom (‘temperature’) and water velocity at the bottom (‘water velocity’) were averaged over the week before the dredge sampling dates.

2.3. Sandeel distribution models

For all three sandeel species a generalized linear mixed effect model (‘glmm’) was used (formula (1)). Because of the high percentage of

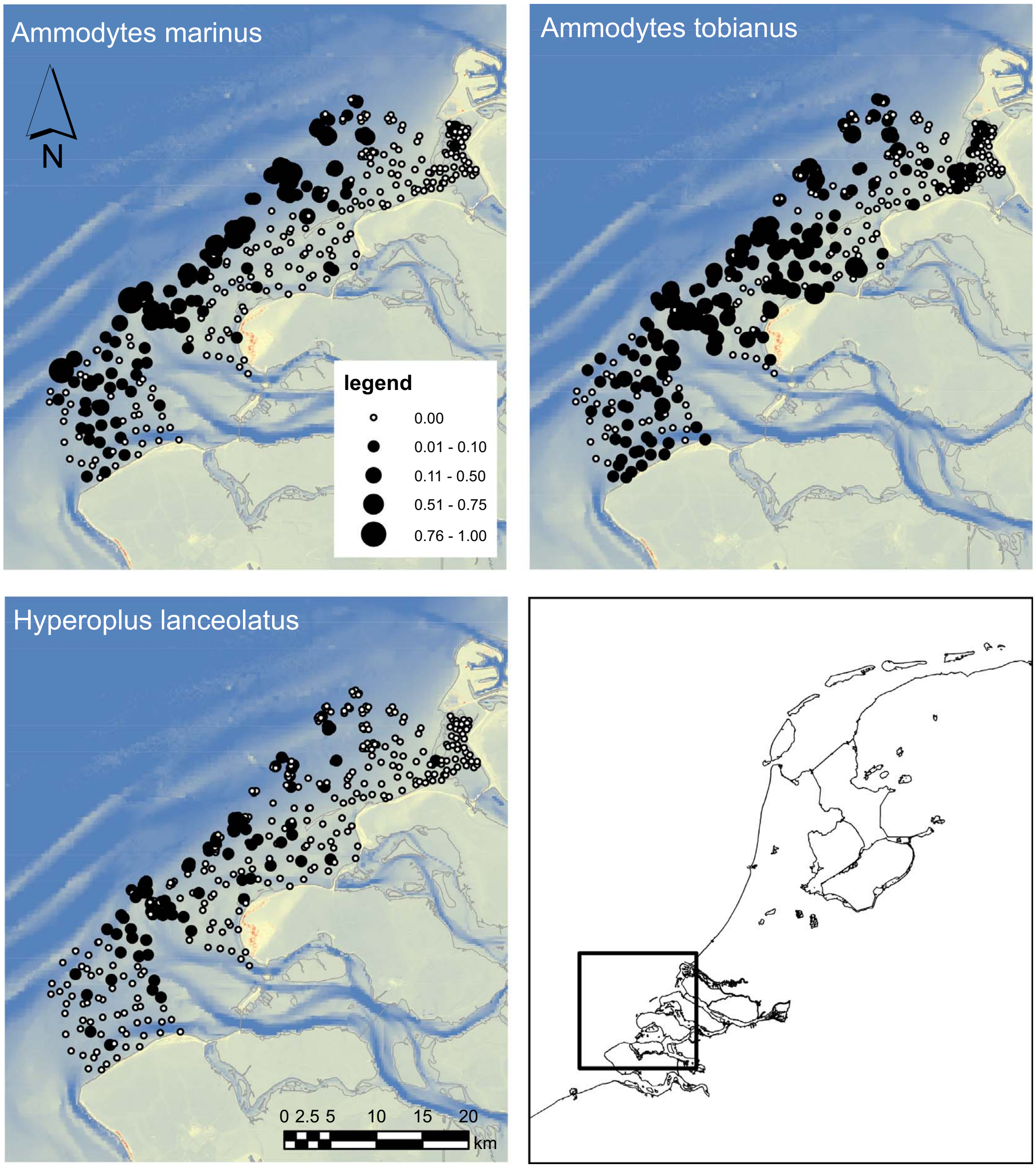

Fig. 1. Average density (nm^{-2}) of complete individuals of the three sandeel species, averaged over the survey years 2009–2012, for the 406 stations in the Voordelta. Note that only complete, unharmed sandeel are considered.

samples without sandeel (see Results section) we modelled presence/absence of sandeel using a glmm with a binomial distribution, and a logit link function. The following factors were added to the model as fixed factors: year, %silt, %medium-coarse sand, depth, salinity, temperature, water velocity and the fishing effort of the beam trawl fleet targeting flatfish ('fishing effort flatfish') and targeting shrimp ('fishing effort shrimp'). Station was added as random factor, whereby we allowed for a random intercept in the model.

