



A Ship Traffic Disturbance Vulnerability Index for Northwest European Seabirds as a Tool for Marine Spatial Planning

Katharina Leonia Fliessbach*, Kai Borkenhagen, Nils Guse, Nele Markones, Philipp Schwemmer and Stefan Garthe

Research and Technology Centre, University of Kiel, Büsum, Germany

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*Correspondence:

Katharina Leonia Fliessbach
fliessbach@ftz-west.uni-kiel.de

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Ship traffic in Northwestern European seas is intense and continuing to increase, posing a threat to vulnerable seabird species as a result of disturbance. However, information on species-specific effects of ship traffic on seabirds at sea is limited, and tools are needed to prioritize species and areas to support the integration of conservation needs in Marine Spatial Planning. In this study, we investigated the responses of 26 characteristic seabird species in the German North and Baltic Seas to experimental ship disturbance using large datasets collected as part of the Seabirds at Sea counts. We developed a Disturbance Vulnerability Index (DVI) for ship traffic combining indicators for species' shyness, escape costs, and compensatory potential, and analyzed the relationships among shyness, escape costs, and vulnerability. The DVI was calculated using the following eight indicators: escape distance, proportion of escaping birds, proportion of birds swimming prior to disturbance, wing loading, habitat use flexibility, biogeographic population size, adult survival rate, European threat and conservation status. Species-specific disturbance responses differed considerably, with common scoters (*Melanitta nigra*) and red-throated loons (*Gavia stellata*) showing the longest escape distances and highest proportions of escaping individuals. Red-throated loon, black guillemot (*Cepphus grylle*), Arctic loon (*Gavia arctica*), velvet scoter (*Melanitta fusca*), and red-breasted merganser (*Mergus serrator*) had the highest DVI values, and gulls and terns had the lowest. Contrary to theoretical considerations, shyness correlated positively with escape costs, with the shyest species also being the most vulnerable among the species studied. The strong reactions of several species to disturbance by ships suggest the need for areas with little or no disturbance in some marine protected areas, to act as a refuge for vulnerable species. This DVI can be used in combination with distribution data to identify the areas most vulnerable to disturbance.

Keywords: seabirds, ship traffic, disturbance, behavior, escape distance, vulnerability index, risk-disturbance hypothesis, marine spatial planning

INTRODUCTION

The German North Sea and Baltic Sea are heavily impacted by ship traffic (OSPAR, 2010; Bahlke, 2017; HELCOM, 2018). A growing maritime economy in general and the construction and maintenance of offshore wind farms in particular will lead to further increases in ship traffic, including outside designated shipping lanes (Ecorys et al., 2012; Fridell et al., 2015; Bahlke, 2017; Matczak, 2018). Ship traffic is known to be associated with various negative environmental impacts as a result of emissions into the water and air (OSPAR, 2010; HELCOM, 2018). In addition, approaching vessels may present a threatening stimulus to marine birds, with subsequent risk-avoidance behavior reducing the time available for other activities such as feeding, resting, or mating (Gill et al., 1996; Frid and Dill, 2002; Beale and Monaghan, 2004b). Observable responses by seabirds include flying off, escape diving, and increased alertness, which can result in loss of energy and opportunities, displacement, and net habitat loss (Béanger and Bédard, 1990; Madsen and Fox, 1995; Béchet et al., 2004). Disturbance by ships may thus reduce survival and reproductive success and affect population dynamics (Goss-Custard et al., 1995a; Madsen, 1995; Carney and Sydeman, 1999; Sutherland, 1998).

The German North and Baltic Seas are important wintering sites for a large number of seabirds (Mendel et al., 2008; Markones et al., 2015). Several species are listed in Annex 1 of the European Union Birds Directive, which obliges member states to conserve their “most suitable territories” as Special Protection Areas. Winter and spring are considered to be the most critical times for accumulating body fat and establishing pair bonds in most waterbirds (Madsen and Fox, 1995; Knapton et al., 2000). However, despite the importance of the area and the high frequency of vessel traffic, disturbance of seabirds as a result of ship traffic is often neglected in (cumulative) impact assessments and planning processes. This can be partly attributed to the lack of detailed information and tools to identify and prioritize vulnerable species and areas.

Vulnerability indices have been established as tools to estimate levels of concern for species and areas, and have been developed for several human activities in the marine environment (surface pollutants: Williams et al., 1995; oil pollution: Camphuysen, 1998; traffic disturbance: Camphuysen et al., 1999; set-net fishery: Sonntag et al., 2012; wind energy: e.g., Kelsey et al., 2018). When combined with distribution data, they can be used to identify the most vulnerable areas (e.g., Garthe and Hüppop, 2004; Sonntag et al., 2012; Bradbury et al., 2014). An extensive literature has documented the effects of disturbance on breeding and non-breeding waterbirds in coastal and freshwater habitats (Carney and Sydeman, 1999; Rodgers and Schwikert, 2002; Steven et al., 2011; Glover et al., 2015; Krüger, 2016; McFadden et al., 2017), but information on disturbance responses of seabirds at sea to vessel traffic is limited to a few species (Bellebaum et al., 2006; Kaiser et al., 2006; Schwemmer et al., 2011).

Disturbance responses differ among species, with some species being more sensitive than others. Responses are measurable as escape distances, the proportions of escaping birds, and as physiological responses such as heart rate and corticosterone

levels. Given that the physiological responses of free-ranging seabirds at sea are extremely difficult to measure, most studies of disturbance effects have reported escape distances as a measure of effect (Blumstein et al., 2005). However, a species' vulnerability to disturbance cannot be assessed based on escape distance alone, given that the decision of when to take flight represents a trade-off between safety and fitness-enhancing activities (Ydenberg and Dill, 1986; Lima and Dill, 1990; Gill et al., 2001; Frid and Dill, 2002; Gill, 2007). A bird in good body condition and with sufficient feeding alternatives might flush earlier than a bird short of resources, as demonstrated in an experimental study with waders (Beale and Monaghan, 2004a). Visible disturbance responses alone are thus generally not considered to be a good indicator of vulnerability (Gill et al., 2001; Frid and Dill, 2002; Beale and Monaghan, 2004a; Beale, 2007). Vulnerability analysis should therefore consider the total costs of disturbance events including the ability to compensate for losses at the individual and population levels.

This study aimed to further our knowledge of species-specific behavioral disturbance responses at sea for all common and characteristic seabirds in German waters using experimental disturbance. We also aimed to develop a Disturbance Vulnerability Index (DVI) for ship traffic, combining indicators for species' shyness, escape costs, and compensatory potential, which can be used as a management tool to assess different vulnerabilities of a given sea area with respect to disturbance by ships. Finally, we aimed to investigate the general relationships among shyness, escape costs, and vulnerability in seabirds by cross-species comparisons of disturbance-related factors.

