



## Research article

## Impact of disturbance on common scoter carrying capacity based on an energetic model

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## ABSTRACT

Shallow coastal zones are intensely used by humans but simultaneously are biodiversity hotspots, with a crucial role in the life cycle of many marine species. The competition for food or space between humans and protected wildlife intensifies under pressure of an increased need for marine resources for human consumption. For successful management it is important to establish the key components driving such conflicts of interest. Here we focus on the protected common scoter (*Melanitta nigra*), a sea duck wintering in coastal habitats that are rich in food, but also among the most disturbed marine systems worldwide. Due to the scoters' shyness disturbance impacts the birds' ability to forage and poses a conflict for balancing bird conservation and economics, including a fishery on its main bivalve prey *Spisula subtruncata*. In this study, we use an energy budget model to quantify the consequences of depth, currents and disturbance on scoter energetics and carrying capacity. Energetics were described using physical parameters and field data on food availability and disturbance. Results reveal non-linear relationships and a threshold value for when a scoter can no longer maintain its energy balance. This is caused by limited foraging time, rather than food availability. From a conservation perspective, this implies that a precautionary principle should be used, because there will be no warning when an area becomes unsuitable. In addition, the model was applied to study the effects of disturbance from different kinds of shipping in a coastal area of the North Sea, north of The Netherlands. Cargo shipping has the largest impact on the carrying capacity, where there is spatial overlap of prey and an intensively used shipping lane. In other prey distribution situations shrimp vessels may cause most disturbance. *Spisula*-Ensis fisheries did not limit the potential carrying capacity due to the limited catches and number of fishing trips. Scoter protection should be aimed at flexible spatial management and on only those vessel types above a *Spisula* bed with a large number of trips, and above all should work from a precautionary principle given the critical thresholds for scoter presence.

## 1. Introduction

Shallow coastal waters, in the vicinity of densely populated areas, are, in many cases, intensively used by man, while at the same time these are often biologically rich and important sites for nature conservation. With increasing interest for conservation of biodiversity, and increasing demands for food to feed expanding human populations, challenges arise to fish these waters, while keeping sufficient resources and space, for wildlife (e.g., Cury et al. (2011)). Many studies deal with direct competition for resources between humans and wildlife, such as the competition for forage fish and the demonstrated effects on

reproduction and survival (e.g., Cook et al. (2014)). In addition to advocating prey biomass reservations for seabirds (Cury et al., 2011) there has been an increased focus on the spatial aspect of prey availability, for example in relation to seabird breeding sites to increase the efficiency of protective measures (e.g., Hentati-Sundberg et al. (2021)). Only few studies deal with indirect interactions such as disturbance (e.g., Fliessbach et al. (2019)). The increasing demand for marine spatial planning is especially challenging in crowded coastal areas and the Dutch coastal zone provides a valuable case study to test the impact of different sources of disturbance on an internationally protected seabird, the common scoter (*Melanitta nigra*). Under Dutch national legislation

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the conservation status of scoter wintering habitat is seen as rather unfavourable and conservation efforts aim to maintain a carrying capacity of 68,500 wintering individuals (Ministry of Agriculture Nature and Food Quality, 2008). However, although this number of wintering ducks was reached 6 times in the years 1993–2004 since the start of monitoring in 1993, it was only reached once in the years 2005–2021 (Sluijter et al., 2021).

Common scoters are charismatic sea ducks that form large wintering flocks along the eastern Atlantic seaboard. The ducks are protected under the EU Bird Directive (79/409/EEC) and largely feed on bivalve shellfish, which also serve as human food. The ducks migrate annually from their northern breeding areas to more temperate coastal zones to spend the non-breeding season. From late summer to late spring they form large flocks along the coasts of western Europe and NW Africa, ranging from Norway, Iceland and the Baltic Sea to Mauritania (Leopold and Skov, 1997). These coastal waters are among the most disturbed marine habitats by human activities and common scoters are, after centuries of being hunted, wary birds that have large escape distances from approaching vessels (Fliessbach et al., 2019). The combination of its shyness, winter habitats in shallow yet disturbed areas and its protective status creates a need to address potential threats for common scoters in their preferred wintering areas.

Statistical models relate scoter presence with food abundance (Kottsieper et al., 2019) and the absence of disturbance (Kaiser et al., 2006; Zuur et al., 2014). These studies found that low numbers and absence of scoters in areas with high food density could be explained by disturbance. This implies that the needs of common scoters during winter include prey-rich, shallow coastal habitat with little disturbance: daily energy requirements cannot be met if the prey base is too poor, or poorly accessible either through environmentally unfavourable conditions (such as too deep waters) or frequent disturbance. In a study where disturbance did not play a role, prey abundance and depth explained most of scoter presence (Schwemmer et al., 2019), but the additional impact of disturbance on the foraging possibilities of these ducks remains poorly studied.

The nearshore waters along the Dutch coast, north of the Wadden Sea Islands are known for their high numbers of scoters (Leopold et al., 1995; Sluijter et al., 2021), and their association with *Spisula subtruncata* beds (Ens et al., 2006; Skov et al., 2008; Tulp et al., 2010). Population dynamics of *Spisula subtruncata* exhibit large temporal variations, mainly associated with stochastic recruitment (Arzel and Elmberg, 2015; Baptist and Leopold, 2009; Cardoso, Witte, and van der Veer, 2007; Troost et al., 2021). In recent years a large *Spisula* bed has formed north of the island of Ameland which attracted tens of thousands of scoters. In these coastal waters ducks encounter many sources of human disturbance, such as fisheries, both by a variety of beam trawlers, fishing for shrimp and a mixed demersal fish assemblage, and by vessels fishing for the same organisms the ducks go after: *Spisula subtruncata*. The latter commenced again in autumn 2018 after almost 2 decades without *Spisula* fishing (pers. comm. B. Keus). Large merchant ships are bound to a shipping separation system, immediately seaward of the –20 m isobath, but smaller vessels, including coasters, are free to sail closer to shore. In addition, large vessels are involved in sand extraction and coastal nourishment in the same area to combat the effects of sea level rise on the coastline. To address the effects of the different sources of disturbance on common scoter presence in the area we used anonymized Automatic Identification System (AIS) data to map disturbance, and an individual-based model describing scoter energetics in detail. The AIS data allowed us to distinguish between vessel types, such as fishing, shipping or dredging, while the scoter model assesses the energy needs and energy gains from foraging with a strong base in physics, based on the model of Brinkman et al. (2002) and the reviews of Kaiser (2002) and Krijgsveld et al. (2008) who focussed on disturbance. This approach is not a statistical scoter model such as presented by Zuur et al. (2014) or Schwemmer et al. (2019), where generalized additive models (GAM) and generalized linear models (GLM) were used to predict scoter

presence based on food and abiotic parameters. The mechanistic approach used here calculates energy income and expenditure to assess if there is a net gain or a net loss of energy, given food availability and abiotic conditions.

The model was first applied to a single bird with *ad libitum* food to assess the effects of depth, current velocity and disturbance on its energetics and time budget. After this sensitivity analysis for a single duck we assessed the effects of depth, current velocity and disturbance on the potential carrying capacity at realistic food densities for a standardized surface area. Finally, we applied the model to the North Sea coastal waters to assess the relative impact of the different sources of disturbance in the main wintering area of common scoters in The Netherlands (Fig. 1), with *Spisula subtruncata* as prey. We did so by comparing three winter seasons using *Spisula* densities and scoter numbers based on survey data, ambient abiotic conditions (meteorological information and depth) and disturbance in the area based on vessel movement.

