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A freshwater species wintering in a brackish environment: Habitat selection and diet of Slavonian grebes in the southern Baltic Sea

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ABSTRACT

After the breeding season, Slavonian grebes (*Podiceps auritus*) leave their freshwater breeding habitats and migrate to wintering grounds in marine or brackish waters. The most important wintering area in northwestern Europe is located in the southern Baltic Sea, with the largest concentrations in the offshore area of the Pommeranian Bight. Analysis of ship-based surveys revealed that the habitat selection of Slavonian grebes in this brackish area is significantly influenced by water depth and bottom sediment type. The grebes prefer shallow waters of 4–14 m depth and occur only over sandy sediments. While the diving depths of endothermic animals is limited due to energetic constraints and thermoregulation, sediment type is regarded to be a proxy for food choice. The diet of Slavonian grebes in the Pomeranian Bight consists mainly of demersal gobies (Gobiidae) that frequently occur over sandy bottom substrates.

1. Introduction

Apart from their morphological and physiological adaptations to the marine environment, there are various physical, biological and anthropogenic factors that influence the distribution of birds at sea (e.g. Furness and Monaghan, 1987; Shealer, 2002). During the breeding season, the occurrence and location of suitable nesting sites, in combination with sufficient food supply, predominantly determine the distribution of seabirds within their geographical breeding range. In winter, however, they may be able to disperse to a much wider range of habitats. As seabirds interact closely with the marine environment, physical conditions and processes at sea substantially influence their distribution (e.g. Briggs et al., 1987; Hunt and Schneider, 1987; Haney and Solow, 1992; Ainley et al., 2005). However, these factors affect seabirds only indirectly, while food availability and foraging options are the dominant factors underlying the relationship between seabirds and physical parameters at sea (Hunt and Schneider, 1987; Shealer, 2002).

The Slavonian grebe (*Podiceps auritus*) is a small limnic waterbird species that mainly breeds in the boreal zone of the Holarctic. The breeding grounds are inland freshwater habitats: mostly isolated eutrophic or mixotrophic pools and ponds, marshes as well as sheltered bays and inlets of larger lakes. Occasionally, breeding is also recorded on brackish sounds, highmoor and crater lakes or in open oligotrophic waters with sterile exposed shores (Fjeldså, 1973; Birds of the Western Palearctic interactive, 2004; Fjeldså, 2004). Around the Baltic Sea, the species is mainly restricted to small and shallow mixotrophic forest lakes, with open water interrupted by patchy, not too high and dense vegetation (Fjeldså, 1973, 2004). Winter grounds, on the contrary, are predominantly marine, often in coastal or inshore waters and estuaries, but also in offshore areas. Only small numbers winter on large freshwater lakes (Birds of the Western Palearctic interactive, 2004; Fjeldså, 2004). Thus, this freshwater breeding waterbird species turns into a seabird during winter.

Slavonian grebes are small and quite inconspicuous in non-breeding plumage, and due to the fact that the winter localities may also be situated far away from the coast, they are difficult to discover and investigate (see also Fjeldså, 2004). Ship-based surveys revealed a large winter population of Slavonian grebes in the offshore area of the Pomeranian Bight in the southern Baltic Sea (Durinck et al., 1994; Skov et al., 2000; Sonntag et al., 2006), which, according to Durinck et al. (1994), is the most important wintering area for this species in northwestern Europe.

At the breeding sites, Slavonian grebes mainly feed in shallow water and perform only shallow dives up to 2 m depth (Fjeldså, 2004). In the offshore area of the Pomeranian Bight, however, water depth reaches values up to 20 m. Another important wintering area

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with fairly deep water is in the archipelago from 62° N up to the Arctic Circle in northwestern Norway (Fjeldså, 2004). Diving depth has a strong effect on the energetic costs of foraging in endothermic animals (e.g. Enstipp et al., 2006). Water depth should thus constitute an important parameter for the habitat choice of Slavonian grebes in the wintering areas, as has already been described for other species in the southern Baltic Sea, e.g. benthivorous sea ducks (Kube and Skov, 1996). However, food availability is considered to be the key factor determining the distribution of seabirds at sea. We chose bottom sediment type as a proxy for the availability of the preferred prey of the grebes on/near the sea bottom. Based on 8 years of extensive work at sea, we present in this paper detailed information on the occurrence of Slavonian grebes in the Baltic Sea and test the hypothesis that water depth and bottom sediment type are relevant factors for the habitat selection of this species in its most important wintering area in northwestern Europe. To evaluate the results regarding bottom sediment, we additionally studied the diet of individuals drowned in set nets in the Pomeranian Bight.

2. Methods

2.1. Study area

The Baltic Sea in northeastern Europe is one of the largest brackish water seas in the world and with a mean depth of 55 m a very shallow water body. Salinity is one of the most important influencing factors and the Baltic Sea is characterised by strong salinity gradients from west to east (Telkänranta, 2006). This study focuses on the southern part of the Baltic Sea (Fig. 1). At a smaller scale, the Pomeranian Bight, bordered by the coasts of Germany and Poland in the west and south and extending to the north approximately up to the 20 m water depth contour (Lass et al., 2001), is of particular interest (large box in Fig. 1). The bight is characterised by the largest riverine freshwater influx into the western Baltic Sea, which strongly influences its hydrographic regime and leads to an average salinity of 7.5 psu (Lass et al., 2001). The shallow Oderbank comprises the central part of the offshore area. Water depth contour lines and distribution of bottom sediment types for the study areas are shown in Figs. 1 and 2, respectively.