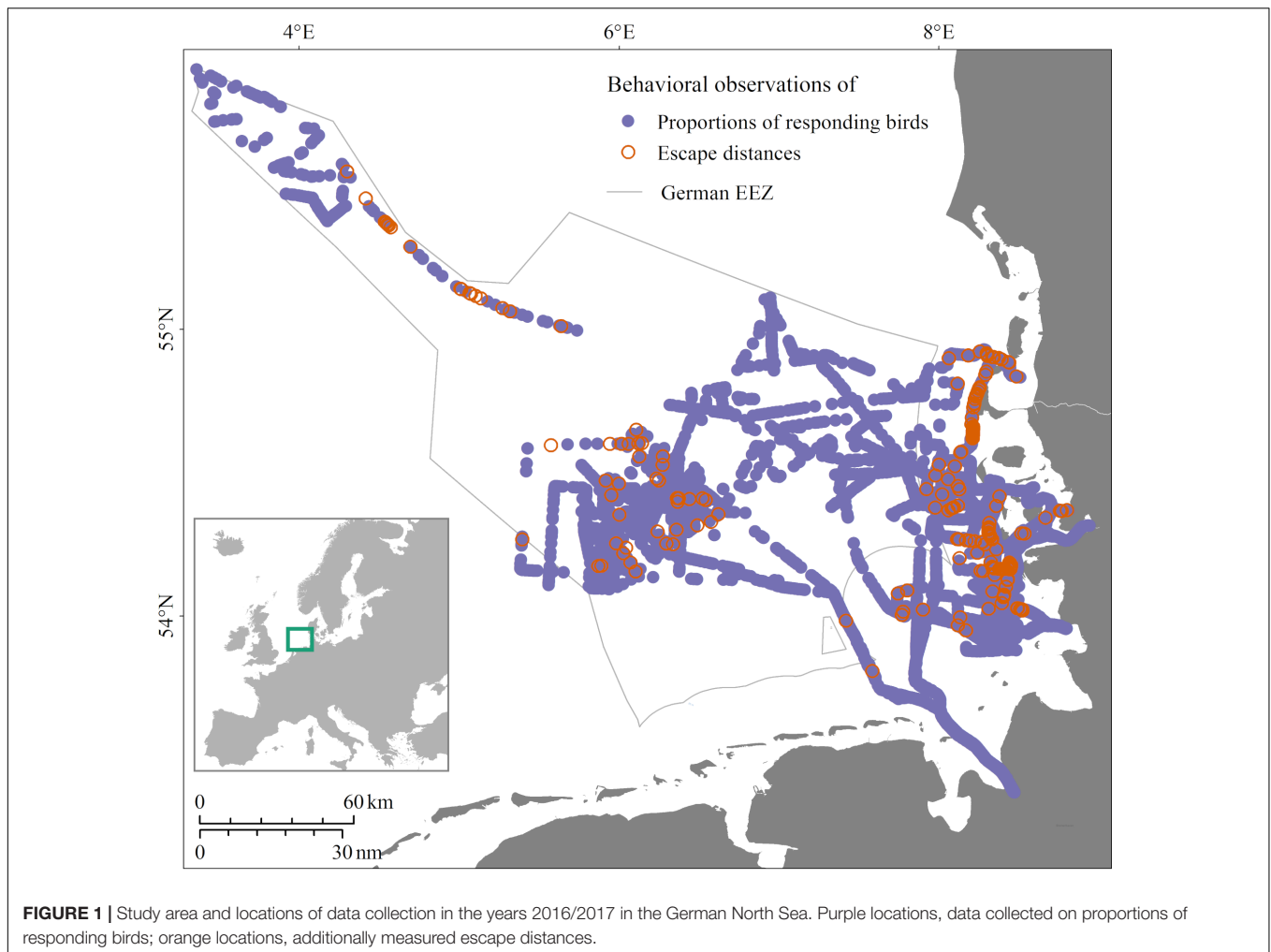
MATERIALS AND METHODS

Behavioral Observations

All behavioral observations were carried out during ship-based Seabirds at Sea counts in the coastal and offshore zones of the German North Sea (**Figure 1**) and Baltic Sea (**Figure 2**), following internationally standardized methods (Tasker et al., 1984; Webb and Durinck, 1992; Garthe et al., 2002; Camphuysen and Garthe, 2004). All birds were classified as either swimming or flying. Swimming birds were counted continuously within a 300 m wide transect parallel to the ship's keel line. Flying birds were only counted at full minutes and within a distance of 300 m to the side and to the front of the vessel, to avoid overestimation. We analyzed three different datasets collected within this framework from all seasons combined, described in the following paragraphs.

Proportion of Swimming Birds

We calculated the proportion of swimming birds for each species from data collected on more than 1,200 survey days in the years 2000 to 2017. Distance-correction factors (Garthe et al., 2007, 2009; Markones et al., 2013) were applied to the number of swimming birds to account for overlooked birds, resulting in a dataset of over 1.1 million birds. In our context 'swimming' encompassed all activities performed on the water surface, including resting, preening, active swimming, or others,



each of which implies slightly different, but low energetic costs compared with flying (Norberg, 1996). Because birds reacted to the approaching vessels, we looked far ahead to detect swimming birds before flushing, and always recorded flushed birds as swimming birds prior to disturbance.