## 2. Methods

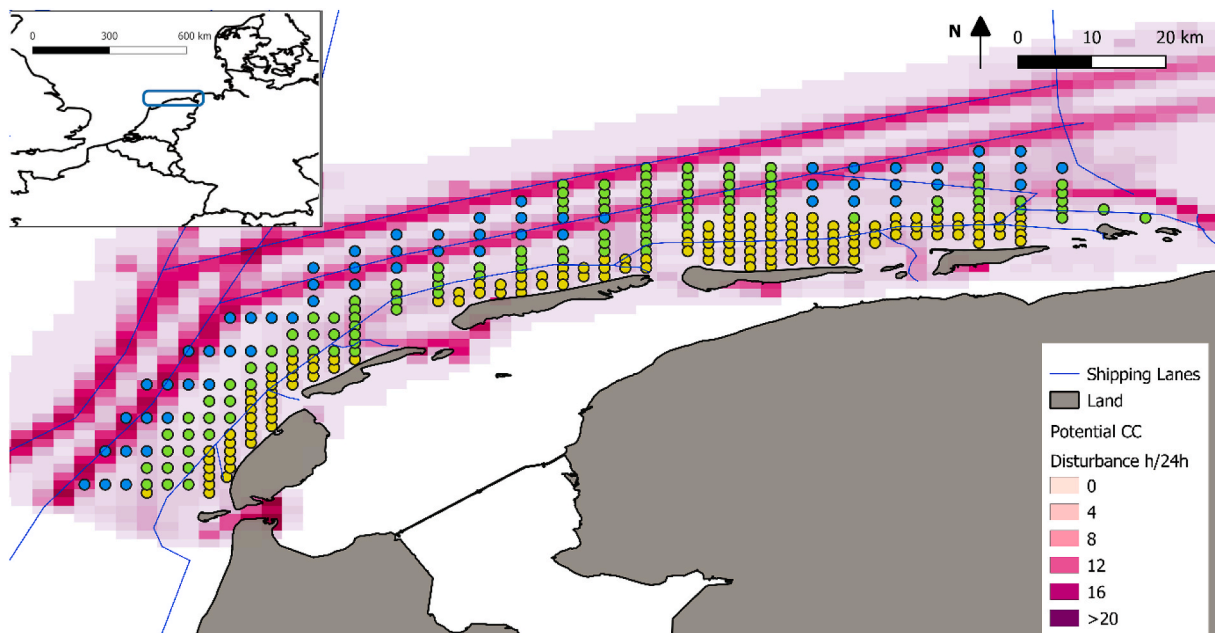
The model is based on an energy as well as a heat balance for an individual bird (Brinkman et al., 2002), named SCOTERS. Activity of the bird may or may not affect these balances. Heat is gained by digestion and muscle action while heat is lost to the environment (air and water) and by the heating of ingested benthic prey from ambient to body temperature. Energy can be gained from ingested prey, while all activities cost energy, including those for finding and handling prey. We acknowledge that this is a simplification. Social behaviour, such as courting, is not included in the model. A general description is given below while a detailed description including equations is given in the appendix.

### 2.1. Daily energy expenditure, food consumption and losses

A duck must perform different activities: flying, active swimming, diving and resting after a dive (always at sea in this species in the non-breeding season), and dealing with prey. Flying occurs when birds need to return to the feeding grounds, after they were displaced by tidal or wind drift (e.g., Fijn et al. (2017)), or in response to disturbance. Swimming is needed to stay at the feeding grounds while countering drift by the current. Diving is needed to obtain food and requires costs to counter drag and buoyancy forces during descent and foraging at the sea floor. After each dive a duck rests, resting is therefore considered as part of a dive. Dealing with prey includes searching and handling but also crushing shells in the muscular gizzard (Nehls, 1996) and digestion.

The model is based on the simplifying assumption that a duck needs to maintain its body mass and thus has to assure a net zero energy balance for survival and leaves if this condition is not met. The model makes an assessment of energy available from food and the energetic costs of getting and dealing with food. For each prey length class the profitability is a function of prey density and quality. First, net profitability per prey length is defined as the amount of energy a duck can get out of one prey based on its flesh content, divided by the time needed to catch and process that prey during a dive (in  $\text{Js}^{-1}\text{prey}^{-1}$ ). This profitability per prey of a given length is multiplied by its density, resulting in the food value density of the area ( $\text{Js}^{-1}\text{m}^{-2}$ ). Prey is swallowed and this mass is heated to body temperature. The flesh is digested with a conversion efficiency and provides energy. There is a digestion cost due to enzyme production incorporated in the assimilation efficiency (Table 2). There is also a cost to excrete the salt that was ingested with the prey, which is based on the water content of the prey. The shell of the prey needs to be crushed to obtain the flesh and in order leave the gut as faeces. Faeces production itself is not a cost term.

All heat losses and gains and all energy costs and gains are summed to yield the net energetic gains per dive, given the depth, water temperature, disturbance and food to be consumed. A net heat loss requires energy for heating. Based on the heat and energy balance, and the net



**Fig. 1.** Area of interest with the coastline, with disturbance indicating the major shipping lanes and the location of the benthos sampling stations. The sampling stations differ in the surface area they represent, with a finer grid closer to the coast (5.3 km<sup>2</sup>; 11 km<sup>2</sup>; 21 km<sup>2</sup>). Disturbance is the mean disturbance of all fleets for the three winter seasons (2017–2018, 2018–2019 and 2019–2020) combined. Small onset: Map of western Europe and in the blue rectangle the area of interest. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

gain per dive, the number of dives needed to fulfil the demands can be calculated for a given prey landscape (prey size and densities). The time needed per dive is a function of depth. This time needed for descent and ascent, searching and handling prey, digesting and recovery determines the possibility for a duck to cover the daily expenditure. We also assume that a bird does not spend more than 80% of a 24 h day on foraging, allowing nocturnal feeding if needed. Common scoters have been recorded above a *Spisula* bank in this particular area at night (Dirksen et al., 2005), but more information on nocturnal behaviour would improve parameterization. This 80% is the maximum time and does not have to be met. However, time spent flying, swimming or being disturbed is a loss to the time a bird has for foraging. This restricts the maximum number of dives per day a duck can make given the circumstances. If the time needed to get enough food exceeds the allowed foraging time the net energy gain is negative and a duck cannot fulfil its energy demand. The number of birds that sustain themselves on the (declining) resource throughout a full winter season with a non-negative net energy is the estimated carrying capacity.

## 2.2. Prey

Common scoters have a flexible diet (Fox, 2003) but are, in Dutch coastal waters, often associated with beds of *Spisula subtruncata* or *Ensis leei* (Leopold et al., 1995; Tulp et al., 2010). The model deals with one prey species, with the benefit that prey species-specific information can be used, rather than interspecific averages. For this study, *Spisula subtruncata* was used as prey because over the years, in the area of interest scoters were mostly associated with *Spisula* beds and not with other potential prey species (personal observation MFL).