2.2. Recording of birds at sea

The distribution of Slavonian grebes was studied by ship-based transect counts following an internationally standardised method for northwest European waters (e.g. Tasker et al., 1984; Camphuysen and Garthe, 2004). From the top deck or bridge-wing of the research vessel two or three observers recorded all flying and swimming individuals within a 300 m wide band transect running parallel to the ship's track on one or both sides. The observers searched for Slavonian grebes with unaided eyes, but in addition the census area was regularly scanned with binoculars to look for birds diving or flushing in front of the approaching vessel. For flying individuals the "snapshot method" according to Tasker et al. (1984) was applied to avoid overestimates. The length of the transect segments ahead was the distance the ship covered in successive 1-min counting intervals and therefore depended on ship speed. The surveyed area was calculated from the transect length and the transect width (300 m). Geographic positions were recorded in 1-min intervals.

2.3. Distribution maps

All data used in this study were taken from the German Seabirds at Sea Database version 5.12 (June 2008; Garthe et al., 2007), which contains more than 30,000 ship kilometres in the southern Baltic Sea for the years 2000–2008. Counting intervals with a seastate higher than 4 were excluded from analysis as such conditions prevent a thorough recording of small bird species like Slavonian grebes. Distribution maps are based on abundances, i.e. number of individuals per area surveyed for each counting interval. In this way, data were corrected for counting effort. Due to the fact that some swimming birds, particularly those in the more distant parts of the transect bands, might have been overlooked, we applied a correction factor of 1.4 according to Garthe (2003) by multiplying the abundance of swimming birds. Numbers of flying birds were not corrected. Maps were created by radial basis function interpolation in Surfer 8.0, using *Multiquadratic* as function method and 20 km as search radius. Visualisation was based on 3 × 3 km grid cells.

2.4. Phenology

To study the seasonal dynamics of Slavonian grebes we selected an area of the southern Baltic Sea, hereafter referred to as "Oderbox". This box covers an area (a) within the core distribution of Slavonian grebes, (b) which was intensively studied (high counting effort), and (c) with reasonably similar habitat parameters, i.e. water depth and bottom sediment type. The box is situated in the offshore area of the Pomeranian Bight covering the shallow bank

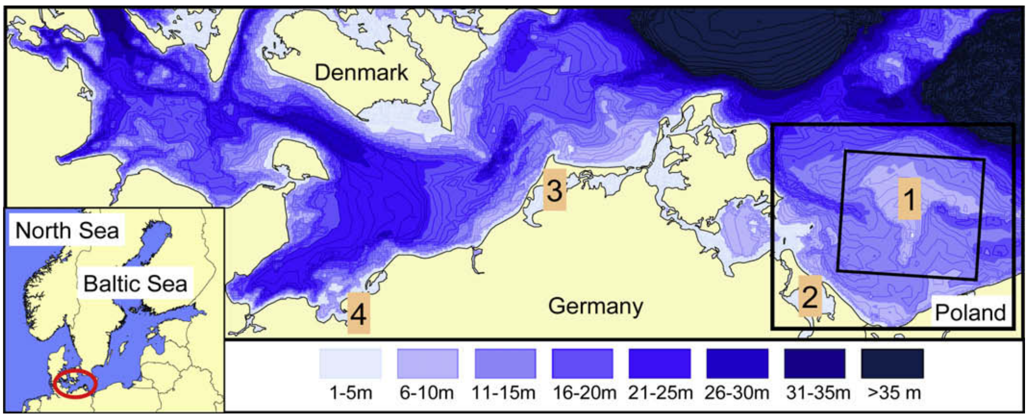

Fig. 1. Location and water depths of the study area in the southern Baltic Sea, with the Pomeranian Bight (large box) and the Oderbox (small box). The numbers describe localities referred to in the text: (1) Oderbank, (2) Usedom peninsula, (3) Darß-Zingst peninsula, (4) Wismar Bay. [Online version: The thin contour lines correspond to areas with equal water depths (isobathes)].