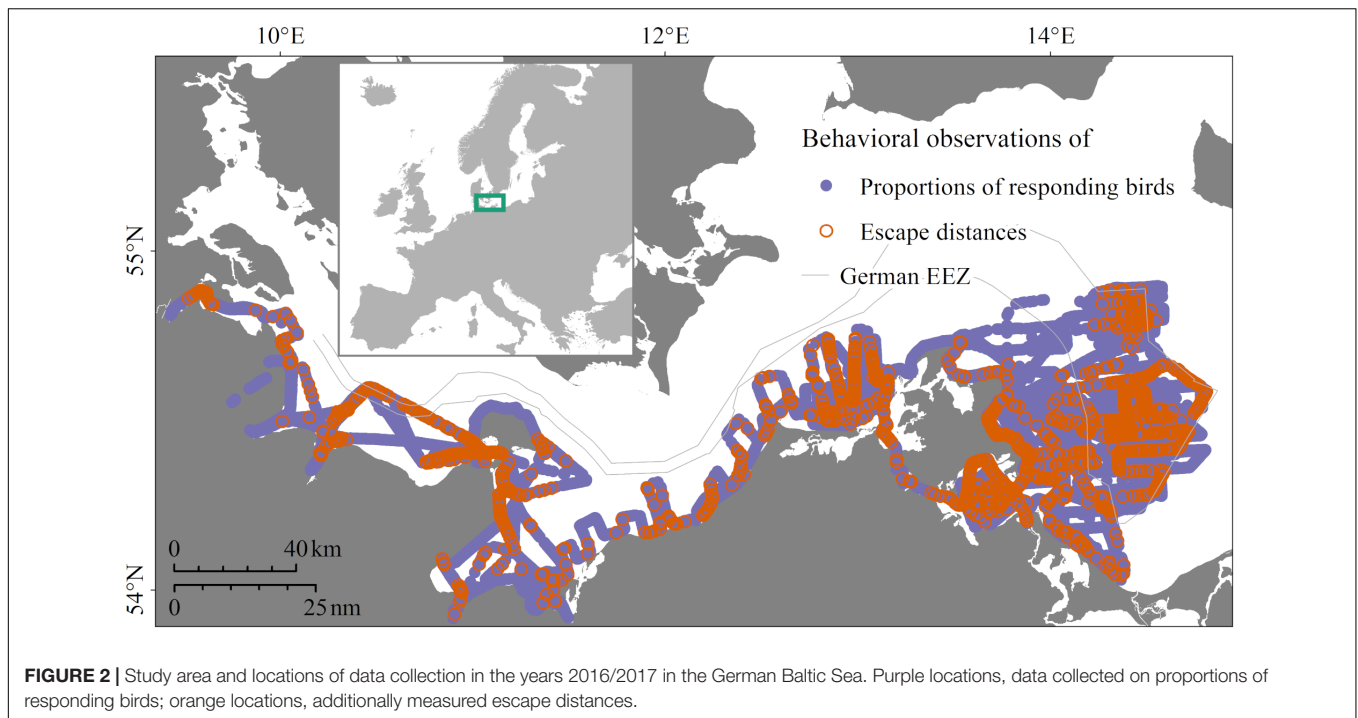
Proportion of Escaping Birds

Species-specific disturbance responses were recorded on 139 survey days in 2016 and 2017 (Figures 1, 2). We distinguished between two types of disturbance responses: flying off and escape diving. Common murres (*Uria aalge*) with young were excluded from the analysis, because we assumed that adult birds escaped less often to stay in the vicinity of their offspring. We further excluded species with fewer than 15 observations from the analysis of the proportion of escaping birds. The total dataset comprised 221,071 individuals from 25 species and species groups (loons and auks).

Escape Distance

We additionally measured the escape distances of disturbed birds, also called flight initiation distance (e.g., Bonenfant and Kramer, 1996; Blumstein, 2006) or flush distance

(e.g., Rodgers and Smith, 1995; Schwemmer et al., 2011), on 51 of the 139 survey days in the years 2016 and 2017. Our method was based on the distance estimation using geometrical functions, as described by Heinemann (1981). We recorded escape distances following the same principle as Schwemmer et al. (2011), but using individualized rulers instead of calipers or binoculars with reticles. To keep a consistent method, we refrained from measuring distances with radar or rangefinder, which are not consistently feasible under conditions at sea (Schwemmer et al., 2011; Borkenhagen et al., 2017). We randomly selected flocks of different sizes and measured the distance between the observer vessel and the first escaping bird in a flock at the moment of flushing or escape diving. Measurements were taken in directions between 90° and 0° of the course of the ship. Five research vessels were used: MS Haithabu (39 m long, $n = 465$ measurements); FS Heincke (55 m long, $n = 42$ measurements); MS Odin (32 m long, $n = 161$ measurements); MS Prandtl (31 m long, $n = 1575$ measurements); and MS Skoven (42 m long, $n = 17$ measurements). The measurements were taken at an average speed of 18.5 ± 1.8 km/h. We scanned the water surface constantly using binoculars to ensure that birds further away were not missed. Because escape distance



generally increases with flock size (Burger and Gochfeld, 1991; Mori et al., 2001; Kaiser et al., 2006; Schwemmer et al., 2011), we calculated the mean escape distance per individual for later use in the DVI. Escape distance per flock was also presented to allow comparisons with other studies. A considerable proportion of auks and loons cannot be identified to species level, especially at greater distances. If differences between species (e.g., red-throated loon) and their respective species group (loons) occurred, we presented both values separately to ensure that all behavioral observations were included. Only species with at least five observations were included in the analysis of escape distances. We calculated mean escape distances for a total of 22 species and species groups (loons and auks) based on 2,260 measurements. Statistical analysis was performed in R 3.2.4 using simple summary statistics (R Core Team, 2016; RStudio Team, 2016).

Disturbance Vulnerability Index

We constructed the DVI for ship traffic to reflect the total costs of disturbance, defined by three components: (1) the probability of a disturbance event based on species' shyness; (2) the energetic costs of escape of each disturbance event; and (3) the costs on the population level based on status factors. We chose eight factors as indicators of the described components:

(1) Shyness:

- Proportion of escaping birds: species with a high proportion of escaping birds flush or dive more often to escape from ships.
- Escape distance: the affected area is larger for species with a long escape distance.

(2) Escape costs:

- Proportion of swimming birds: flying is energetically much more costly than swimming (floating), and a flushing event is thus proportionally more costly for birds that seldom fly than for frequently flying birds.
- Wing loading: species differ in the energy expenditure required for reactions such as flushing or diving because of morphological and physiological differences. Birds with a higher wing loading have higher energetic costs for flushing (Norberg, 1996).
- Habitat use flexibility: disturbance may displace birds from suitable habitat. Species relying on specific habitat features thus have higher costs than species with less specific habitat preferences.

(3) Population status:

- Biogeographic population size: energetic losses, displacement, and habitat loss may increase mortality and reduce reproduction. Species with small biogeographic populations are considered more vulnerable to additional losses.
- Adult survival rate: species with high adult survival rates are more affected by additional adult mortality than species with low adult survival rates (Sæther and Bakke, 2000).
- European threat and conservation status: species with a high conservation status are considered more vulnerable to any additional pressures.

Each factor was scored on a 5-point scale from 1 (low) to 5 (high). Factors (a–c) above were based on data collected in the

present study. We used the weighted mean value of species and species group for auks and loons in factor (b), because birds could often not be identified to species level at longer distances. Factor (e) was assessed by subjective considerations based on at-sea experience by Garthe and Hüppop (2004). If data for one species was missing, we used scores for closely related species. The sources of the values for each factor and their scores are given in **Table 1**. An average score was calculated for each component and subsequently multiplied by each other to produce the DVI for each species, following the methodology of the wind farm sensitivity index developed by Garthe and Hüppop (2004):

$$DVI = \frac{(a + b)}{2} \times \frac{(c + d + e)}{3} \times \frac{(f + g + h)}{3}$$

The relationships among the three components of the DVI were investigated by Spearman's rank-order correlations in R 3.2.4 (R Core Team, 2016; RStudio Team, 2016; Wickham, 2016).

RESULTS

Behavioral Observations

Proportion of Birds Swimming

The proportion of time the birds spent swimming differed strongly among species (**Figure 3**). Grebes, seaducks, auks, and loons were detected swimming most often, with proportions ranging from 91% (red-throated loon) to 100% [red-necked grebe (*Podiceps grisegena*) and horned grebe (*Podiceps auritus*)]. Moderate proportions of great cormorants (*Phalacrocorax carbo*), gull species, northern fulmars (*Fulmarus glacialis*), and northern gannets (*Morus bassanus*) were seen swimming, while terns had the lowest proportions of swimming birds (16–23%).

Proportion of Escaping Birds

The proportion of individuals showing disturbance responses such as flushing or escape diving differed greatly between species (**Figure 4**). Overall, flushing was the most common disturbance response, with 73% of all recorded birds flushing in front of the vessel, compared with 1% that escaped by diving. Even among species capable of diving, only a small proportion of birds dived, except for Arctic loons, common murre, and red-necked grebes.

The highest total proportions of birds with observed disturbance responses were calculated for unidentified loons (96%), red-throated loons (95%), unidentified auks (94%), and black guillemots (92%), followed by red-breasted mergansers (*Mergus serrator*; 86%), common scoters (83%), velvet scoters (82%), horned grebes (80%), razorbills (*Alca torda*; 78%), and long-tailed ducks (*Clangula hyemalis*; 81%). The lowest proportions of disturbance responses were found in gull species and northern fulmars, among which black-legged kittiwakes (*Rissa tridactyla*) had the highest (32%) and black-headed gulls (*Croicocephalus ridibundus*) the lowest (10%) proportions.