The fixed factors were explored with regards to outliers, collinearity, spatial autocorrelation and potential need for transformations. Outliers did not play a role and collinearity among fixed factors was never high, with a maximum of 71% correlation of velocity with depth (see the Appendix for the table with Pearson's product moment correlation). Both the fishing effort of the flatfish fisheries and shrimp fisheries were transformed to the 4th root (after comparing several transformations), due to a high fraction of low values. The parameter for silt content exhibited a high fraction of zero-values but no appropriate transformation could be found.

The base statistical model was:

$$log\,it\,(p_{ij}) = \alpha + \beta_1\,x\,silt_{ij} + \beta_2\,x\,sand_{ij} + \beta_3\,x\,depth_{ij} + \beta_4\,x\,velocity_{ij} + \beta_5\,x\,salinity_{ij} + \beta_6\,x\,temperature_{ij} + \beta_7\,x\,year_{ij} + \beta_8\,x\,(fishing\ effort\ flatfish)^{1/4}{}_{ij} + \beta_9\,x\,(fishing\ effort\ shrimp)^{1/4}{}_{ij} + a_i \tag{1}$$

P_{ij} is the probability that in trawl j at station i sandeel is present, using the logistic link (*logit*). $Silt_{ij}$ is the silt-value in trawl j at station i, etc. a_i is the random intercept, assumed to be normally distributed with mean 0 and variance σ^2_a.

The glmm was run using the R-software and the glmm-package 'lmer' (Team, 2011). Non-significant fixed factors were identified by a X^2-test and removed one by one. Taking into account the approximation of the glmm-tests (Zuur et al., 2009), p-values that were on the boundary (defined as $0.04 < p < = 0.05$ in a X^2-test) were also deemed non-significant.

The QQ plots of the final model were tested for unexpected residual patterns. Potential spatial autocorrelation was tested using correlog analysis on the full model. Both analyses were performed on the results of the glmm as described by Zuur et al. (2009) and showed no problems with the residuals of the models.

3. Results

3.1. Occurrence of the three sandeel species

All sandeel species were found in only a minority of the 1661 samples: *Ammodytes marinus* in 19%, *A. tobianus* in 24% and *H. lanceolatus* in 7% of the samples. The average density over all samples was similar for the two *Ammodytes* species: 0.05 ± 0.19 and 0.06 ± 0.23 individuals per m^2 for *A. marinus* and *A. tobianus*, respectively (mean ± standard deviation, see also Fig. 1). The mean density of *H. lanceolatus* was ten times smaller: 0.006 ± 0.023 (Fig. 1). Care has to be taken with the interpretation of the density information, since only intact fish could be identified to the species level. The total number of sandeel was roughly 2.5 times the number of intact (and thus identified) sandeel.

3.2. Relation with abiotic variables

Silt content of the sediment in the survey samples was on average low (mean = 3.81%, see Table 1 and Fig. 2). Most samples (73%) contained no silt and only 19% of the samples had a silt content higher than 4%, but silt content could be as high as 66.84%, mostly near the coast. All three sandeel species were only found at sampling locations with very low silt content (Figs. 3, 4 and 5). The medium-coarse sand content was on average high (mean = 49.94%), but varied largely between samples (Table 1, Fig. 2), from < 1% to almost 100%. The lowest sand content was near the most northern fresh water outlet, which also harboured high silt content (Fig. 2). The presence of all three sandeel species increased with increasing levels of medium-coarse sand (Figs. 3, 4 and 5).

The estimated average water velocity ranged from 0 to 0.52 ms^{-1} (Table 1, Fig. 2). All three species were rarely caught at sites with lower average velocities (Figs. 3, 4 and 5). Depth of the sampled locations varied between 0.3 and 27 m (Table 1, Fig. 2). *Ammodytes marinus* was mostly found at intermediate depths (12–20 m, Fig. 3), while *A. tobianus* and *H. lanceolatus* were rarely found at the deepest sites (Figs. 4 and 5). All three sandeel species were more present at the higher estimates of average salinity values (Figs. 3, 4 and 5). Average temperature ranged from 9 to 20 °C, but the relation between all three sandeel species and temperature was the least pronounced of all environmental variables (Figs. 3, 4 and 5).

Table 1
Statistics of the explanatory fixed variables. Mean, minimum and maximum value of the samples and the standard deviation of the mean (sd). Data source: Survey = measured during the survey. HD = estimated in the hydrodynamic model, and averaged over the week prior to trawling. VMS = estimated from VMS and logbook data, for a radius of 50 m, summed over the year prior to the survey.