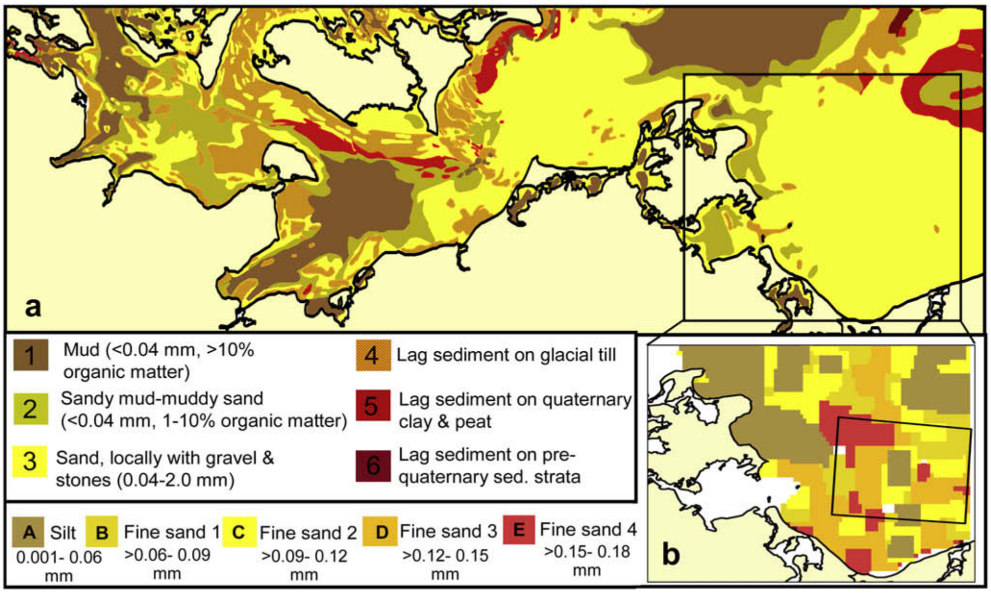

Fig. 2. Bottom sediment types in the southern Baltic Sea (a) and in the Pomeranian Bight (b). Data for the Pomeranian Bight are based on a high resolution classification of the main sediment type sand into five sub-classes according to grain size. The black box in (b) indicates the Oderbox used for the small-scale habitat analysis.

Oderbank (small box in Fig. 1). For every day in the study period 2000–2008 we calculated the abundance of Slavonian grebes as number of birds per area surveyed. Only days with a survey effort of at least 5 km^2 within the box area were included in the analysis. Sample size varied between 1 day (June) and 9 days (April) per month, with a total of 43 days. Monthly means ± confidence intervals are based on bootstrapping 10,000 times the original values.

2.5. Diet

We analysed the diet of four Slavonian grebes accidentally caught and drowned in set nets in the Pomeranian Bight off the coast of the Usedom peninsula (see Fig. 1). The sample comprised one female of unknown age (drowned in January 2002), one immature female (February 2005), one adult female (April 2005) and one immature male (April 2005). Following a scoring according to van Franeker (2004), body condition was good in three birds and moderate in one bird. Stomach and guts were removed from the dissected birds and all prey items were collected. Fish remnants were identified to the lowest possible taxon based on otoliths or hard parts of the skeleton like premaxillae and vertebrae according to Härkönen (1986), Watt et al. (1997), Leopold et al. (2001) and our own reference collection. Invertebrates were identified by jaws (polychaete worms), carapace elements (crustaceans) or chitinous parts of the exoskeleton (insects). Prey numbers were calculated as the smallest definite number by considering all remnants of a given species. Items that occur in pairs (like otoliths or jaws) were paired based on species, orientation, size, wear and shape. Otoliths were measured to derive original fish length and biomass using regressions obtained from Leopold et al. (2001) after correction for wear. To assess the biomass of unidentified clupeids, the average value of herring and sprat was calculated as these are the most frequent clupeid fish species in the Pomeranian Bight. Unidentified fishes were excluded from biomass calculations as were crustaceans, as we had no indications of the size of crustaceans found in the samples. Regressions for polychaete worms were adopted from Debus and Winkler (1996).

As is always the case in grebes, the dietary remains in the stomachs of our samples were embedded in a feather ball that also formed a plug in the pyloric exit and prevented the passage of hard prey items into the intestines (see e.g. Piersma and van Eerden, 1989; Fjeldså, 2004). Therefore, the guts only contained a few unspecific fish bones and a single heavily worn fragment of an otolith and were thus excluded from further analyses.

Due to the low sample size the results were not analysed statistically.

2.6. Habitat selection

Water depth and bottom sediment type were selected as two abiotic factors with a potential influence on the distribution of Slavonian grebes in the southern Baltic Sea. Data on water depth within the study area were obtained from the Danish Hydraulic Institute (DHI). These data are classified into 1-m categories and visualised in Fig. 1. Sediment data were obtained from the Geological Survey of Denmark and Greenland (GEUS; Hermansen and Jensen, 2000). These data are classified into six different sediment types based on grain size and content of organic material (Fig. 2a). Additionally, we used high resolution data for the Oderbox area that comprise a more detailed classification of the main sediment type sand into five sub-classes (grain size 0.001–0.180 mm, Fig. 2b). They were provided by the Institute for Applied Ecology (IfAÖ) Ltd, Neu Broderstorf, within the IMKONOS project.

The influence of water depth and bottom sediment type on Slavonian grebe distribution was tested by modelling the abundance of birds (individuals per area surveyed) in relation to both factors with a generalised additive model (GAM; Wood, 2006) using the mgcv package (Wood, 2000) in version 2.8.1 of R (R Development Core Team, 2008). Bird abundance served as response variable while water depth and sediment type were used as covariables. A cubic regression spline was used as smoothing function for the covariate water depth and a thin plate regression spline for the covariate sediment type. Because the latter variable included only a few different categories, the degrees of freedom for curve smoothing were restricted to 3. As the data set was based on count data, the Poisson function should usually form the basis of the analysis (Zuur et al., 2007). However, to prevent overdispersion, quasi-Poisson was selected as underlying function in the model frame. In a first step we conducted the habitat analysis for the total study area. At a smaller scale, we further analysed the core distribution area within the Oderbox. For both areas calculations were performed for the total time period where Slavonian grebes occurred in the study area (October to April) as well as separately for three time periods based on the results of the phenology analysis: autumn (October, November), winter (December to February) and spring (March, April).