There were sometimes large differences in the proportions of individuals of closely related species displaying certain behaviors; 92% of red-throated loons took flight in front of the vessel and only 3% dived to escape, while only 30% of Arctic loons took flight, and 32% dived to escape. The proportion

TABLE 1 | Data sources and scoring of factors used in the DVI.

Factor	Source	Scoring
(a) % Escaping birds	Present study: experimental disturbance, German Seabirds at Sea database (years 2016 and 2017); total proportion of birds that either flushed or dived to escape within the transect	0–20%: 1 21–40%: 2 41–60%: 3 61–80%: 4 81–100%: 5
(b) Escape distance	Present study: experimental disturbance, German Seabirds at Sea database (years 2016 and 2017); distance from the vessel in m in the moment of flushing or diving	0–200 m: 1 201–400 m: 2 401–600 m: 3 601–800 m: 4 >800 m: 5
(c) % Swimming	Present study: German Seabirds at Sea database (data from 2000 to 2017); proportion of birds swimming within the transect	0–20%: 1 21–40%: 2 41–60%: 3 61–80%: 4 81–100%: 5
(d) Wing loading	Greenewalt, 1962; Guillemette, 1994; Alerstam et al., 2007; FLIGHT 1.22 for Windows (Pennycuik, 2008)	<50 N/m ² : 1 50–79 N/m ² : 2 80–109 N/m ² : 3 110–150 N/m ² : 4 >150 N/m ² : 5
(e) Habitat use flexibility	Garthe and Hüppop, 2004	1–5
(f) Biogeographic population size	Wetlands International, 2018 Northern gannet, Northern fulmar and Auks: BirdLife International (2017); excluding Greenland, individuals were multiplied by 1.5 and breeding pairs by 3 for consistency with Wetlands International	>3,000,000: 1 1,000,001–3,000,000: 2 500,001–1,000,000: 3 100,001–500,000: 4 ≤100,000: 5
(g) Adult survival rates	Horswill and Robinson, 2015	≤0.75: 1 0.751–0.80: 2 0.801–0.85: 3 0.851–0.90: 4 >0.90: 5
(h) European threat and conservation status ¹	BirdLife International, 2017	Non-SPEC: 1 Non-SPEC ^E : 2 SPEC3: 3 SPEC2: 4 SPEC1: 5

¹ Categories after BirdLife International (2017):

Non-SPEC: species whose global population is not concentrated in Europe, and whose European population status is currently considered to be 'Secure.' Non-SPEC^E: species whose global population is concentrated in Europe, but whose European population status is currently considered to be 'Secure.' SPEC3: species whose global population is not concentrated in Europe, but which is classified as 'Regionally Extinct,' 'Critically Endangered,' 'Endangered,' 'Vulnerable,' 'Near Threatened,' 'Declining,' 'Depleted,' or 'Rare at European level.' SPEC2: species whose global population is concentrated in Europe, and which is classified as 'Regionally Extinct,' 'Critically Endangered,' 'Endangered,' 'Vulnerable,' 'Near Threatened,' 'Declining,' 'Depleted,' or 'Rare at European level.' SPEC1: European species of global conservation concern, i.e., classified as 'Critically Endangered,' 'Endangered,' 'Vulnerable,' or 'Near Threatened' at global level.

of flushed individuals was very high among black guillemots (90%), compared with razorbills (65%) and common murre (17%). In contrast, the proportion of individuals that dived was considerably higher among common murre (20%) compared with razorbills (13%) and black guillemots (2%). Horned grebes (75%) flushed more often than red-necked grebes and great crested grebes (*Podiceps cristatus*; each 46%), but red-necked

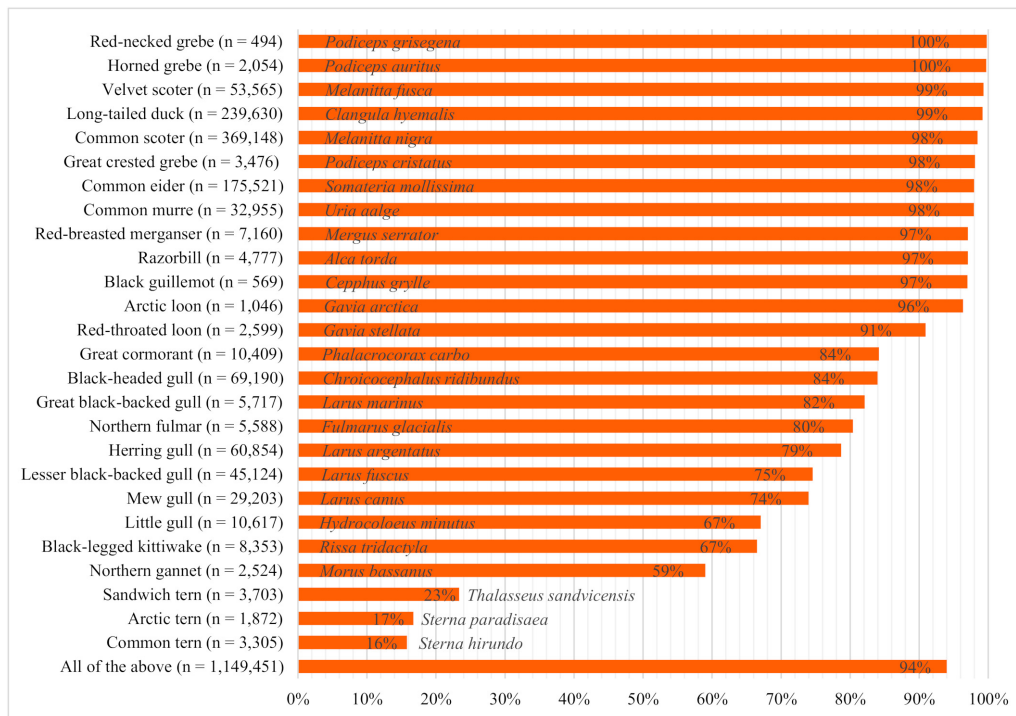


FIGURE 3 | Proportion of swimming birds observed during ship-based surveys in the German North and Baltic Seas in the years 2000 to 2017 (n = total number of individuals considered).