A modelled winter starts in September and ends in April the next year. Food density data are based on the Wageningen Marine Research yearly benthos monitoring before September. Prey density decreases due to consumption during the modelled winter season. This benthos survey is part of the statutory task related to Dutch legislation in shellfish fisheries management and has been carried out since 1995 along the Dutch coast, following a stratified approach (Tulp et al., 2010). For this study data from 2017, 2018 and 2019 were used, covering the area north

of the Dutch Wadden Sea islands (Fig. 1). Samples were taken with a trawled dredge with a 5 mm sieve and sorted. All *Spisula* in the samples were measured to the nearest mm (Perdon et al., 2019; Troost et al., 2021). For each sampling station we calculated *Spisula* densities per 5 mm size class (number m<sup>-2</sup>), while water depth was measured at the time of the haul. The surface area of the grid cell in which the sample was taken was calculated post-hoc. The size of the study area is about 3300 km<sup>2</sup>.

## 2.3. Disturbance

Disturbance was estimated using Automatic Identification System (AIS) data of all vessels in the area larger than 15 m, for which the system is mandatory (Burger et al., 2019). AIS transposes ships' geographic positions to announce their location to other ships and the Dutch coast guard. An identification field Maritime Mobile Service Identity (MMSI) and a time stamp are included in the signal. The coast guard forwards all signals to MARIN (Maritime Research Institute Netherlands). This institute made the data anonymous and accessible for research purposes. Vessel types were identified by linking the MMSI identification field to ships databases (Lloyds and Samson), which lead to the identification of the ship types 'cargo', 'dredging', 'recreation', 'fishing' and a rest category. Identification of different fishing fleets was done by MARIN with information from the Vessel Monitoring Data (VMS) information provided by Wageningen Marine Research (Hintzen et al., 2012). Fishing vessel subtypes identified were 'shrimp', 'Ensis-*Spisula*' and 'other'. MARIN could then provide an anonymous database for seven "fleets" (Table 1).

We assume a 1 h period before disturbed birds return to the area and resume feeding and a distance of 1 km from a vessel at which the scoters would fly away from the area (Krijgsveld et al., 2008). Calculation of the disturbance caused by vessels was performed on a spatial grid based on the benthos sampling grid, with dimensions of 1 min north (1.852 km) and 2.5 min east (2.728 km), for the complete study period in 3-min time intervals. This interval was chosen to prevent AIS signals of ships skipping a grid cell when sailing. For every 3-min interval, all AIS data were selected up to 1 h back in time. The selected AIS data points were given a

**Table 1**

Effect of excluding distinct disturbance sources in the study area for each winter period on total disturbance, with disturbance expressed as mean hours of disturbance per 24 h. The mean and SD of disturbance are calculated using the AIS data with all vessel types causing disturbance *minus* the AIS data without the selected type. The statistics are taken over all benthos sampling points for the appropriate winter period.

Excluded disturbance source	Mean disturbance (h 24h <sup>-1</sup> ), SD (in brackets) and % reduction in mean disturbance compared to all fleets combined		
	2017–2018	2018–2019	2019–2020
Shrimp fishing	2.6 (3.6) 19.5%	2.9 (3.9) 21.6%	2.9 (4.4) 17.3%
Ensis and spisula fishing	3.2 (3.4) 0.6%	3.7 (3.7) 0.3%	3.5 (4.3) 0.01%
Fishing other	3.0 (3.4) 6.7%	3.5 (3.7) 4.6%	3.0 (4.2) 4.3%
Cargo shipping	1.7 (1.7) 47.7%	1.9 (1.7) 48.2%	1.7 (1.7) 49.5%
Dredging	3.0 (3.4) 7.5%	3.6 (3.7) 6.1%	3.3 (4.3) 11.9%
Recreational	3.1 (3.5) 3.4%	3.6 (3.7) 2.9%	3.3 (4.3) 3.2%
Rest category (e.g., ferry)	3.0 (3.4) 7.8%	3.4 (3.7) 9.1%	3.3 (4.3) 6.0%
	Mean disturbance and SD (in brackets)		
All sources	3.3 (3.44)	3.76 (3.7)	3.5 (4.3)

1000-m radius and combined into one spatial polygon. The percentage overlap of the spatial polygon with each grid cell was calculated and multiplied with the part of the day the calculation stands for (i.e. 3 min interval means 3 out of 1440 min, or 0.002083 day). For each grid cell and each day, the total time disturbed was calculated by summation of the 3-min disturbances per grid cell in 24 h, from which the monthly means per grid cell were derived, expressed as mean hours of disturbance per 24 h (Fig. 1). In order to isolate the effect of each vessel type on the total disturbance, calculations are done for all vessels (acting as a baseline) as well as for all vessels minus the vessel type of interest. This resulted in nine disturbance scenarios based on the identified vessel types (see Table 1): one without disturbance, one with all types included, given background disturbance from the other fleets (see Table 1): one without disturbance, one with all fleets included, and then seven scenarios with one fleet excluded from the AIS analysis. By excluding a vessel type disturbance will not be reduced if other vessel types are present in an area. The exclusion approach assesses the effect of fleet type exclusion from a bird's perspective. Disturbance values were assigned to each benthos sampling grid cell. Note that disturbance varies strongly between grid cells (Coefficient of variance = 1.04) and

less so in time (Coefficient of variance = 0.39) (all sources of disturbance and three winters combined), confirming the variability of the spatial pattern (Fig. 1) and annual stability.

The cost of disturbance is twofold. Not only is there an energy costs of flying away from and returning to the feeding grounds, there is also the time lost that otherwise could have been spent on foraging leading to a reduced energy gain. Note that the effect of *Ensis* and *Spisula* fishing only relates to disturbance and not to a decrease in prey density in the model.

#### 2.4. Parameter values

Scoter parameter values are listed in Tables 2 and 3 and are described below in more detail. There is no information on seasonal patterns in total body mass of the common scoter. We therefore used information from scaup (*Aythya marila*) as common scoter and scaup have a similar pattern of habitat use in The Netherlands and have similar diets, body mass and phenology. We used data on lean mass and seasonal changes in fat mass from scaup reported by De Leeuw (1997) to generate the relative seasonal change in body mass for common scoter, as required by the model (Table 3). As benchmark for the seasonal pattern we use the mean of male and female scoter average mass given by Durinck et al. (1993) for March. We use this body mass benchmark because these data are from healthy birds that drowned in fishing nets. Results of the seasonal scaling of mass and the mean for the winter period used in the model are provided in Table 3.

Basal Metabolic Rate (BMR) for the common scoter was assessed to be 3.8 W/kg using the relationship from Aschoff and Pohl (1970) and a lean biomass of 0.73 kg of starved scoters reported by (Cramp and Simmons, 1977) (Table 2). BMR was then multiplied with body mass to calculate the absolute cost in J, which varies seasonally.

Cost of flying is based on the information available for tufted duck (*Aythya fuligula*) and scaup from De Leeuw (1997), by interpolating the costs (68 W for a 1 kg tufted duck and 84 W for a 1.3 kg scaup using an average mass of 1270 kg, yielding 81 W (conform Kaiser (2002)). For each month the cost of flying is calculated based on body mass. The flying time per day is a function of disturbance and compensation for drift by currents. Half of the drift is assumed to be compensated by flying and the other half by swimming. We use a flying speed of 75 kmh<sup>-1</sup> (Christensen et al., 2004). We use monthly mean velocity data to assess the drift.

Ducks stop swimming to compensate for drift when the current velocity exceeds 0.7 ms<sup>-1</sup> (Prange and Schmidt-Nielsen, 1970; Woakes and

**Table 2**

List of scoter parameter names, values, units, description and references.