In the process of developing our habitat model with the available data set, two aspects had to be considered. Firstly, in the total set of more than 64,000 data points, the occurrence of Slavonian grebes was a very rare event compared to a large number of zero-counts. Standard statistical functions might thus be inappropriate. In addition to the (original) model described above, we therefore applied a two-stage GAM according to Jensen et al. (2005). In the first stage of this analysis, presence or absence of Slavonian grebes in relation to both habitat factors were modelled using a binomial distribution function. In the second stage only presence data (bird abundance > 0) were modelled as a function of the environmental covariates using the quasi-Poisson distribution. Afterwards, the predicted bird abundance was calculated as the product of both stages (combined model). The residuals of the original and combined model were then compared using a Student's *t* test. As there were no significant differences between these residuals for the total data set as well as the three seasons ($P > 0.995$, respectively), we selected the more simple, original model for our analysis.

Secondly, bird numbers are probably spatially autocorrelated. To avoid spatial autocorrelation within the model, an autocorrelation structure for latitude and longitude usually has to be included, using a generalised additive mixed model (GAMM) with the autocorrelation structure corEXP for spatial data (Pinheiro and Bates, 2000). However, by comparing the residuals of the model with and without this autocorrelation structure, we found no difference between both model types. This held true for the model of the total study area ($R^2 > 0.996$) as well as for the Oderbox ($R^2 > 0.998$) and was separately tested for the total data set and the three different time periods autumn, winter and spring. Thus, to keep the model as simple as possible, no autocorrelation structure was applied.

3. Results

3.1. Distribution and phenology

Slavonian grebes occurred in the southern Baltic Sea in winter and during migration periods. So far, we recorded only a single bird in the summer months. A clear hotspot occurred in the Pomeranian Bight, with the largest numbers in the offshore area around the shallow Oderbank, at about 30–50 km from the coast. This core distribution area was pronounced in winter as well as during migration (Fig. 3a–c). Locally moderate numbers were observed north of the Darß-Zingst peninsula in winter and spring while in more western parts of the study area only a few birds were recorded. During spring migration, the coast of Usedom was an important staging area in addition to the hotspot around the Oderbank. Most observations of Slavonian grebes comprised single individuals or two birds, and only a few aggregations of three or four birds were recorded.

The analysis within the Oderbox revealed a more detailed seasonal pattern (Fig. 4): After leaving their breeding localities, Slavonian grebes first appeared at the Oderbank in October. Autumn migration peaked in November while numbers were lower during the winter resting period. Birds left the southern Baltic Sea

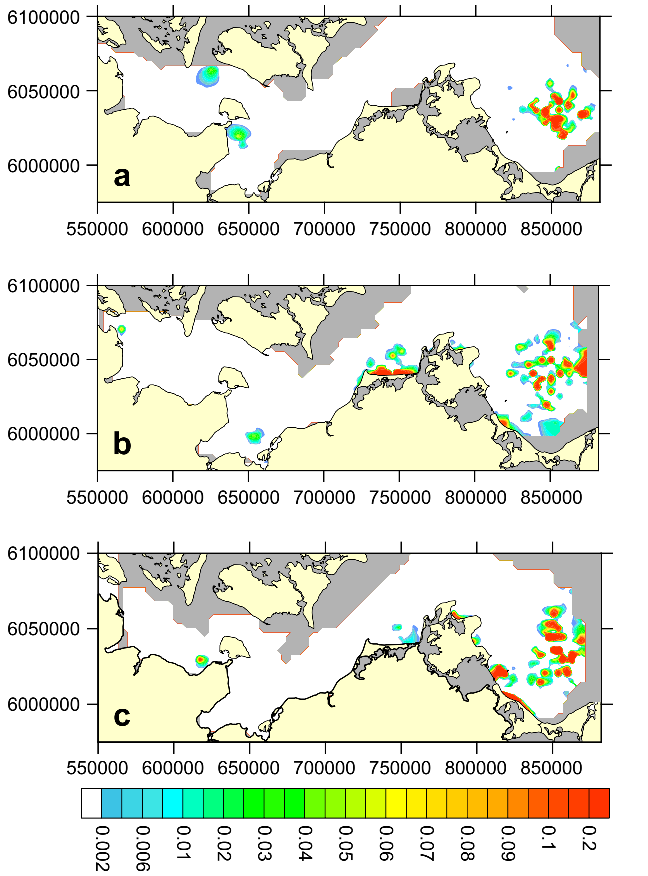

Fig. 3. Distribution of Slavonian grebes in the southern Baltic Sea during (a) autumn (Oct–Nov), (b) winter (Dec–Feb), and (c) spring (Mar–Apr) 2000–2008. The scale indicates the abundance as birds per square kilometre on a logarithmic scale. Hatched [online version: grey] areas mark regions that were not studied.

in March and April. Compared to autumn, numbers during spring migration were considerably lower.