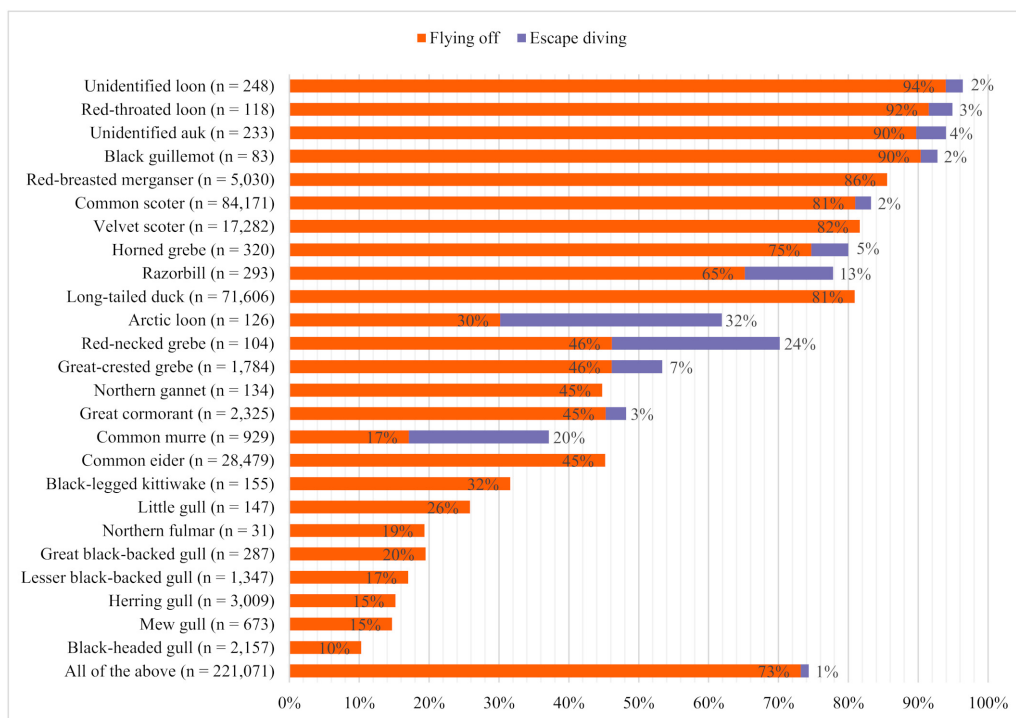


FIGURE 4 | Species-specific proportions of birds showing different disturbance responses in front of approaching research vessels in 2016 and 2017 (n = total number of individuals considered).

grebes dived more often (24%). Velvet scoters, common scoters, and long-tailed ducks showed similar proportions of flushed individuals (82%, 81%, and 81%, respectively), while the proportion of common eiders that flushed was only about half (*Somateria mollissima*; 45%).

Escape Distance

Escape distances differed widely among species. The mean escape distance per individual was higher than the mean escape distance per flock in most species (Table 2). This effect was most pronounced in red-breasted mergansers (1,178 m per individual vs. 681 m per flock) and common scoters (1,600 m per individual vs. 1,015 m per flock). Of all species, common scoters had the highest mean escape distance per individual (1,600 ± 777 m), followed by unidentified loons (1,374 ± 416 m), red-breasted mergansers (1,178 ± 617 m), red-throated loons (750 ± 437 m), unidentified auks (750 ± 379 m), and Arctic loons (721 ± 616 m). The escape distances of the remaining seabird species, razorbills, black guillemots, grebes, and great cormorants were considerably lower, with mean values between 474 ± 304 m (velvet scoter) and 221 ± 171 m (red-necked grebe). The lowest mean escape distances were calculated for gull species (lesser black-backed gull (*Larus fuscus*): 157 ± 105 m, herring gull (*Larus argentatus*): 133 ± 83 m, mew gull (*Larus canus*): 118 ± 113 m, black-headed gull: 84 ± 70 m, great black-backed gull (*Larus marinus*): 79 ± 81 m), northern gannets (127 ± 82 m), and common murres (127 ± 110 m) (Table 2). The maximum escape distance was

observed in common scoters (3,200 m). Other seabird species and loons also had high maximum escape distances between 1,500 m and 2,000 m. Seabirds sometimes flushed at a distance of around 3,000 m, but could not be identified to species level and were not included in the analysis.

Disturbance Vulnerability Index

The species differed strongly in their DVI values (Table 3). The highest values were calculated for red-throated loon, black guillemot, and Arctic loon, followed by velvet scoter, red-breasted merganser, razorbill and horned grebe. Mew gull, black-headed gull, common tern (*Sterna hirundo*) and Arctic tern (*Sterna paradisaea*) were the least vulnerable species. Rankings based on behavioral sensitivity (shyness × escape costs) and population sensitivity diverged in some cases, and we therefore presented both values separately. Behavioral sensitivity was highest in red-throated loon, common scoter, red-breasted merganser and Arctic loon and lowest in Sandwich tern (*Thalasseus sandvicensis*), lesser black-backed gull, common tern and Arctic tern. Common eider and black guillemot ranked highest in terms of population sensitivity, and common scoter, great-crested grebe, black-headed gull and Arctic tern lowest. In the DVI, common scoter thus ranked lower and common eider ranked higher than suggested based on behavioral sensitivity alone.

The scores for the three components of the index (shyness, escape costs, population status) correlated positively with each

TABLE 2 | Escape distances of seabirds in the German North and Baltic Seas.

Species	Individual		Min	Max	Flock		
	Mean ± SD	N			Mean ± SD	Median	N
Common scoter	1,600 ± 777	9,417	40	3,200	1,015 ± 727	800	591
Unidentified loon	1,374 ± 416	64	340	2,000	1,281 ± 424	1,200	40
Red-breasted merganser	1,178 ± 617	193	120	2,000	681 ± 485	500	41
Red-throated loon	750 ± 437	31	250	1,700	702 ± 348	600	21
Unidentified auk	750 ± 379	4	200	1,000	667 ± 416	800	3
Arctic loon	721 ± 616	31	80	2,000	562 ± 450	450	18
Velvet scoter	474 ± 304	1,062	30	2,000	444 ± 307	350	241
Black guillemot	417 ± 186	6	180	700	417 ± 186	410	6
Razorbill	395 ± 216	53	30	900	330 ± 219	280	23
Long-tailed duck	389 ± 227	8,274	10	1,500	325 ± 235	250	604
Horned grebe	343 ± 255	33	30	1,100	325 ± 268	265	24
Great-crested grebe	308 ± 248	58	50	900	288 ± 245	165	36
Common eider	277 ± 218	1,496	20	1,600	255 ± 195	200	290
Great cormorant	258 ± 215	187	30	1,500	287 ± 241	225	124
Red-necked grebe	221 ± 171	7	80	600	230 ± 186	175	6
Lesser black-backed gull	157 ± 105	51	30	500	159 ± 106	130	50
Herring gull	133 ± 83	115	15	300	110 ± 85	65	60
Northern gannet	127 ± 82	7	20	250	127 ± 82	120	7
Common murre	127 ± 110	86	15	500	137 ± 123	100	48
Mew gull	118 ± 113	12	20	400	118 ± 113	70	12
Black-headed gull	84 ± 70	9	20	250	86 ± 75	60	8
Great black-backed gull	79 ± 81	7	25	250	79 ± 81	40	7

Values presented for individuals and flocks for comparability reasons. Values for individuals calculated from value for flock, weighted by the number of individuals. Distances given in meters.

TABLE 3 | Factor scores and resulting Disturbance Vulnerability Index (DVI) values for 26 common European seabird species.