Name	Value	Unit	Description	References
BMR	3.8	Wkg <sup>-1</sup>	Basic metabolic rate	Cramp and Simmons (1977), De Leeuw (1997)
Flycost	62	Wkg <sup>-1</sup>	Energetic cost of flying	Based on De Leeuw (1997) and the estimated mean mass of scoter
FlySpeed	21	ms <sup>-1</sup>	Flying speed	Christensen et al. (2004)
Flytime	Variable	sd <sup>-1</sup>	Flying time per day	based on drift and disturbance
Swimcost	7.2	Js <sup>-1</sup>	energetic cost of swimming	based on Prange and Schmidt-Nielsen (1970)
Swimtime	variable	sd <sup>-1</sup>	Swimming time per day	based on drift
SwimmingSpeed	0.5	ms <sup>-1</sup>	Swimming speed	(Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983)
DivingSpeed	0.9	ms <sup>-1</sup>	diving speed on descent	Kaiser (2002)
DivingSpeedAmpl	0.1	ms <sup>-1</sup>	amplitude of diving speed	estimate
DivingAmplFreq	3.8	s <sup>-1</sup>	stroke frequency when diving	Richman and Lovvorn (2008)
BottomSpeed m/s at bottom	0.1	ms <sup>-1</sup>	speed at the bottom	Estimate AG Brinkman
BottomSpeedAmpl	0.2	ms <sup>-1</sup>	amplitude of speed at the bottom	estimate
BottomAmplFreq	3.2	s <sup>-1</sup>	stroke frequency when at the bottom	Richman and Lovvorn (2008)
Lung volume constant	1.61	–	Lung volume is calculated as	Lasiewski and Calder (1971)
Lung volume exponent	0.91	–	1.61Mass <sup>0.91</sup>	Lasiewski and Calder (1971)
EnergyCont	22500	JgdW <sup>-1</sup>	Energy content of scoter	Brinkman et al. (2002)
Search time	4	s	Search time at the bottom	Brinkman et al. (2002)
Handling time	4	s	Handling time	Brinkman et al. (2002)
Assimilation efficiency	0.7	–	Food Assimilation efficiency	Brinkman et al. (2002)
Friction factor	0.15	–	Friction factor for drag force	Brinkman et al. (2002)
Grid cell size	1e6	m <sup>2</sup>	Standard area size	



**Table 3**

Body mass values of scoter in gram used in the model. Note that the birds are not present in significant numbers in the Dutch coastal zone from June until September.

Body Mass	value	Reference
January	1326	Seasonal scaling based on lean mass and seasonal change in fat ratio of scaup (De Leeuw, 1997) and fitted to match scoter data (Durinck et al., 1993).
February	1292	
March	1271	
April	1300	
May	1312	
October	1165	
November	1193	
December	1298	
Season	1270	
Average		

Butler, 1983). We assume that this also holds as threshold for swimming below water and that foraging ceases at higher current velocities, which results in a zero-energy gain. Below this threshold swimming time is based on the time needed to overcome half of the drifted distance. This assumption was made to prevent swimming from taking up most of the time in a day, leaving no time for foraging. Swimming speed was set at  $0.5 \text{ ms}^{-1}$  assuming it to be the most cost-efficient speed with a cost of  $7.2 \text{ Js}^{-1}$  (Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983).

Swimming underwater when diving for food has additional costs because of drag. The drag force underwater was estimated using fluid mechanics. Based on the frontal aspect of a living bird, taken as a sphere, when the speed relative to the fluid equals the diving speed ( $v$ ), the drag force  $F = f(0.5 \rho v^2)(0.5\pi D^2)$ , with  $f = 0.15$ , the friction factor;  $\rho = 1020 \text{ kgm}^{-3}$ , the specific mass of the fluid;  $v = 0.5 \text{ ms}^{-1}$ , the speed; and  $D = 0.15 \text{ m}$ , the diameter of the duck, projected as a disc perpendicular to the flow direction (Brinkman et al., 2002).

Kaiser (2002) provides an overview of vertical diving speeds with an average of  $0.9 \text{ ms}^{-1}$  over a range of species. We use this average value of  $0.9 \text{ ms}^{-1}$  for our model. Stroke frequency from the closely related and similarly sized white-winged scoter *M. deglandi* was used (body mass  $1.092 \text{ kg}$ ; Richman and Lovvorn (2008) (Table 2).

We assume that the ducks could spend a maximum of 80% of their time foraging, leaving a minimum of 20% for resting, preening etc. Time needed for swimming and flying based on drift and disturbance duration is subtracted from the maximum foraging time. The maximum foraging time is hence limited based on specific circumstances. The amount of time actually spent on foraging is the result of energy demand and food availability. In favourable circumstances there may be time left unaccounted for in the time budget.

For the prey species allometric relationships were taken from literature or fitted on data. Total mass, ash-free dry weight (AFDW), and shell mass were calculated as functions of length (Table 4). The mass of water within a prey item, needed to calculate the cost of salt excretion, is calculated as the total mass minus shell and ash-free dry weight. Ash-free dry weight is scaled per month, reflecting the seasonal change in the condition of the animal (Cardoso, Witte, and van der Veer, 2007). It is assumed that the scalar for AFDW is 1 during June and July and drops to 0.5 in January and February, increasing again to 1 in summer.

In addition to these different mass compartments, the cost of crushing the shell is needed on a length base. The power needed for crushing *Spisula subtruncata* shells as a function of shell length was based on experiments of bivalves inhabiting the coastal zone (taken from Fijn et al., 2017) (Table 4).

The crushing power needs to be converted into the energy it costs in order to use it in the duck energy budget. Both Nehls (1996) and Piersma et al. (1993) provide an allometric relationship for crushing as a function of mussel size (*Mytilus edulis*). Based on Nehls (1996), who provides crushing energy (J) and on Piersma et al. (1993) who provide crushing power (N) for the same species, we calculated the conversion factor between energy and power, assuming that the crushing energy is

**Table 4**

The allometric relationships for *Spisula subtruncata* to calculate gains and costs when dealing with prey, as function of shell length (mm) with the form  $\log_{10}(X) = a + b \log_{10}(L)$ , where X can be mass (g), AFDW (g), shell mass or crushing power (N).

Function	a	b	R <sup>2</sup>	df	P	Reference
Length-Mass	-3.747	3.045				Cardoso, Witte, and van der Veer (2007)
Length-AFDW	-4.6	2.822	0.942	459	<0.0001	WMR data
Length-Shell mass	-3.599	2.687	0.968	101	<0.0001	WMR data
Length-crushing power	-0.213	1.559	0.833	549	<0.0001	WMR data

proportional to crushing power  $P_C$ . This conversion factor, estimated at  $7 \cdot 10^{-3} \text{ kJN}^{-1}$  (Brinkman et al., 2002), was then used to convert the estimated crushing power into crushing energy. The cost of crushing is then  $C_C = 0.007 \cdot P_C$ , with crushing cost in kJ and  $P_C$  as a function of shell length.

For estimating the carrying capacity of the area north of the Wadden Sea islands we used the densities of *Spisula subtruncata* in the years 2017, 2018 and 2019, assuming that 3 *Spisula* per dive are taken. *Ensis leei* (with a maximum of 9 cm) was much less abundant during this period in the study area, a factor of 20 less compared to *Spisula* densities in the first 2 winters (Troost et al., 2021). In the last winter higher densities of *Ensis* were found, with a maximum of ca 4000 individuals  $\text{m}^2$ , but this was very local, not a bank, and in the western part of the study area where the observed number of scoters was low that winter. We, therefore, focus on *Spisula subtruncata*, the main food source in the area, and consider this as the only prey.