	Data source	Mean	Min	Max	sd
%Silt	Survey	3.81	0.00	66.84	10.13
%Medium-course sand	Survey	49.94	0.82	99.75	27.04
Depth (meter)	Survey	10.14	0.29	26.95	5.26
Water velocity ($m s^{-1}$)	HD	0.30	0.001	0.52	0.12
Temperature (°C)	HD	15.24	9.39	19.53	2.25
Salinity (PSU)	HD	31.74	15.16	34.39	2.64
Fishing effort flatfish (fraction area trawled)	VMS	0.04	3×10^{-11}	0.99	0.09
Fishing effort shrimp (fraction area trawled)	VMS	0.48	4×10^{-6}	4.74	0.63

3.3. Relation with fishing effort

The average fishing effort of the flatfish fisheries in the direct vicinity of the sampled locations was estimated at 0.04 (Table 1, Fig. 6). This means that on average 4% of the area within 50 m from a sampled location was trawled by the flatfish fisheries in the year prior to the trawl. The maximum effort of the flatfish fisheries was 0.99. The average fishing effort of the shrimp fisheries was higher: 0.48 (Table 1, Fig. 6). The maximum effort of the shrimp fisheries was 4.74, and 15% of the samples had an estimated fishing effort of > 1.0. Due to the method used (kriging), no areas with zero fishing effort were present, but many of the locations had very low estimates (Fig. 6), especially regarding the flatfish fisheries.

All three species of sandeel were predominantly found at the lower range of the fishing effort of both the shrimp and the flatfish fisheries and never found at the higher range of the fishing effort (Fig. 7).

3.4. Habitat modelling

The final model regarding *A. marinus* included seven fixed explanatory factors (Table 2). The presence of *A. marinus* decreased through the years 2009–2012, and was negatively correlated with silt concentration in the sediment and with the fishing effort of the flatfish fisheries. Its presence was positively correlated with the concentration of medium-coarse sand in the sediment, and with water velocity, depth and salinity. Fishing effort of the shrimp fisheries ($X^2 = 0.74$, $p = 0.4$) and the water temperature ($X^2 = 1.71$, $p = 0.2$) were sequentially removed as non-significant explanatory factors.

The final model regarding *A. tobianus* included seven fixed explanatory factors (Table 2). The presence of *A. tobianus* decreased through the years 2009–2012, and was negatively correlated with silt concentration in the sediment, depth and the fishing effort of the flatfish fisheries. Its presence was positively correlated with the concentration of medium-coarse sand in the sediment, and with water velocity and depth. Salinity ($X^2 = 0.05$, $p = 0.8$) and the fishing effort of the shrimp fisheries ($X^2 = 1.23$, $p = 0.3$) were sequentially removed as non-significant explanatory factors.

The final model regarding *H. lanceolatus* included six fixed explanatory factors (Table 2). The presence of *H. lanceolatus* was negatively correlated with silt concentration in the sediment, depth, temperature and the fishing effort of the shrimp fisheries. Its presence was positively correlated with water velocity and salinity. Year ($X^2 = 1.43$, $p = 0.2$), the fishing effort of the flatfish fisheries ($X^2 = 3.02$, $p = 0.08$) and the percentage of medium-coarse sand in the sediment ($X^2 = 4.14$, $p = 0.042$) were sequentially removed as non-significant explanatory factors.

Thus, for both *Ammodytes* species the hypothesized influence of both sediment characteristics, water velocity and the beam trawl fisheries targeting flatfish is confirmed by these results. For *H. lanceolatus* the hypothesized influence of water velocity, silt content and the beam trawl fisheries targeting shrimp is confirmed by these results.

4. Discussion

As hypothesized, sandeel of all three species were only found at locations with low silt content and all three models showed significant negative relations of sandeel presence with silt content. Sandeel of all three species were rarely found at locations with low medium-coarse sand content and for both *Ammodytes* models a significant positive relation with medium-coarse sand content was found. Low silt and high medium-coarse sand content of the sediment facilitate easy penetration and a sufficient and constant supply of oxygen in the sediment; which is important for sandeel since it has no permanent burrow an no inhalant opening (Reay, 1970; Wright et al., 2000). A preference for low silt content may also be related to the possibility of silt clogging the gills