Bird species	a % Escaping	b Mean escape distance	c % Swimming	d Wing loading	e Habitat use flexibility	f Biogeographic population size	g Adult survival rate	h European threat and conservation status	Behavioral sensitivity ((a + b)/2) × (c + d + e)/3	Population sensitivity (f + g + h)/3	DVI
Red-throated loon	5	5	5	5	4	4	3	3	23.3	3.3	77.8
Black guillemot	5	3	5	4	5	4	4	4	18.7	4.0	74.7
Arctic loon	4	5	5	5	4	4	3	3	21.0	3.3	70.0
Velvet scoter	5	3	5	5	4	4	2	5	18.7	3.7	68.4
Red-breasted merganser	5	5	5	4	4	4	2	3	21.7	3.0	65.0
Razorbill	4	3	5	4	3	2	4	5	16.0	3.7	51.3
Horned grebe	4	2	5	4	5	5	1	5	14.0	3.7	51.3
Common eider	3	2	5	5	4	3	4	5	11.7	4.0	46.7
Common scoter	5	5	5	4	4	3	2	1	21.7	2.0	43.3
Long-tailed duck	5	2	5	4	4	2	1	5	15.2	2.7	40.4
Red-necked grebe	4	2	5	3	5	5	1	1	13.0	2.3	30.3
Great cormorant	3	2	5	3	3	3	4	1	9.2	2.7	24.4
Great crested grebe	3	2	5	4	4	4	1	1	10.8	2.0	21.7
Common murre	2	1	5	5	3	1	5	3	6.5	3.0	19.5
Northern gannet	3	1	3	3	1	3	5	2	4.7	3.3	15.6
Little gull	2	1	4	1	3	4	2	3	4.0	3.0	12.0
Great black-backed gull	1	1	5	2	2	4	5	2	3.0	3.7	11.0
Black-legged kittiwake	2	1	4	1	2	1	4	3	3.5	2.7	9.3
Northern fulmar	1	1	5	2	1	1	5	3	2.7	3.0	8.0
Sandwich tern	1	1	2	1	3	4	4	2	2.0	3.3	6.7
Lesser black-backed gull	1	1	4	1	1	4	4	2	2.0	3.3	6.7
Herring gull	1	1	4	2	1	1	3	4	2.3	2.7	6.2
Mew gull	1	1	4	1	2	2	3	2	2.3	2.3	5.4
Black-headed gull	1	1	5	1	2	1	3	2	2.7	2.0	5.3
Common tern	1	1	1	1	3	2	4	1	1.7	2.3	3.9
Arctic tern	1	1	1	1	3	2	3	1	1.7	2.0	3.3

other (Figure 5). There was a strong significant correlation between shyness (mean of factors a and b) and escape costs (mean of factors c–e) ($r = 0.81$, $p \leq 0.001$, $n = 26$). Escape costs also correlated significantly with population status (mean of factors f–h) ($r = 0.43$, $p \leq 0.05$, $n = 26$), but the positive correlation coefficient between shyness and population status was not significant ($r = 0.27$, $p = 0.189$, $n = 26$).

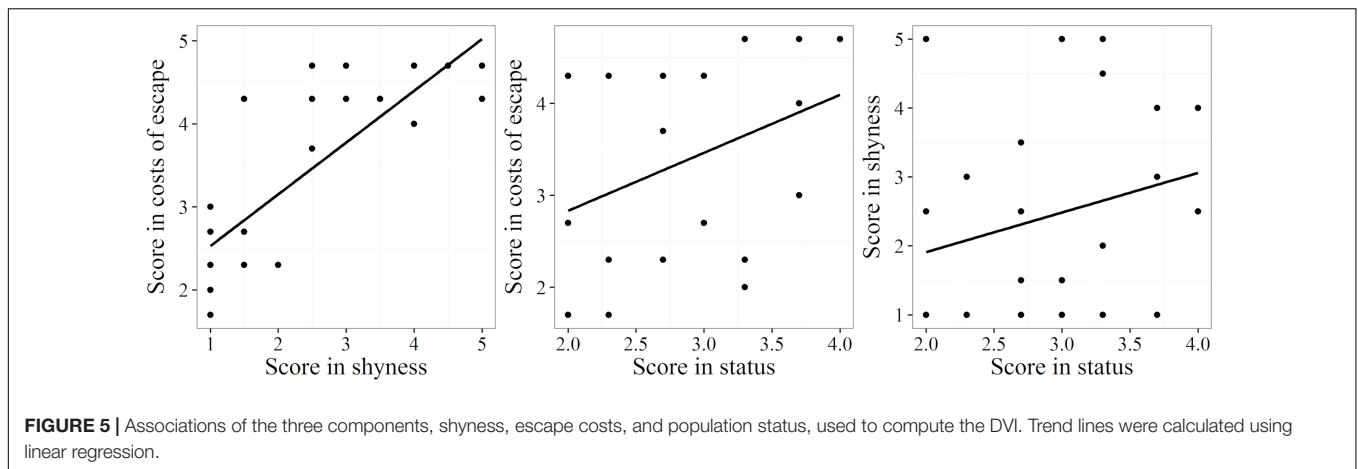
DISCUSSION

Behavioral Observations

The current study detected large interspecific differences in the proportions of swimming birds prior to disturbance, associated with species' ecology. Species adapted to diving for (relatively) stationary prey exhibited the highest percentages of swimming individuals. Flying is the energetically most demanding form of locomotion per unit time (Norberg, 1996), and can be

up to 31 times more costly than the basal metabolic rate (see Elliott et al., 2013 for an example in thick-billed murres, *Uria lomvia*). Short flights are especially costly per unit time, because take-off, ascent, and descent form a large part of the total flight time (Nudds and Bryant, 2000). Birds that rarely fly under normal circumstances thus suffer proportionally higher flight costs due to disturbance than birds that fly more frequently.

Disturbance responses to ships differed strongly among species. Species with long escape distances were also among the species with the highest proportions of escaping birds, reflecting the fact that these parameters are related and measure the same trait (shyness). However, differences between the shyest species were much more pronounced in terms of escape distances than in the proportions of escaping birds. Investigating both factors thus gave a more detailed picture of interspecific differences in disturbance behavior, and both were included as indicators for species' shyness in the vulnerability index.



The detected differences in disturbance responses among species could largely be explained by different perceptions of predation risk, and less by the cost of escape. The decision on when to take flight is the result of a trade-off between safety and feeding or other fitness-enhancing activities (Ydenberg and Dill, 1986; Lima and Dill, 1990; Frid and Dill, 2002). Birds will thus flush when the costs of remaining and escape are equal (Ydenberg and Dill, 1986). In theory, escape distance should increase with higher flight costs (high wing loadings) and higher costs due to lost opportunities (low habitat flexibility). In our study, however, species with higher escape costs were overall also those with stronger disturbance responses (except for common eider and common murre), suggesting that these species must have highly different predation risks, i.e., costs of remaining (Ydenberg and Dill, 1986), which dominated the influence of escape costs on escape distances. Birds with high wing loadings are generally less maneuverable in flight, need a longer time to take off, and thus have more difficulty escaping from predators. Many of those species are also subject to hunting by humans (Hirschfeld and Heyd, 2005; Hirschfeld and Attard, 2017), which might have increased their shyness toward human activities. In contrast, purely pelagic seabirds such as northern gannets, northern fulmars, and terns have a lower predation risk, and like gulls, often benefit from increased feeding opportunities in the presence of ships by using discards (Garthe and Hüppop, 1994; Garthe et al., 2016).