## 2.5. Environment

Monthly data on air temperature and wind speed were obtained from the Royal Dutch Meteorological Institute station De Kooy (KNMI 2021), monthly data on water temperature were obtained from Rijkswaterstaat (Dutch Ministry of Infrastructure and the Environment; station Schiermonnikoog noord), recorded close to and within the study area, respectively. These data are for the specific years involved but are not spatially explicit (Table 5 and Table 6).

The current velocity data are on a spatial grid and monthly basis and obtained from a tidal model driver using the regional model ES2008 (TMD obtained from <https://www.esr.org/research/polar-tide-models/tmd-software/>). For the model application of a single duck constant values for current velocity were used, for the model application on the benthos survey data points monthly mean current velocity values

**Table 5**

Monthly values of abiotic parameters used for the runs with a single scoter for winter season 2018–2019. Air temperature and wind data were obtained from KNMI (Royal Meteorological Institute) and water temperature was obtained from buoy data from RWS. The column on the far right indicates the scaling of prey AFDW, assuming 1 in summer.

	Air Temperature (°C)	Water Temperature (°C)	Wind ( $\text{ms}^{-1}$ )	AFDW scalar
September	15.36	17.85	5.18	0.9
October	12.86	14.75	5.03	0.8
November	7.12	10.31	5.77	0.7
December	6.97	6.88	6.9	0.6
January	4.44	6.41	5.56	0.5
February	6.19	5.93	5.28	0.5
March	7.54	7.63	6.96	0.6
April	10.12	9.58	5.28	0.7
May	11.13	12.26	4.75	0.8

derived from the tidal model were used. The abiotic data were obtained for the winter seasons 2017–2018, 2018–2019 and 2019–2020 (Table 6).

## 2.6. Bird counts

Visual, aerial surveys were used to get the total number of common scoters in the three winters studied here. In The Netherlands, these ducks are counted once every year, in mid-winter, to monitor numbers present relative to the national target of 65,000 wintering individuals. For these counts, Dutch nearshore waters are subdivided into counting sub-areas. In the current study area, these run from the shoreline of the Wadden Sea islands, out to the shipping lane, at the –20 m isobath, and are each adjacent to one large, or several small Wadden Sea islands. From West to East, these sub-areas are, respectively: Texel, Vlieland, Terschelling, Ameland and Schiermonnikoog/Rottum (see Sluijter et al. (2021) for the most recent report on these counts). As the ducks often flock in only a few major concentrations, the plane flies alongshore until such concentrations are found. These are then circled to count the ducks. There is, however, growing concern that smaller flocks might be missed and since January 2019 additional counts were conducted that used a regular grid of transect lines, running north to south instead of along shore. By either method, the total numbers of ducks observed within each sub-area are used, rather than the exact positions of each flock seen. The ducks show considerable alongshore movement, driven by the tides and by disturbance and this is compensated to some extent by using total numbers per sub-area.

## 2.7. Model application for a single duck, carrying capacity estimates and application

The model was first run for a single duck and fixed values of disturbance, current velocity and depth to study the heat, energy and time budget in detail (disturbance zero or 3 h 24 h<sup>-1</sup>; current velocity 0.5 ms<sup>-1</sup>; depth 5 m). Thereafter, different values of depth, current velocity and disturbance were used to explore the abiotic boundaries for a common scoter that must meet its energy demands. These runs with a single duck were with the assumption of *ad libitum* food. For estimating the carrying capacity for the sensitivity run we used a food density based on the survey data (length classes and individuals m<sup>-2</sup>: 10–15 mm: 1500; 15–20 mm: 15; 20–25 mm: 35; 25–30 mm: 35; 30–35 mm: 15).

In a second step the model was applied to the North Sea coast north of the Wadden Sea Islands (Fig. 1) to study the potential carrying capacity based on *Spisula* densities for the same three winter seasons. For each sampling grid cell from the benthos sampling program (described above), we assessed the potential carrying capacity. This was done given the grid cell-specific depth, current velocity, disturbance, and specific

values for air and water temperature and wind speed. Since the benthos sampling is on a finer grid closer to the islands the grid cells are smaller here than further offshore where a coarser sampling grid is applied (Fig. 1). The model assumes that there is no exchange of birds between sampling grid cells.

The model was programmed in C++.

## 3. Results

### 3.1. Individual heat, energy and budgets

In the first model runs there is no food depletion, and results vary only with the environmental variability. Heat loss was mostly due to cooling and breathing (Fig. 2). Heat gains are based on the basal metabolic rate (BMR) and activity. The heat gain from BMR is most important, followed by the heat gain from swimming and the net heat gain from foraging. The difference between heat losses and gains varies with season and is dealt with by active heating or cooling, accounted for through the energy budget, to maintain a constant body temperature. In this example, there is always a heat surplus, which is accounted for in the energy balance by active cooling. Disturbance changes the heat balance. This is due to increased flying time but also indirect effects such as increased heat gains due to additional foraging to provide the energy needed for flying due to disturbance.

Energy gain solely stems from consumed prey and the model is set so that gains match the total costs. On average, BMR constitutes 30% of the total energy costs. The energy costs are diverse and vary during the season due to seasonal changes in environmental conditions and the energy content of the food (Fig. 3). During the second half of winter the foraging costs increase. This is due to the increased number of dives needed to get enough energy for heating. In addition, each prey item contains less energy due to the seasonal decline in energy content, so more dives are needed to gain the same amount of energy, while more is needed. When disturbance is included in the model the energy needed for flying and foraging increases. Disturbance adds almost 50% to the costs when summed over the winter period for this parameter setting.

The time spent on the different activities also has a seasonal pattern, especially related to foraging (Fig. 4). Without disturbance most time is spent on swimming, to compensate for current drift. When disturbance is included more time and energy is spent on flying but especially more time is spent on foraging to compensate for the energy lost, responding to disturbance. As a result, disturbance has a profound effect on the time budget.