3.2. Diet and prey size

All four stomachs contained dietary remains. A total of 576 fish specimens (76% of all prey remnants) from three different families could be identified (Table 1). Gobies (common goby *Pomatoschistus microps* and sand goby *P. minutus*) occurred most frequently in the stomachs and accounted for 95% of all fish remains, followed by sandeel comprising 4%. Most sandeels could not be identified to species level as the otoliths found in the stomachs were too heavily worn. All stomachs contained jaws of polychaete worms that

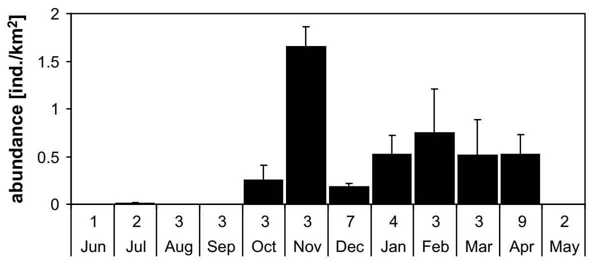

Fig. 4. Seasonal abundance (with 95% confidence interval) of Slavonian grebes within the Oderbox area (small box in Fig. 1). Numbers on the *x*-axis indicate the sample size (days surveyed during each month).

Table 1
Diet of four Slavonian grebes drowned in set nets in the Pomeranian Bight. Frequency of occurrence is the number of stomachs containing the respective prey category. Numerical abundance is the total number of the respective prey category (brackets indicate the percentage of the total number of items). Biomass is the percentage of total biomass calculated for all stomachs.

Prey category			Frequency of occurrence	Numerical abundance	[%]	Biomass (%)
Fish	Gobies (Gobiidae)	*Pomatoschistus microps*	4	175	[23.1]	17.4
		Pomatoschistus minutus	2	14	[1.8]	1.2
		Pomatoschistus microps/minutus	4	360	[47.6]	68.0
	Sandeel (Ammodytidae)	*Ammodytes tobianus*	2	3	[0.4]	0.9
		Hyperoplus lanceolatus	1	1	[0.1]	1.7
		Sandeel indet.	3	20	[2.6]	10.3
	Clupeids (Clupeidae)		1	1	[0.1]	0.1
	Fish indet.		1	2	[0.3]	–
Polychaete worms			4	174	[23.0]	0.4
Crustaceans			4	3	[0.4]	–
	Crangon crangon		3	4	[0.5]	–
Insects			2	?	?	–

accounted for 23% of all dietary remains. Fragments of insects were found in the stomachs of the two birds drowned in April, but they were too heavily worn to be counted.

Gobies dominated the diet not only with regard to numerical abundance but also concerning biomass (Table 1). They accounted for almost 87% of the total prey biomass. Polychaete worms were found in the stomachs in relatively high numbers, but their proportion of the total prey biomass was less than 1% due to their small median length of only 1.3 cm ($N = 84$ individuals measured). Total length of gobies ranged from 3.1 to 5.7 cm ($N = 230$). Consumed common gobies (*Pomatoschistus microps*) were slightly smaller than sand gobies (*P. minutus*). Sandeels were considerably longer than gobies with a total length of 5.7–14.5 cm ($N = 13$).

Although there was considerable variation in the total number of prey items found in each stomach, the overall results held true for all four individual birds: gobies were the most important prey in terms of numerical abundance as well as biomass.

3.3. Habitat selection

Water depth and bottom sediment type both proved to have a clear effect on the habitat choice of Slavonian grebes in the southern Baltic Sea. The results of the model revealed a significant influence of the two habitat factors on bird distribution in all time periods analysed except for spring when the influence of bottom sediment type was less pronounced (Table 2). The two variables explained between 14.8% (winter) and 32.1% (autumn) of the variation in abundance.

Preferred water depth ranged from 4 to 14 m with optimum values at approximately 6–9 m (Fig. 5a). Almost all birds (93%) were observed in waters less than 15 m deep and only one bird was recorded in waters more than 20 m deep. Preferred bottom sediment type was sand (category 3, Fig. 5b) where 99% of all birds occurred. The few remaining individuals were observed in areas with sediment type 4 (lag sediment on glacial till). Based on the result that Slavonian grebes occurred only in areas with water depths up to 20 m, we repeated the model excluding all data with higher water depths to re-evaluate the influence of sediment type. With these restricted data the model resulted in the same findings as the model based on the total data set (Table 2).

Although water depth and bottom sediment type had a significant influence on the distribution of Slavonian grebes in the southern Baltic Sea, the larger proportion of the deviance could not be explained by these two variables. Additionally, the error analysis of the GAM clearly indicated regions within the study area where the original observations of Slavonian grebes differed from the distribution predicted by the model. Numbers observed in the field were lower than predicted by the model especially in some inshore areas (e.g. Wismar Bay) and in the offshore areas north of the Darß-Zingst peninsula.

Within the Oderbox, water depth and bottom sediment type also had a significant influence on bird distribution in all time periods analysed (Table 2). Although water depth in the box mainly ranged from 6 to 14 m, it exceeded the latter in some parts of it. These areas were clearly avoided by Slavonian grebes. No uniform trend was recognisable for waters 6–14 m deep as they lie within the preferred depth zones found for the southern Baltic Sea region.

Table 2
Results of the generalised additive model for the habitat selection of Slavonian grebes in the southern Baltic Sea and within the Oderbox. Significance codes: ***0.001; **0.01; *0.05.