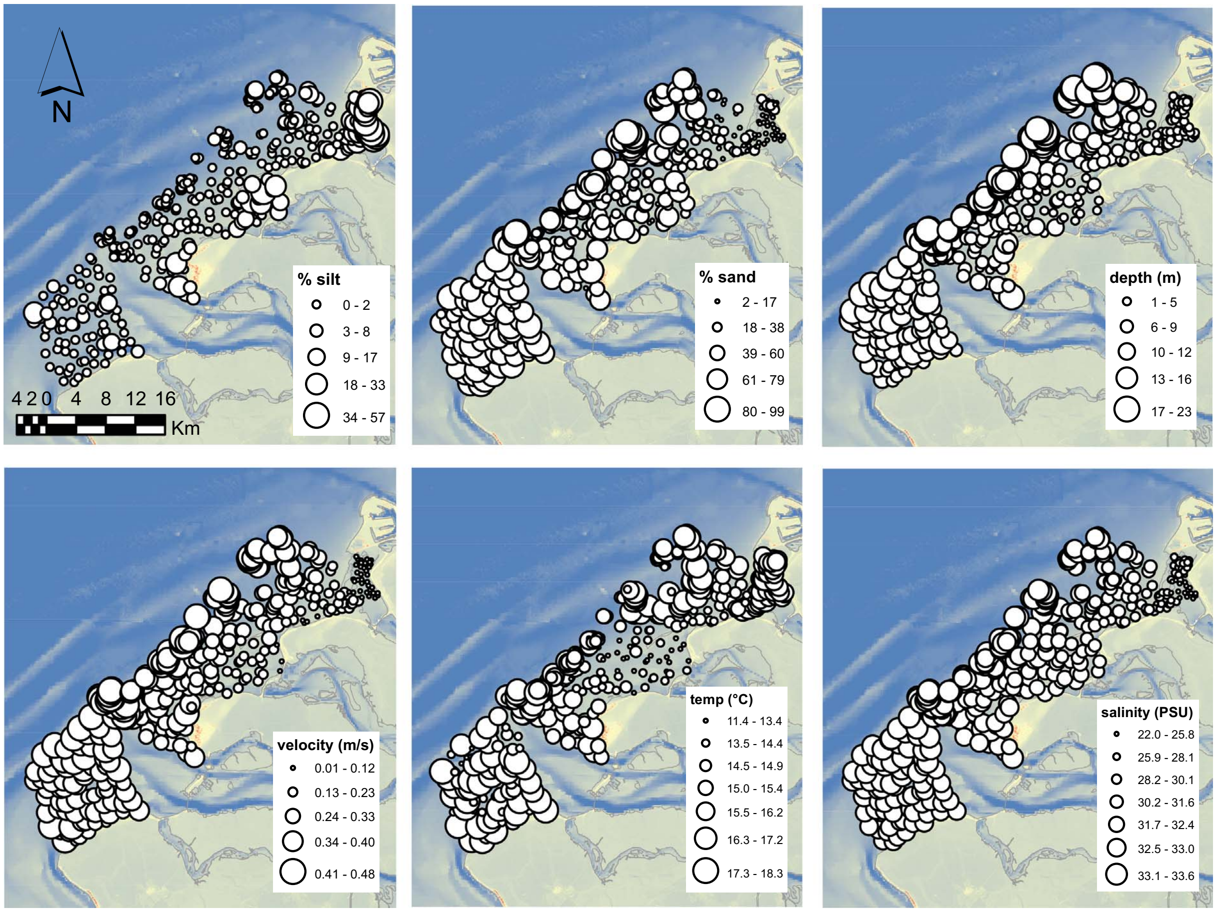

Fig. 2. Spatial patterns of all abiotic parameters, averaged over the years 2009–2012, for the 406 stations in the Voordelta.