### 3.2. Effects of depth, current velocity and disturbance

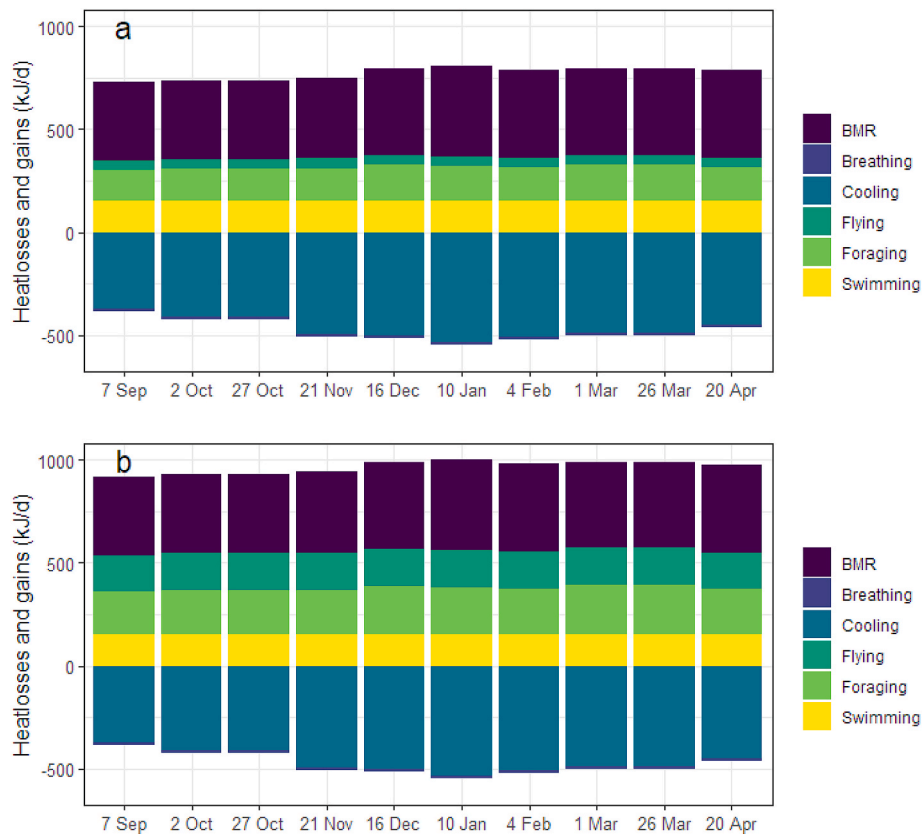
While energy and heat budgets vary over time at a given set of environmental parameter values, the budgets will also vary when those values are changed in the model. Here we illustrate the effects of depth, current velocity and disturbance and the range of values for which a scoter can sustain itself *ad libitum* food conditions. Note that these are model simulations and that this exercise scopes the parameter ranges that can be found in coastal zones.

Both the heat and energy budgets change with depth. At increasing depth, more energy is needed to acquire food, while the longer dives have a positive effect on the heat budget due to increased muscle activity. The time budget also changes with depth due to an increase in foraging time, as more time is needed to get to the seafloor and to deal with the increased amount of food needed to cover the energy demand. Time turns out to be the limiting factor at increasing depths when disturbance is included in the model (Fig. 5). When time runs out, despite *ad libitum* food availability, the energy demand cannot be fulfilled. In this specific example, time runs out at a depth of 47 m, based on the ambient conditions (meteo, current velocity = 0.5 ms<sup>-1</sup> and disturbance 3 h 24 h<sup>-1</sup>). In conclusion, diving depth is not limiting because of food availability *per se*, but because of the time needed to

**Table 6**

Monthly values of abiotic parameters used for the model application for the coastal waters north of the Wadden Sea Islands for seasons 2017–2018 and 2019–2020. Values for winter season 2018–2019 are provided above in Table 5. Air temperature (°C) and wind data (ms<sup>-1</sup>) were obtained from KNMI (Royal Meteorological Institute) and water temperature was obtained from buoy data from RWS.

	2017–2018			2019–2020		
	Air T.	Water T.	Wind	Air T.	Water T.	Wind
September	14.61	17.52	4.68	15.51	19.06	5.08
October	13.86	14.86	7.00	11.98	15.33	5.80
November	8.58	11.24	5.54	6.97	11.30	4.82
December	5.76	7.66	6.52	6.73	8.46	6.09
January	5.44	6.13	7.16			
February	1.45	4.77	5.85			
March	3.77	2.28	6.0			
April	10.33	8.96	5.0			
May	15.25	13.15	4.4			



**Fig. 2.** Heat budget per time step during winter season for a single duck. a: the budget without disturbance and b: with disturbance set at a constant of 3 h 24 h<sup>-1</sup>. Current velocity is set at a constant of 0.5 ms<sup>-1</sup> and depth equals 5 m.

obtain the food to fulfil the energy demand. Note that the maximum depth of the study site is 31 m and scoters have been observed diving up to 30 m (Cramp and Simmons, 1977).

Increasing current velocity limits the depth at which a duck can fulfil its energy demand (Fig. 6a). When the current is zero the model predicts that scoters can gain enough energy to sustain themselves up to a depth of 59 m (given the parameter setting of ambient conditions and disturbance used in this setting). An increase in the current velocity starts to have a negative effect on the energy budget at 0.4 ms<sup>-1</sup> thereby limiting diving depth. At a current velocity of 0.7 ms<sup>-1</sup>, the value where scoters stop swimming against the current (Prange and Schmidt-Nielsen, 1970; Woakes and Butler, 1983), the diving depth is limited to 22 m.

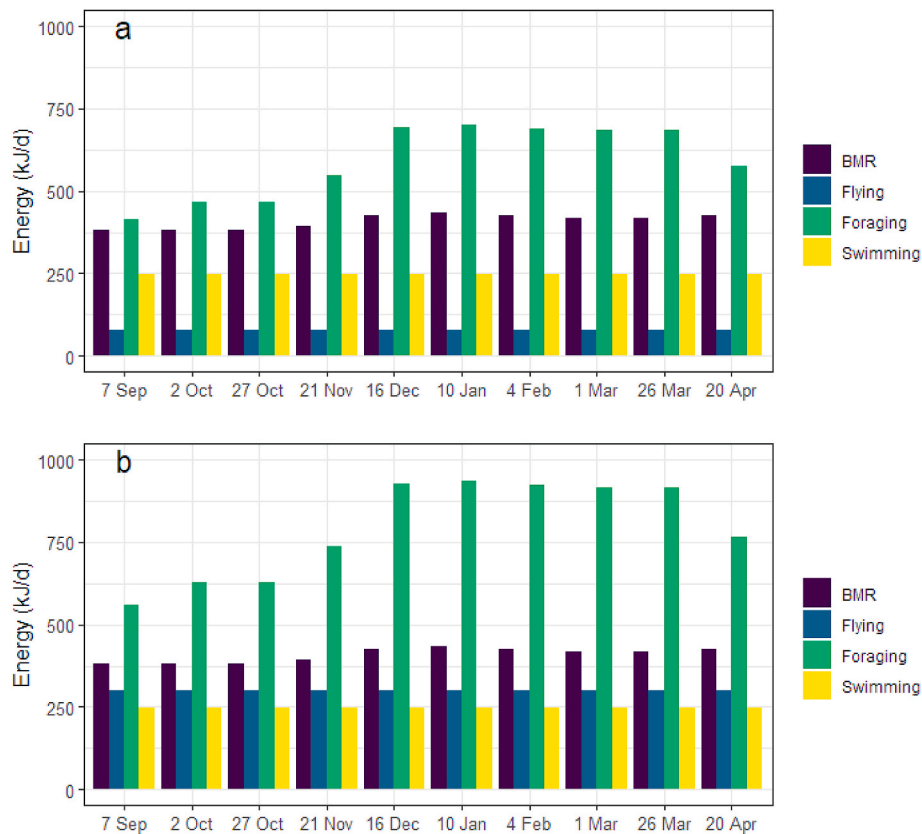
When disturbance is included in the model the energy demand goes up due to increased flying time, increased energy expenditure and lost foraging time (Fig. 4). The interplay between depth and disturbance is illustrated in Fig. 6b (current velocity = 0.5 ms<sup>-1</sup>). For lower values of disturbance a scoter can sustain itself at larger depths. With increasing disturbance, the depth at which scoters can persist decreases in a non-linear way. This implies that a small amount of disturbance in a deeper area can be detrimental for scoters, despite abundant food availability. A similar amount of disturbance has less impact in more shallow areas because there is more room in the time budget. Note that these calculations illustrate the effect of the interplay of depth, current velocity and disturbance on the time budget. The natural variability in abiotic and especially biotic conditions will further determine time budget limitations, quantitatively affecting the relationship between depth, current velocity and disturbance.