	Number of counting intervals (bird density > 0)	Water depth		Bottom sediment		Bottom sediment (water depth ≤ 20 m)	
		F	*P*	*F*	*P*	*F*	*P*
Southern Baltic Sea							
Total (Oct–Apr)	64168 (431)	81.4	<2e−16***	259	<2e−16***	201.1	<2e−16***
Autumn (Oct–Nov)	14993 (98)	2.947	0.0154*	114.641	<2e−16***	82.4	<2e−16***
Winter (Dec–Feb)	26084 (135)	39.29	<2e−16***	111.57	<2e−16***	87.01	<2e−16***
Spring (Mar–Apr)	23091 (198)	38.674	<2e−16***	0.768	0.486	0.913	0.417
Oderbox							
Total (Oct–Apr)	10177 (353)	12.38	<2e−16***	17.74	7.09e−10***		
Autumn (Oct–Nov)	1984 (94)	13.432	<2e−16***	7.851	0.000131***		
Winter (Dec–Feb)	3687 (103)	5.567	9.83e−07***	16.802	4.67e−09***		
Spring (Mar–Apr)	4506 (156)	6.849	1.54e−09***	8.215	7.93e−05***		

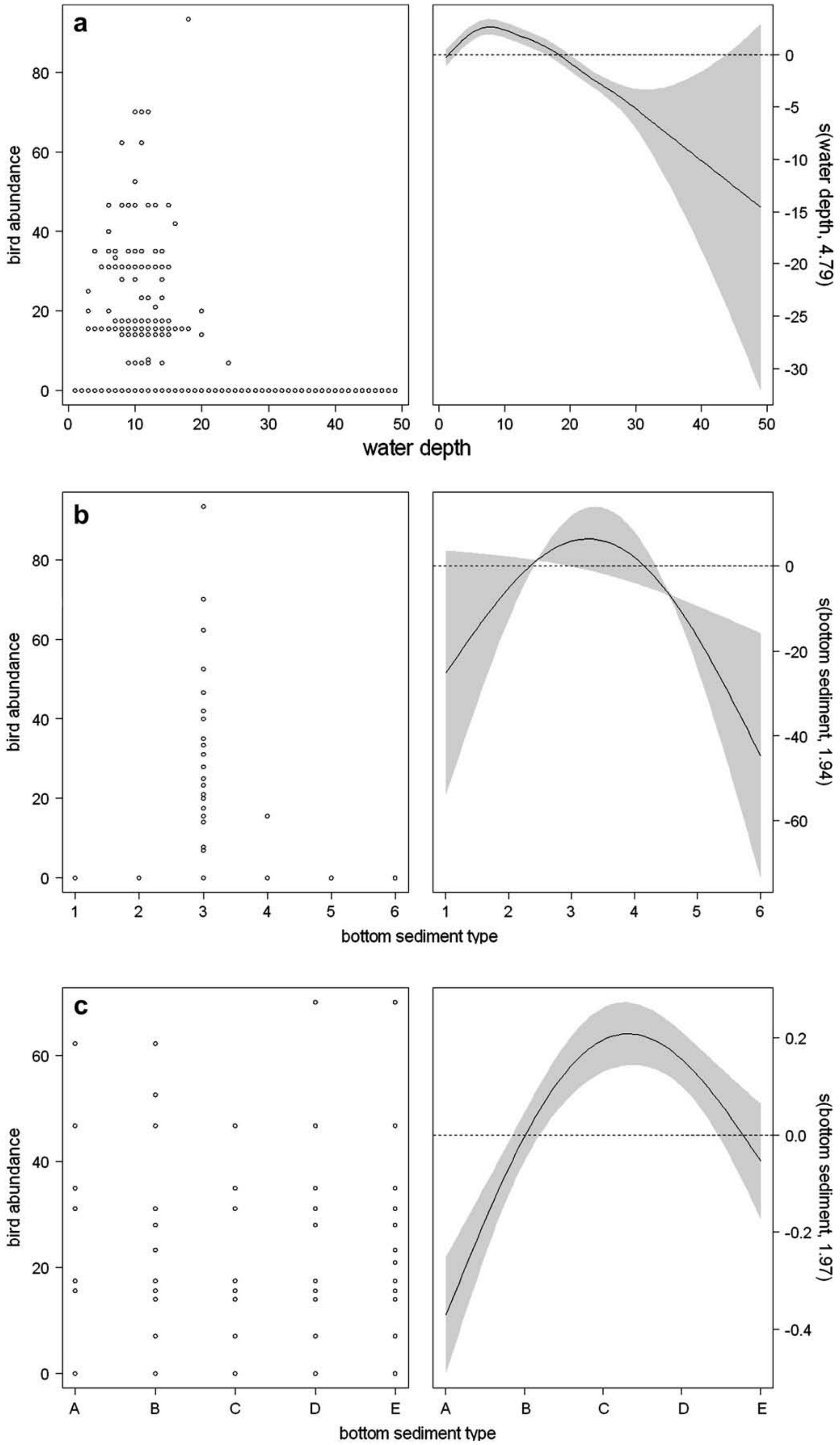

Fig. 5. Results of the habitat analyses for the total data set (Oct–Apr 2000–2008), showing the original data matrices on the left and the GAM smoothing curves describing the effect of the predictor variables on bird abundance on the right panels, respectively. Dashed lines represent mean values which were scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines). Bird abundance is represented as a function of water depth (a; $F = 81.4$, $P < 0.001$), bottom sediment type for the southern Baltic Sea (b; $F = 259$, $P < 0.001$) and bottom sediment type within the Oderbox (c; $F = 17.74$, $P = 7.09\mathrm{e}{-10}$).