Wing loading, as an escape cost, might partially explain differences in disturbance behavior between closely related species. Common murres and Arctic loons each have approximately 30% higher wing loading than the closely related razorbills and red-throated loons (Thaxter et al., 2010; Alerstam et al., 2007; Pennycuick, 2008). Common murres had a much lower escape distance than razorbills, while Arctic loons seemed to escape slightly later than red-throated loons. We also observed fewer common murres and Arctic loons escaping compared with razorbills and red-throated loons, and a much higher percentage dived to escape instead of flying off. Similarly, the wing loading of common eiders is higher than in other seabird species (Guillemette, 1994; Alerstam et al., 2007), and the mean escape distance and proportion of birds taking

flight was considerably lower (see also Schwemmer et al., 2011). However, differences among the other seabird species cannot be explained by wing loading. The positive relationship between body mass and escape distance reported in several other studies (Blumstein, 2006; Fernández-Juricic et al., 2006; Weston et al., 2012) did also not seem to exist in the seabird species studied here. A detailed knowledge of the costs, habitat and resource uses, and predation risks for each species would be required to understand the interspecific differences fully.

We also detected high intraspecific variability in escape distance. Escape distances can be influenced by various environmental (season, weather condition, location, habitat quality, size, speed, and noise of approaching vessels, angle of approach) and individual parameters (body condition, body size, flock size, previous experiences, molting stage, state, personality; e.g., Madsen, 1985; Burger and Gochfeld, 1991; Schwemmer et al., 2011). Notably, habitat quality and the state of the individual are likely to have strong effects on escape distances, leading to differences between populations and between different life cycle stages for the same individual. For example, high habitat quality and few habitat alternatives may lead to lower escape distances because birds should avoid leaving profitable areas (Frid and Dill, 2002); however, birds feeding in a high-quality habitat might be in better body condition and thus be able to maximize their safety by flushing earlier (Beale and Monaghan, 2004a). Some species undergo a flightless period during molting, leading to reduced escape distances (own observations); however, the energy demand during this period is high and individuals are thought to be more vulnerable to disturbance (Thiel et al., 1992). During courtship, males are less prepared to leave females and breaking of pair bonds due to disturbance might have a direct negative effect on reproduction. These examples illustrate the facts that escape distances are context-dependent and thus highly variable within species, and that escape distances alone do not translate into vulnerability (Beale, 2007). Although the above parameters generated variation in our study, a recapitulation of their effects was beyond the scope of the current study. Our data were collected over a large study area and at different seasons to represent birds in different states and different habitats to allow the calculation of a mean escape distance per species, which could

serve as an indicator of the probability of disturbance responses for that species.

Common scoters and loons are known to escape at long distances in front of ships or low flying planes and helicopters (Camphuysen et al., 1999; Garthe and Hüppop, 2004; Kaiser et al., 2006; Thaxter and Burton, 2009; Schwemmer et al., 2011), but documented information on the disturbance behaviors of other species at sea is limited. The flush distances of seaduck flocks presented by Schwemmer et al. (2011) were similar to the current results, in terms of both absolute values and proportions between species, suggesting consistency of our method and a negligible observer effect (see also Guay et al., 2013). Kaiser et al. (2006) measured flush distances of common scoter flocks of 1,000–2,000 m using radar, which also falls within the range of our observations. The values for velvet scoters, long-tailed ducks, and loons given by Bellebaum et al. (2006) were not directly comparable because of the different methods used, but the ratios between species were similar to those in the present study. Flush distances at sea appear to be considerably higher than in estuarine areas (Ronconi and Clair, 2002; McFadden et al., 2017). This could be explained by habituation to vessel traffic, which is usually high in estuarine areas. Another explanation might be longer sighting distances in the open seascape. Differences in escape distances between habitats highlight the importance of studying the responses within the area of interest to define setback distances (Rodgers and Schwikert, 2002; Blumstein et al., 2003; McFadden et al., 2017) for a specific habitat.

Notably, use of the mean escape distances calculated here must take account of the fact that they were based on ships of a specific size and speed, and bigger and/or faster ships might induce longer escape distances and higher proportions of flushed birds. Furthermore, the mean escape distances were still likely to be underestimated, because birds flushing at longer distances were less likely to be detected or the species was less likely to be identified. Finally, we only measured visible disturbance responses, which are energetically the most costly reactions to disturbance. However, physiological stress responses, measurable as corticosterone levels (Cockrem, 2007; Fowler, 1999) and increased heart rate (e.g., Nimon et al., 1995), which is linked to an elevated metabolic rate (Green, 2011), commence well before behavioral changes become visible (Weimerskirch et al., 2017). Similarly, individuals might still experience stress despite behavioral habituation, as shown in penguins habituating to human disturbance (Walker et al., 2006). Thus a reduced escape distance in certain areas, which could be interpreted as indicating habituation or lowered vulnerability, might also be a consequence of limited alternative habitat. Setback distances should thus be considerably higher than mean escape distances to minimize the physiological effects of disturbance.

Disturbance Vulnerability Index

Ship traffic disturbance has been the subject of a few vulnerability indices in the past. Camphuysen et al. (1999) evaluated the behavioral sensitivity of seabird species to traffic disturbance, but did not include conservation status. In Garthe and Hüppop (2004), sensitivity to disturbance by ship and helicopter traffic was ranked by expert judgment as one factor for assessing

seabird vulnerability to offshore wind energy developments. Both these indices ordered species similarly to the current index with respect to behavioral sensitivity, highlighting the consistency and reliability of expert-based evaluations, even when different methodologies are used.

Similar to other vulnerability indices, the current DVI depends on the selected factors, the scoring system, and the relative grouping and weighting of the factors. Another limitation of our index is that it only covers species occurring in German waters, and therefore does not include some especially sensitive species such as common loon (*Gavia immer*). We therefore suggest including measurements of escape distances and records of disturbance responses from other European monitoring programs to broaden the set of species. This might also provide more information on intra-specific behavioral differences and allow adjustment of population-specific vulnerability indices to account for variations in the selected factors between populations.

For the DVI, we only chose those factors that we considered to be most relevant for estimating the total costs of disturbance, and thus gave all the chosen factors the same weight. We included behavioral factors as well as population status factors, and combined them in a systematic way to estimate the total costs of disturbance. All but one factor, habitat use flexibility (evaluated by Garthe and Hüppop, 2004), were based on real data. Habitat use flexibility was used to indicate how well a bird can compensate for the cost of lost opportunities. Feeding time needed to meet energetic requirements would be a meaningful additional indicator for the ability to compensate for losses (Mayhew, 1988; Madsen and Fox, 1995; Wisniewska et al., 2016). However, integration of this factor in the index would require a detailed knowledge of the species' activity budgets, including activity at night, and time needed for digestion and recuperation from diving. Although such information can be obtained from telemetry studies, it is not yet available for most species. The application of telemetry data in behavior-based and individual-based models also helps to improve predictions regarding the impacts of disturbance on habitat use, survival, and reproduction (Goss-Custard et al., 2006a). However, even sophisticated modeling techniques may not be able to describe the whole complexity of the interactions between wildlife and humans (May et al., 2019). We therefore consider that vulnerability indices like the one presented here provide the best available solution for assessing the potential vulnerabilities of a large set of species.