### 3.3. Carrying capacity

In reality, more than one scoter needs to fulfil its energy demand and resources will be depleted to some extent during the winter period. The

model is therefore run to calculate the number of birds that can sustain themselves during a winter season, given environmental conditions identical to those used for the analysis of one bird. For this evaluation we used realistic food densities to assure that resource depletion can occur. Note, however, that interactions between individual ducks, e.g., the phenomenon that the birds might suffer from mutual interference (see for example Van der Meer and Ens (1997)) are not included in the model.

Increases in either current velocity or disturbance lead to a decrease in the number of scoters (Fig. 7). However, the maximum depth at which scoters can be present is lower compared to the situation with a single scoter due to food depletion. With increasing current velocity or disturbance, the decrease in numbers is abruptly followed by a shear drop towards zero birds, when the threshold value is reached from which point onwards no scoters can persist. This implies that even a small increase in current velocities or disturbance levels may all of a sudden cause the carrying capacity to drop to zero, without a warning signal based on changes in the number of birds. With increasing depth, the potential carrying capacity first decreases and then temporarily increases, followed by a decrease again until no scoter can persist. This non-linear pattern is caused by a temporary benefit of deeper diving. Although a deeper dive costs more energy it also produces more heat. In addition, the increase in pressure reduces the buoyancy forces to stay at the bottom by pressing the air out of the feathers. This additional heat and reduced force to stay at the bottom generated by a slightly deeper dive reduces the food intake needs for each bird. This in turn reduces the intake and prey depletion, allowing for a higher carrying capacity. However, a further increase in depth increases the energy demand per bird such that the carrying capacity decreases rapidly.



**Fig. 3.** Energy costs during a winter season without (a) and with disturbance (b); disturbance is 3 h 24 h<sup>-1</sup>. Current velocity is set at a constant of 0.5ms<sup>-1</sup> and depth equals 5 m.

### 3.4. Coastal zone application

Application of SCOTERS to the North Sea coast shows that large differences in potential carrying capacity exist between winters (Table 7). In both winters 2018–2019 and 2019–2020 the potential carrying capacity was much higher than winter 2017–2018. The location of potential carrying capacity hotspots also differs between winters. In winter 2017–2018 two hotspots, albeit with low numbers, are present north-west of Terschelling and just north of Ameland (Fig. 8a). In winter 2018–2019 the foraging hotspot predicted north-west of the island of Terschelling remains and the area north of Ameland now has a higher carrying capacity due to an increased *Spisula subtruncata* density (Fig. 8b). Although the *Spisula subtruncata* bed has extended north-westwards the model predicts little carrying capacity there due to the high level of disturbance. In winter 2019–2020 the model does predict a hotspot there because a high-density patch of *Spisula subtruncata* is in between the eastbound and westbound shipping lanes where there is a strip of low disturbance (Fig. 8c).

The effect of the different types of disturbance depends on the location of the *Spisula subtruncata* bed. The largest effect of disturbance exclusion is caused by cargo vessels (the potential carrying capacity increases by 84% during winter 2018–2019 and increases by 86% during winter 2019–2020 when disturbance from cargo vessels is not included), in the main shipping lane. This is because part of the *Spisula* bed is close to and even in the shipping lane (Figs. 1 and 8). Exclusion of shrimp fishing has the second largest effect, with a 29% increase in potential carrying capacity in the winter of 2017–2018. The relatively large impact of the shrimping fleet in that winter is because the carrying capacity hotspots are located in the area where shrimp vessels were most active; that were located closer to the islands and further away from the cargo shipping lane. The effect of other fleets, including the *Spisula*/Ensis fishery, is much less, between less than 1% up to an 8% increase in

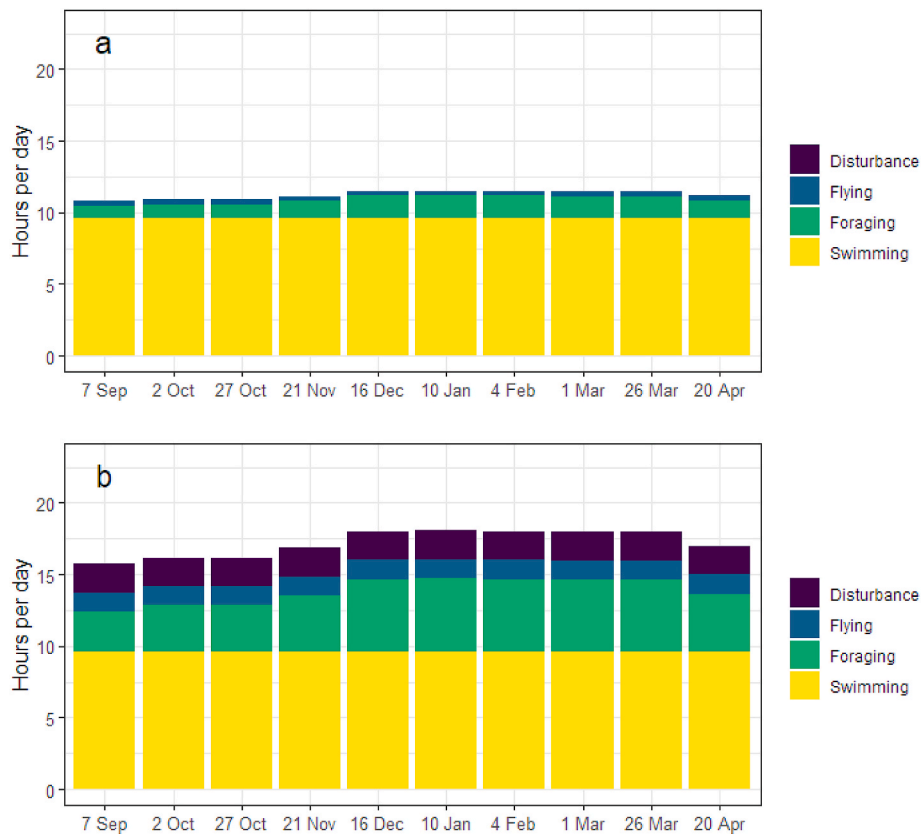
carrying capacity when their share of disturbance is excluded, despite the fact that the mean fleet activity is not that different (Table 1). Without any disturbance at all the estimated potential carrying capacity is much higher. The potential carrying capacity would even more than double in winter 2018–2019, and would reach a figure of over a million individuals in winter 2019–2022. This high potential carrying capacity is due to the high food density that last winter.

The location of potential carrying capacity hotspots and locations where birds were observed matches only partially (Fig. 8) (correlation coefficients based on count areas: 2017–2018 = 0.4; 2018–2019 = 0.35; 2019–2020 = -0.2). Birds were observed where the model predicts the peak of carrying capacity. However, especially during the last winter most ducks were observed in the eastern parts of the study area, despite a lack of *Spisula subtruncata* or high densities of other bivalve species here, resulting in a mismatch with the model results. Also, in winter 2017–2018 birds were observed in the most eastern parts despite the absence of potential prey.