Regarding bottom sediment the results indicated an avoidance of very fine-grained sediment types (especially silt, <0.06 mm) as well as a tendency to avoid areas with sediment type E (fine sand with grain size 0.15–0.18 mm; Fig. 5c).

4. Discussion

4.1. Distribution and seasonal patterns

The occurrence of Slavonian grebes in the Baltic Sea was first described by Durinck et al. (1994). Recently published population sizes refer to a number of 1000 individuals in the German part of the Baltic Sea in winter, with the largest proportions in the Pomeranian Bight (Mendel et al., 2008). In other parts of the Baltic Sea, only low numbers of wintering Slavonian grebes have been recorded so far, for example in the Bay of Gdansk or along the Kursiu Spit (Durinck et al., 1994; Skov et al., 2000). The occurrence of Slavonian grebes in the Pomeranian Bight involves migrants and winter residents. Numbers are highest during autumn migration. Some parts of the northeastern breeding population apparently remain in the Pomeranian Bight for only a short time before moving on to other wintering areas. These are probably in the more western parts of the Baltic Sea (see Fig. 3b) and along the coast of northwestern France, where a winter population has been reported by Gilissen et al. (2002). During the midwinter months, December to February, numbers within the Oderbox hotspot area show distinct variations. It is unclear to what extent local movements (e.g. to the Polish side of the Pomeranian Bight) or general seasonal patterns might be responsible. During spring migration, abundances assessed within the Oderbox are considerably lower than in autumn. This might be due to the fact that in spring high numbers occur outside the Oderbox in the coastal areas of the Pomeranian Bight, especially off the coast of Usedom (Fig. 3c). Furthermore, Slavonian grebes might spend less time in the study area on the way back to the breeding grounds where an early arrival could be advantageous for nest site occupation.

4.2. Feeding ecology

Although the sample size of our diet study is very small, it nevertheless provides valuable insights into the prey composition of Slavonian grebes during winter. Obtaining diet samples of individuals at sea is almost impossible. Non-destructive methods are not applicable and the shooting of this highly protected species is ethically unjustifiable and technically impossible. So far, only two other authors provide information on winter diet in European waters. In a single bird from the Kattegat in late October, Madsen (1957) found small gobies (*Gobius* spec.), 15-spined sticklebacks (*Spinachia spinachia*), a polychaete jaw and some detritus of insects. In Lake IJsselmeer, The Netherlands, Piersma (1988) identified smelt (*Osmerus eperlanus*), a pelagic fish species, as the main diet of wintering Slavonian grebes.

Common gobies, the dominant prey found in our study, are widespread in the coastal areas of the Baltic Sea. They prefer shallow habitats with macrophytes in the litoral zone up to 12 m water depth whereas sand gobies have a wider depth range (e.g. Evans and Tallmark, 1985; Muus and Nielsen, 1999). These habitat preferences are in agreement with the fact that the birds of our diet studies were by-caught in the coastal zone of the Pomeranian Bight. One may speculate that sand gobies are the dominant goby species in the diet of Slavonian grebes on the Oderbank, because, unlike common gobies, they occur in high numbers in this central part of the Pomeranian Bight (Thiel et al., 2007).

Polychaete worms, probably *Hediste diversicolor* due to its high abundance in the study area (Zettler, personal communication), were very small-sized and accounted for less than 1% of the total prey biomass. It is unclear whether such small individuals were directly captured by Slavonian grebes – maybe after exposure due to the digging activities of sea ducks wintering in the Pomeranian Bight, as described for SW Norway by Byrkjedal (2000) – or whether the hardly digestible chitinous jaws reached the bird stomachs via gobies preyed upon by the grebes. (Nereid) polychaete worms are described as prey of common and sand gobies by various authors (e.g. Pihl, 1985; Zander, 1990; del Norte-Campos and Temming, 1994; Leitão et al., 2006).

4.3. Habitat selection

The results of the model support our hypothesis that both factors analysed substantially influence the habitat choice of Slavonian grebes in the study area. We consider water depth to be a more relevant parameter than sediment type, as it acts via the maximum possible diving depth of this small bird species. In the breeding areas, Slavonian grebes forage in shallow water, often only up to 2 m, and perform only shallow dives to catch prey under water (Fjeldså, 2004). This limitation results from the fact that Slavonian grebes mainly breed in fertile lakes where penetration of light is often very low. Thus, prey is difficult to detect and to pursue in the deeper parts of those waters (Fjeldså, 2004). In marine areas, Slavonian grebes are able to feed in much deeper water. However, diving depth of endothermic animals is limited due to physiological constraints and the thermal properties of water, and temperature has a strong effect on daily energy expenditures (e.g. Wiersma et al., 1995; Enstipp et al., 2006). In great crested grebes (*Podiceps cristatus*) wintering on Lake IJsselmeer, lower air and water temperatures caused an increase in food intake rate due to higher energetic costs for e.g. maintenance of body temperature, higher diving activity to catch more food, and the heating of cold prey in the stomach (Wiersma et al., 1995). Because of a negative exponential relationship between body mass and thermal conductance (which is higher in water than in air), de Vries and van Eerden (1995) assumed that energetic expenditure for thermoregulation may indeed be a constraint for small Slavonian grebes that spend the whole winter at sea. We therefore postulate that the birds tend to avoid sea areas of the southern Baltic Sea with water depths exceeding 15 m to reduce high energetic costs while foraging in cold water for their favourite prey, demersal gobies.