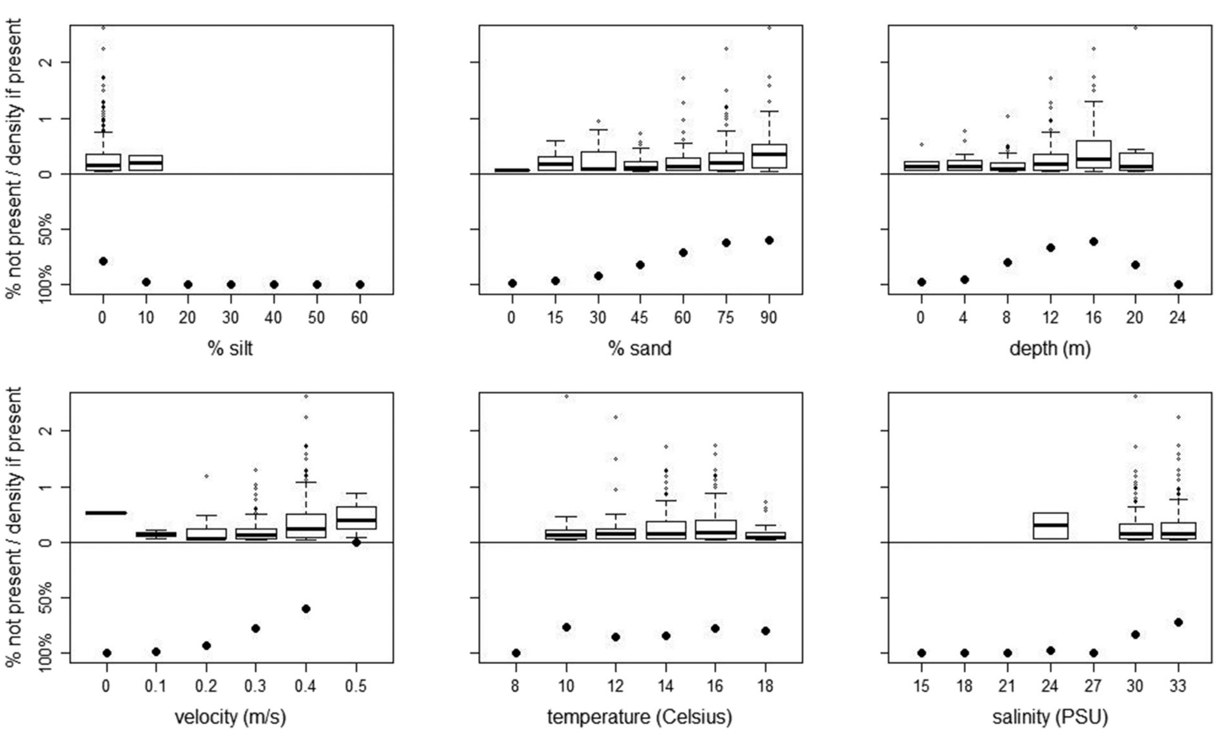

Fig. 3. *Ammodytes marinus*' absence (percentage samples in which not present) below the x-axis and boxplots of the density (nm^{-2}) if present above the x-axis, in relation to the abiotic parameters. Abiotic parameters are binned, with category names representing the minimum value of that category.

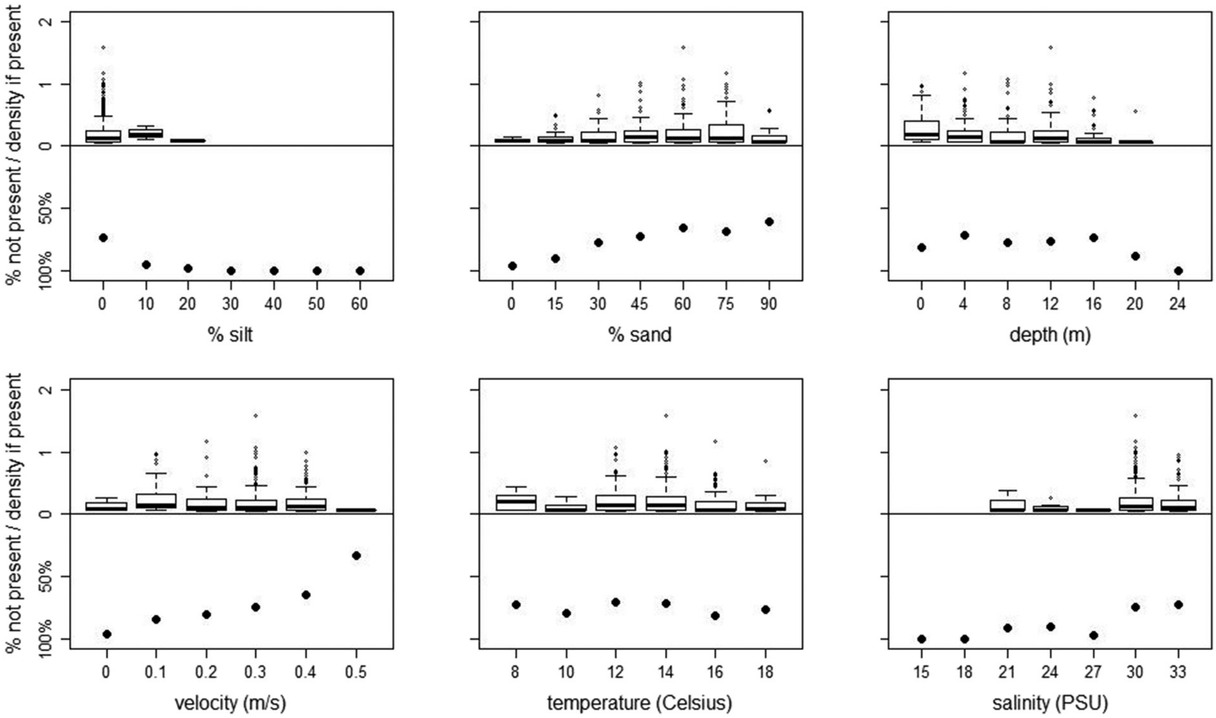

Fig. 4. *Ammodytes tobianus*' absence (percentage samples in which not present) below the x-axis and boxplots of the density (nm^{-2}) if present above the x-axis, in relation to the abiotic parameters. Abiotic parameters are binned, with category names representing the minimum value of that category.

while burrowed (Wright et al., 2000).

Sandeel were rarely found at locations with the lowest estimated water velocities and in all three models positive relations with velocity were found. High water flow will lead to higher oxygen supply to the sediment (Meyer et al., 1979; Reay, 1970; Wright et al., 2000). It may also indirectly influence the presence of sandeel, via a potential negative effect on silt content. However, silt content is relatively low everywhere in the Voordelta (despite low estimated water velocities), which makes it more likely that the negative correlation between velocity and the presence of sandeel here is related via oxygen supply.