Relationship Between Shyness and Vulnerability in Seabirds

Cross-species comparisons and the systematic combination of disturbance-related factors within the DVI also allowed us to draw conclusions about the general relationships among shyness, escape costs, and disturbance vulnerability in seabirds. Theoretical considerations and experimental evidence suggest that visible disturbance responses alone are generally not a good indicator of vulnerability, because birds in good body condition and with sufficient feeding alternatives should flush

earlier than birds short of resources (Gill et al., 2001; Frid and Dill, 2002; Beale and Monaghan, 2004a). In contrast to the expected situation however, shyness and escape costs were positively correlated in the present study. Escape costs also correlated positively with population status, such that several species ranked high in all three factor groups of our index. Among the species studied here, the shyest thus also seemed to be the most vulnerable. We propose that, while escape distance is not a good indicator of vulnerability of individuals within the same species, it may serve as an indicator of vulnerability within a range of species. This is in line with Møller (2008) and Møller et al. (2014), who found that long escape distances were associated with population declines among European and Australian birds. A better understanding of the relationships among shyness, escape costs, and population status might have important implications for conservation management. The next step should thus be to carry out further investigations based on the emerging patterns for seabirds using an extended set of species and possibly populations.

The Dimension of the Problem

Escape costs do not comprise only direct energetic costs and reduced energy uptake through lost time for feeding (Owens, 1977; Bélanger and Bédard, 1989); flushed birds might also be displaced from the best feeding resources (Madsen, 1998; Madsen and Fox, 1995). Altered distribution patterns within shipping lanes (Schwemmer et al., 2011) and in relation to vessel traffic to and from offshore wind farms (Mendel et al., 2019) have already been demonstrated in loons. We observed many common scoter flocks flying so far away after flushing that they could not be seen resettling before moving out of sight. Schwemmer et al. (2011) found that most common scoters did not return within 3 h after disturbance by a vessel, while common eiders and long-tailed ducks returned to pre-disturbance numbers within one to 3 h after disturbance. This suggests that very shy species may abandon an area completely, while others may suffer temporary habitat loss.

If birds cannot compensate for energetic losses, disturbance will affect body condition, reproduction, and survival (Madsen, 1985; Goss-Custard et al., 1995a,b, 2006a,b; McHuron et al., 2018). Ducks and geese have been observed feeding at night to compensate for being disturbed during the day (Bélanger and Bédard, 1990; Knapton et al., 2000; Merkel et al., 2009) and shorebirds were shown to increase feeding rates to compensate for lost feeding time (Swennen et al., 1989; Urfi et al., 1996). However, feeding rates and times cannot be extended limitlessly. The time needed to meet energetic requirements determines by how much feeding rates can be increased.

Seabirds might be able to habituate and even adapt to disturbance by ship traffic, if they were able to identify vessels as non-threatening objects. Habituation of birds to particular types of disturbance and within certain areas has been documented before (Smit and Visser, 1993; Samia et al., 2015). For example, among waterbirds, snow geese became accustomed to gunfire (Bélanger and Bédard, 1989) and common

eiders and long-tailed ducks showed reduced flush distances within shipping lanes (Schwemmer et al., 2011). However, ships differ greatly in size, shape, speed, and engine noise, making recognizing them as non-threatening objects difficult. Furthermore, waterbirds are hunted using motorboats in some parts of Europe (Laursen and Frikke, 2008). In an environment where predation risk exists, either from natural predators or human activity, birds are thus likely to regard big moving objects as potential threats, and the potential for habituation among sensitive species seems very limited under the current conditions. Notably, even after decades of intense ship traffic in European waters, most species still reacted strongly to our experimental disturbance.

CONCLUSIONS AND RECOMMENDATIONS

This study provides further evidence for the disturbance effects of ship traffic on seabirds, and additional information on the species-specific responses. We present the first comprehensive set of data on escape distances and relative numbers of escaping birds, covering most seabird species found in Northwest European waters. Our findings are based on extensive field experience and data sets from up to 17 years of behavioral observations of seabirds at sea. We show that species differ strongly in their disturbance responses. Our DVI is based on a comprehensive set of variables and addresses a wide range of disturbance-related aspects of bird ecology. It allows for objective quantification of species' vulnerability to ship traffic disturbance. It identified red-throated loon, black guillemot, Arctic loon and velvet scoter as the most vulnerable species to ship disturbance, and common and Arctic tern as the least vulnerable. The shyest seabird species also had the highest escape costs and seemed to be the most vulnerable.

The strong reactions of several species to disturbance by ships have important management implications. Because most human activity at sea involves vessel movements, their effects should be considered more comprehensively in environmental impact assessments and conservation planning. Our DVI can be used to inform marine spatial planning, conservation management, and impact assessments to identify and prioritize the most vulnerable areas in a practical way: The values given here can be multiplied by rasterized species abundances and then summed over all species in a raster cell to produce vulnerability maps (see Garthe and Hüppop, 2004; Sonntag et al., 2012 for examples). Following this, a possible management solution would be to implement low-disturbance or disturbance-free zones in some marine protected areas (von Nordheim et al., 2006). An alternative option in other vulnerable areas could involve the spatial and temporal coordination of ship traffic, which might be especially relevant in areas where ship traffic has increased dramatically as a result of the construction and maintenance of offshore wind turbines. The displacement of sensitive seabirds from wind farm areas has been shown to be a combined effect of the wind farm itself and the associated ship traffic, but these effects are difficult to separate (Mendel et al., 2019). Our study

demonstrated strong reactions to ships alone, emphasizing the importance of minimizing wind farm-associated ship traffic in order to achieve an environmentally friendly transition to the use of renewable energies. Vulnerability maps produced using our DVI can be applied in this context to identify the most suitable corridors.

Ship traffic might also have to be included in single-species action plans as a relevant threat to declining seabird species identified as most vulnerable to ship traffic disturbance (see Wildfowl and Wetlands Trust, 2015 for an example of a species action plan under AEWa). The mean flush distances for such species reported in this study can be used to develop species-specific conservation measures, such as setback distances from important feeding and resting sites. In this context, the setback distances should be longer than the mean escape distances in order to minimize the behavioral and physiological effects of disturbance. Setback distances might also be necessary with respect to human activities in the vicinity of marine protected areas to conserve their proposed function as refuges for vulnerable species.

Clearly, the effects of disturbance events by ships are cumulative and equate to net habitat loss (see also Madsen and Fox, 1995). If regulation of ship traffic is applied as a management tool, threshold levels are needed above which species' abundance will be significantly reduced. The results of this study highlight the fact that these thresholds will be species-specific, and need to be investigated further.

ETHICS STATEMENT

Data collection was carried out within the German Marine Biodiversity Monitoring and did thus not require approval of an ethics committee.

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AUTHOR CONTRIBUTIONS

KF and SG contributed to conception and design of the study. PS developed the methodology for measuring escape distances. NM and SG organized the database. KB, KF, NG, and NM conducted field work and recorded data. KF performed the analysis and wrote the first draft of the manuscript. KB, NG, NM, PS, and SG provided critical revision and discussions, and corrected the manuscript. All authors contributed to manuscript revision, and read and approved the submitted version.

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