Slavonian grebes were almost exclusively recorded in waters over sandy bottom. However, some sediment types (1,5,6) predominantly occurred in deeper waters and were thus, according to our results regarding water depth, located in areas not suitable for Slavonian grebes. It is therefore difficult to judge whether certain sediment types were truly avoided or were rather out of reach due to the unfavourable water depth. On the other hand, sediment types 2 and 4 did occur within the suitable depth range, but were avoided by Slavonian grebes, indicating a "real" influence of sediment type. The restriction to sandy sediments indicates that Slavonian grebes mainly feed on benthic or benthopelagic prey occurring over this sediment type. Common and sand gobies, the dominant prey found in our diet samples, are demersal fish species that often occur over sandy bottom sediments, albeit they can also colonise other habitats (Jansson et al., 1985; Zander, 1990; Vorberg and Breckling, 1999). Thiel et al. (2007) found high numbers of *Pomatoschistus minutus* in the sandy Pomeranian Bight. This supports the assumption that, in our study area, Slavonian grebes find their favoured prey species over sandy bottom substrates and consequently occur mainly in areas with this sediment type. The small-scale differences in distribution found within the hotspot area in the Oderbox might reflect spatial and/or temporal variability in the occurrence of the main prey gobies. At a large scale, the distribution of seabirds at sea often corresponds best with physical phenomena, while biological features like foraging range, social interactions and prey availability often determine distribution patterns at smaller scales (Schneider and Duffy, 1985; Hunt and Schneider, 1987). Ragworms, whether direct prey of Slavonian grebes or indirectly taken via gobies, are rather euryoecious and can be found in different sediment types (Hartmann-Schröder, 1996). *Hediste diversicolor* is widespread within the southern Baltic Sea and was frequently observed in the sandy Pomeranian Bight by Zettler and Röhner (2004) and Zettler et al. (2006). In Lake IJsselmeer, where the diet of Slavonian grebes consists of pelagic smelt, water transparency is very low (Piersma et al., 1988), probably impeding foraging near the bottom. Thus, the birds seem to be able to adjust their feeding techniques or prey species according to the environmental conditions they encounter in the wintering areas.

Although water depth and bottom sediment type could be described as important habitat factors, the variance explained by both parameters as well as an error analysis indicate that these variables alone cannot sufficiently predict the distribution of Slavonian grebes in the study area. Consequently, further factors must be effective. Particularly in some inshore areas of the study area, bird numbers observed in the field were much lower than predicted by the model. One reason for this fact is that these areas have low water depths and thus could not be surveyed from ships due to the draught of the survey vessels. Counts carried out from land within the framework of the annual midwinter International Waterbird Census revealed small to medium numbers of Slavonian grebes in several coastal areas (Scheller et al., 2002; Mendel et al., 2008; DDA, 2009) and can explain some of the discrepancies between modelled data and original field observations. Still, there are regions within the study area with suitable habitat conditions regarding water depth and sediment type where no Slavonian grebes occur. We therefore assume that at least two other factors might influence their distribution in the southern Baltic Sea:

(1)Competition with other grebe species: besides Slavonian grebes, high numbers of great crested grebes (*Podiceps cristatus*) and red-necked grebes (*P. grisegena*) winter in the southern Baltic Sea (e.g. Durinck et al., 1994; Sonntag et al., 2006). During the breeding season there is strong interspecific competition between different grebe species, resulting in a spatial segregation into different breeding habitats (Berndt and Drenckhahn, 1990; Fjeldså, 2004). Due to the high abundances of the three grebe species wintering in the study area, and based on our (so far unpublished) own detailed data on their distribution and diet within the study area, we have indications that interspecific competition might affect the distribution patterns even outside the breeding season.

(2)Anthropogenic effects: within the given abilities of seabirds to stay at sea set by physical and biological parameters, anthropogenic activities may cause irregularities in distribution and abundances (e.g. Kaiser et al., 2006). The southern Baltic Sea is strongly influenced by various human activities that affect different seabird species to various extents (Garthe et al., 2003; Mendel et al., 2008). Slavonian grebes are particularly sensitive to ship traffic and show strong fleeing reactions towards approaching ships (Garthe et al., 2004; own unpublished data). Frequently used ship routes are therefore likely to influence the distribution of Slavonian grebes as already described for other species like divers and sea ducks (e.g. Hüppop et al., 1994; Kube and Skov, 1996).

These hypotheses will be the subject of future analyses to further clarify the habitat selection of Slavonian and other grebe species as well as their interactions in the southern Baltic Sea.

5. Conclusions

While various factors may influence the distribution of seabirds at sea (summarised e.g. in Hunt and Schneider, 1987; Shealer, 2002), prey availability and species-specific feeding options and constraints are considered to be of most relevance in the relationship between seabirds and the marine habitat (Montevecchi, 1993). For Slavonian grebes wintering in the Baltic Sea, water depth and bottom sediment type strongly influence the spatial distribution patterns. Both factors can be linked to diet preferences. The maximal possible diving depth while foraging for bottom-living gobies is limited due to physiological and thermoregulatory aspects in this small endothermic bird species. Bottom sediment type can be used as a proxy for the availability of demersal prey and provides particularly valuable information when data on the spatial occurrence of prey species and, as in Slavonian grebes, data on diet in general, are scarce.

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