As hypothesized, for both fishing fleets that are relevant in the Voordelta, all three sandeel species were only found at locations with low fishing intensity. Statistically, for all three species a significant relation was found with only one fleet: the presence of both *Ammodytes* species was negatively correlated with the fishing pressure of the beam trawl fleet targeting flatfish, while the presence of *H. lanceolatus* was

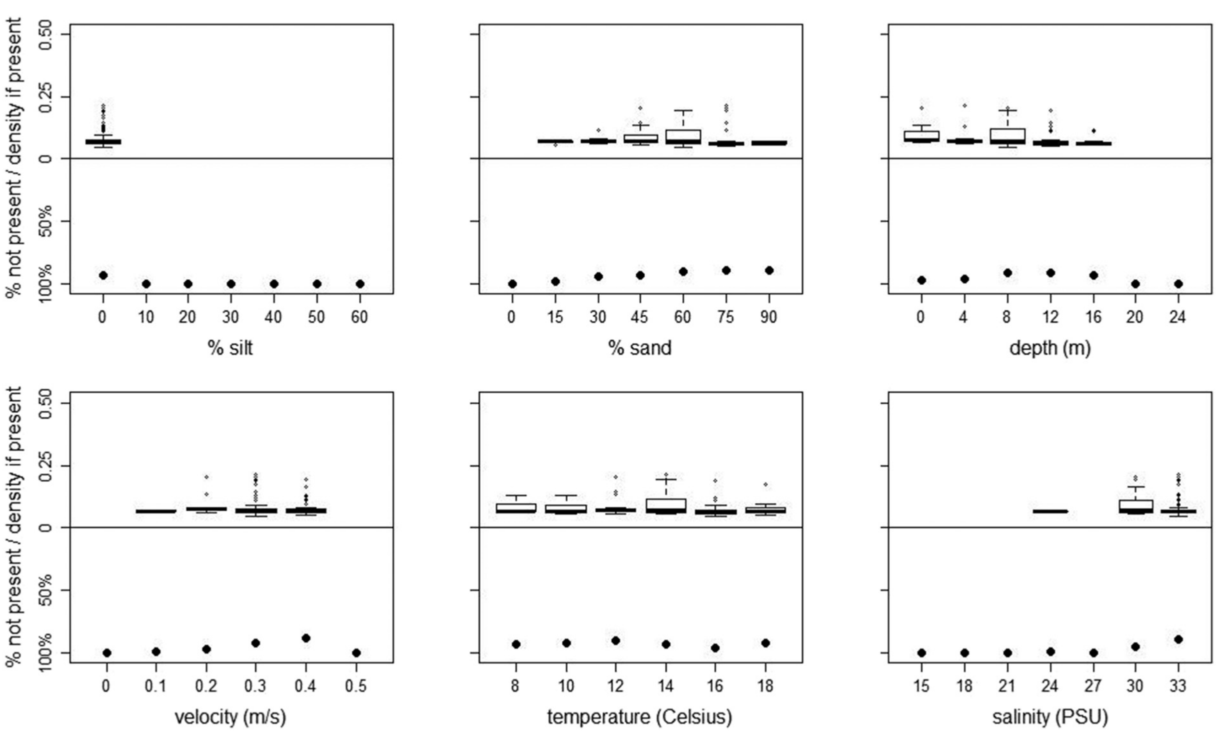

Fig. 5. *Hyperoplus lanceolatus*' absence (percentage samples in which not present) below the x-axis and boxplots of the density (nm^{-2}) if present above the x-axis, in relation to the abiotic parameters. Abiotic parameters are binned, with category names representing the minimum value of that category.

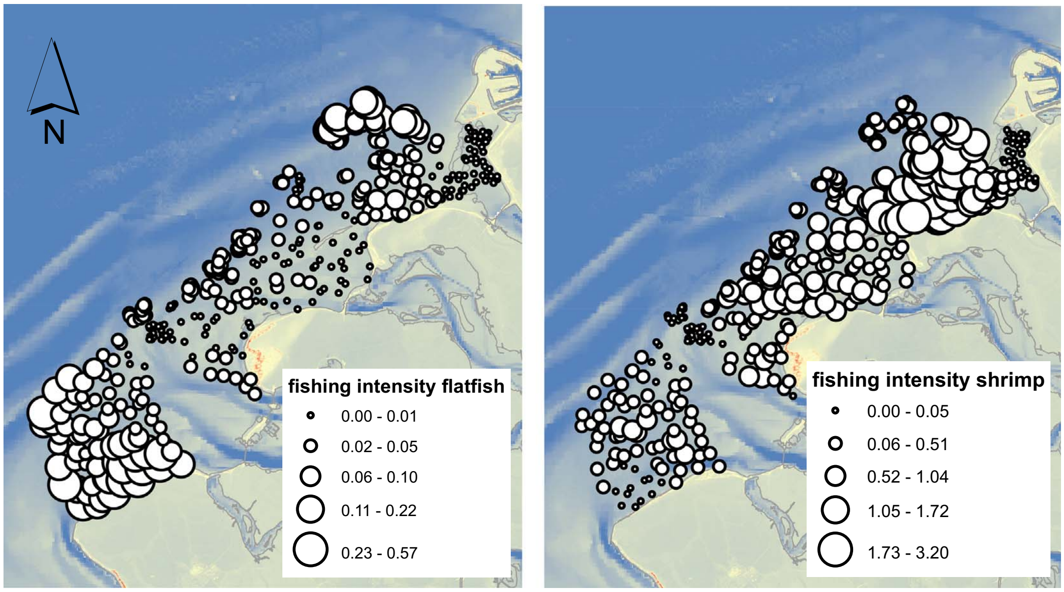

Fig. 6. Spatial patterns of the fishing effort of the flatfish and shrimp fisheries, averaged over the years 2009–2012, for the 406 stations in the Voordelta. Fishing effort is expressed as the fraction trawled area within 50 m of a sampled location.

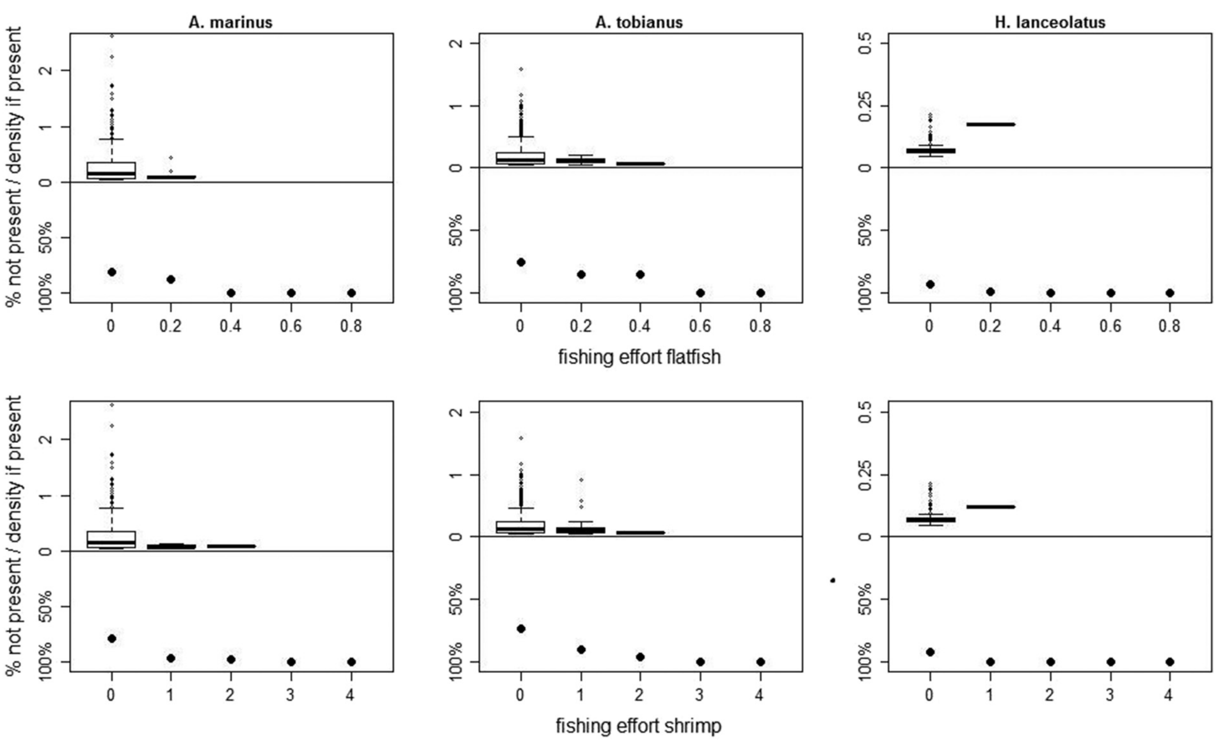

Fig. 7. Absence (percentage samples in which not present) below the x-axis and boxplots of the density (nm^{-2}) if present above the x-axis, of *A. marinus*, *A. tobianus* and *H. lanceolatus*, in relation to the fishing effort of the flatfish and shrimp fisheries. Fishing effort is binned, with category names representing the minimum value of that category. Fishing effort is expressed as the fraction trawled area, within 50 m of a sampled location, in the previous year.

negatively correlated with the fishing pressure of the beam trawl fleet targeting shrimp. The intensity of the fisheries on flatfish, as expressed in fraction area trawled, was much lower than of the fisheries on shrimp. Still, both *Ammodytes* species only exhibited significant relations with the flatfish fisheries. A likely explanation is that the effect of flatfish fisheries is larger: The flatfish targeted by this fishery are partly buried in the sediment. The heavy gear is therefore equipped with tickler chains that are pulled through the upper layer of the sediment, thereby damaging or killing organisms living in the sediment (Kaiser et al., 2002). A shrimp trawl is lighter and has no tickler chains. Contact with the bottom is made by a ground rope with rubber bobbins at the front of the net and by rubber rollers which roll over the surface. The gear used by the shrimp fleet thus likely affects the seafloor and the fish living in it far less destructively.

This explanation on the difference between the two gears builds on an assumed causal relation between the beam trawl fisheries and the presence of burrowed sandeel. However non-causal relations are also possible, the most likely of which is through a negative correlation of

Table 2
Parametrisation of the three final models to estimate sandeel presence. Number of observations = 1611, number of groups (stations) = 406. *The p-value of water velocity in a X^2-test was < 0.04 and thus water velocity was not removed as being on the boundary.

Species	Fixed effects					Random effects		
	Factor	Estimate	Std. error	X^2 value	p (> z)	Factor	Variance	St. dev
A. marinus	Intercept	824.568	184.296	4.474	< 0.001	Station	0.517	0.719
	%Silt	− 0.204	0.071	− 2.883	0.004			
	%Medium-coarse sand	0.029	0.005	5.655	< 0.001			
	Depth	0.088	0.023	3.885	< 0.001			
	Water velocity	6.676	1.528	4.368	< 0.001			
	Salinity	0.274	0.114	2.399	0.016			
	Year	− 0.417	0.093	− 4.512	< 0.001			
	Fishing effort flatfish (^1/4)	− 2.643	0.509	− 5.195	< 0.001			
A. tobianus	Intercept	1169	1472	7.93	< 0.001	Station	0.403	0.635
	%Silt	− 0.099	0.033	− 2.95	0.003			
	%Medium-coarse sand	0.031	0.004	7.80	< 0.001			
	Depth	− 0.015	0.002	− 6.99	< 0.001			
	Water velocity	6.147	1.086	5.66	< 0.001			
	Temperature	− 0.127	0.032	− 3.98	< 0.001			
	Year	− 0.581	0.073	− 7.94	< 0.001			
	Fishing effort flatfish (^1/4)	− 2.195	0.428	− 5.13	< 0.001			
H. lanceolatus	Intercept	− 15.019	3.840	− 3.91	< 0.001	Station	6.7 × 10^-8	0.0003
	%Silt	− 0.329	0.142	− 2.32	0.020			
	Depth	− 0.054	0.026	− 2.07	0.038			
	Water velocity	3.807	1.863	2.04	0.041*			
	Salinity	0.444	0.116	3.82	< 0.001			
	Temperature	− 0.122	0.044	− 2.75	0.006			
	Fishing effort shrimp (^1/4)	− 1.275	0.498	− 2.56	0.010			

the spatial distribution of sandeel with that of the target species of the fleets, due to opposing habitat preferences. However, the fishing intensity of the flatfish fleet was higher at locations with habitat conditions that are preferred by sandeel: e.g., lower silt content, higher sand content and higher velocity (see the correlation matrix in the Appendix). Still sandeel presence was negatively correlated with fishing intensity. This does not support the hypothesis of such an indirect effect via opposing habitat preferences of sandeel and flatfish. Fishing intensity by the shrimp fisheries was generally only weakly correlated with the abiotic conditions. Brown shrimp (*Crangon crangon*), the target species for this fleet, has a wide distribution and no clear-cut habitat preferences (Campos and Van der Veer, 2008). The fact that the shrimp fleet behaves relatively independent of abiotic characteristics is therefore not surprising. It also does not support the hypothesis of an indirect effect, via opposing habitat preferences of sandeel and shrimp.

Although all sandeel species occurred less in areas used more intensely by both fleets, only one significant relation between each sandeel species and a fishing fleet was found. Better insight into the ecophysiology of the three individual sandeel species and/or more studies on the relationship between beam trawl fisheries and the distribution of sandeel are needed to understand whether these statistical differences are indicative of actual biological differences in the sensitivity for various types of fishing pressure.

This is the first study to examine a wide range of environmental factors simultaneously as explanation of the distribution of three coinciding sandeel species. To the best of our knowledge, the influence of water velocity and beam trawling – but also temperature and salinity - have not been previously examined with regard to burrow distribution for any of the sandeel species. Also, for *H. lanceolatus* and *A. tobianus* this is the first study that examines their habitat use in such detail. These findings agree with and greatly expand on previous studies on the relation between sandeel and its environment.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2017.05.001.

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