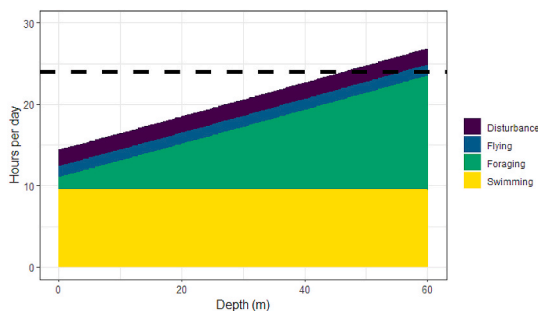
### 4. Discussion

The increasing demand of humans for space and resources in coastal waters increasingly puts pressure on animals utilizing the same area (Cury et al., 2011). Illustrating this conflict of interest with common scoters as a focal species, we show that human use of the area, in this case by disturbance, has far more impact on the common scoter than resource competition, because disturbance limits foraging time for this shy bird, while food was overabundant. We demonstrated that ducks can maintain themselves at a large range of depth, current velocity and disturbance values but also that foraging time runs out when even a small increase in one of these values results in a negative energy balance (c.f., Norberg, 1977). Our spatial application indicates that there appears to be plenty of food in the study area for a vast number of





**Fig. 4.** Time budget of a single duck without (a) and with (b) disturbance corresponding to heat and energy budgets presented above. Note that the time not allocated to an activity is 'spare time' available for preening, courting etc.



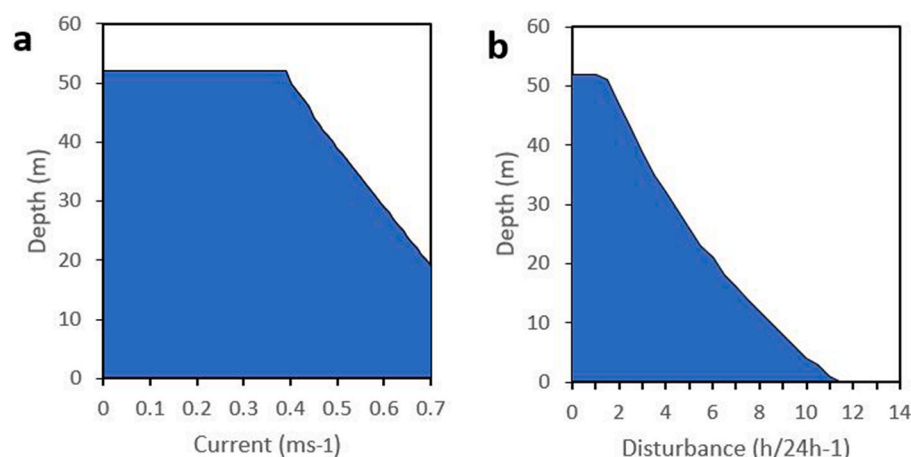
**Fig. 5.** Diving time needed to fulfil the energy requirements as a function of depth for a single individual and *ad libitum* food. The conditions are identical to those used in the figures above with disturbance set to  $3 \text{ h } 24 \text{ h}^{-1}$  and a current velocity of  $0.5 \text{ ms}^{-1}$  (Fig. 4). The data plotted are from time step February 4, which is the time step where time is most limiting. The dashed line denotes 24 h as a reference.

wintering scoters, but actual numbers using the site fell far short of what would be theoretically possible if all this food would be available to the ducks. There was no *Spisula* fishery in 2017 and although fishing occurred in autumn 2018 and 2019 in the area, catches amounted to 0.6% of the estimated *Spisula* stock older than 1 year (Perdon et al., 2018, 2019). This is less than our estimate of scoter consumption of 4%, based on bird counts and energy demand. Such levels of fishing will hardly affect the carrying capacity. In contrast, current levels of disturbance have a relatively large detrimental effect on ducks as this impacts their time budget. If conservation of wintering ducks would be a target, we advocate using a precautionary principle and flexibility in time and space based on actual *Spisula* densities when assigning conservation areas.

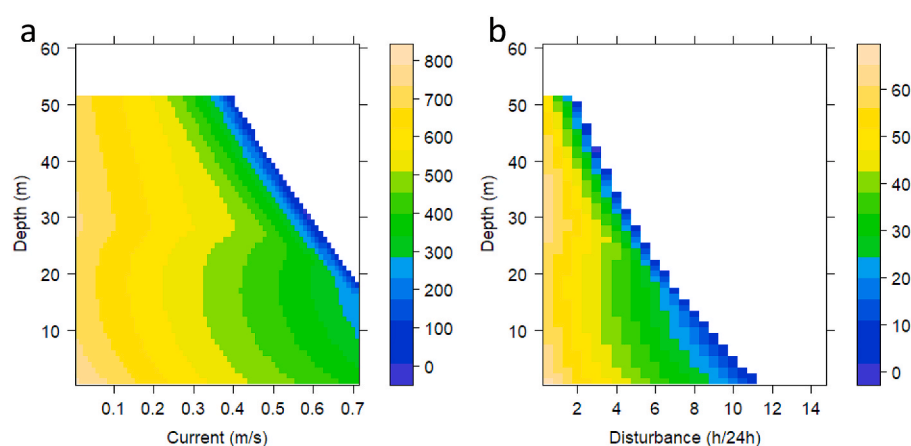
The first results show that a relatively steady and gentle decrease in carrying capacity may drop rapidly to zero close to the threshold of a neutral energy balance. Such a threshold and quick drop advocate using a precautionary principle due to the unpredictability of local circumstances. For example, a combination of disturbance and a sudden winter storm could suddenly become detrimental to the carrying capacity. Especially at larger depth, this can be the case because disturbance has an increasingly negative effect on the time budget here. The model applied to the coastal zone showed a large difference in the potential carrying capacity of the area in time and space, and different effects of vessel types. Not surprisingly, the combination of disturbance intensity and overlap with the location of *Spisula* beds determines whether or not a certain vessel type affects carrying capacity. In winter 2017–2018 *Spisula* was present in an area where shrimp vessels are active (either steaming or fishing), resulting in the largest effect on carrying capacity from these vessels. In winters 2018–2019 and 2019–2020 a large and high-density *Spisula* bed was located close to and in the major shipping lanes, causing cargo shipping to have the largest disturbing effect. Nonetheless, even with disturbance, the model predicts that bed could feed the entire European scoter population (winter 2019–2020), which is estimated at 285,000–350,000 birds (Birdlife, 2022).

#### 4.1. Time limitations

At carrying capacity level, we find a non-monotonous relationship between the number of ducks and depth. The maximum number of ducks decreases somewhat with increasing depth because a deeper dive costs more energy and time. There is however a threshold value for which suddenly ducks can no longer get enough energy, because the number of dives needed to fulfil energy requirements exceeds the number of dives needed to accomplish this within the time available. This implies that at high food density, the resource *per se* is not limiting



**Fig. 6.** Scoter persistence as function of depth and current or disturbance. The blue area indicates those combinations of values of current velocity and depth, or disturbance and depth, for which a scoter can sustain itself under ambient conditions and *ad libitum* food. a: scoter persistence as function of current and depth (disturbance = 3 h 24 h<sup>-1</sup>). b: scoter persistence as function of disturbance and depth (current velocity = 0.5 ms<sup>-1</sup>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 7.** Potential carrying capacity (number of scoters in standard grid cell; colour scale on the right) based on current and depth (a) (disturbance = 3 h 24 h<sup>-1</sup>) and disturbance and depth (b) (current velocity = 0.5 ms<sup>-1</sup>) in an area of 1E6 m<sup>2</sup>. Parameter settings are identical to those in Fig. 6, except that food at the start of the winter season is set at a density 1600 individuals m<sup>-2</sup>, allowing depletion during the season. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

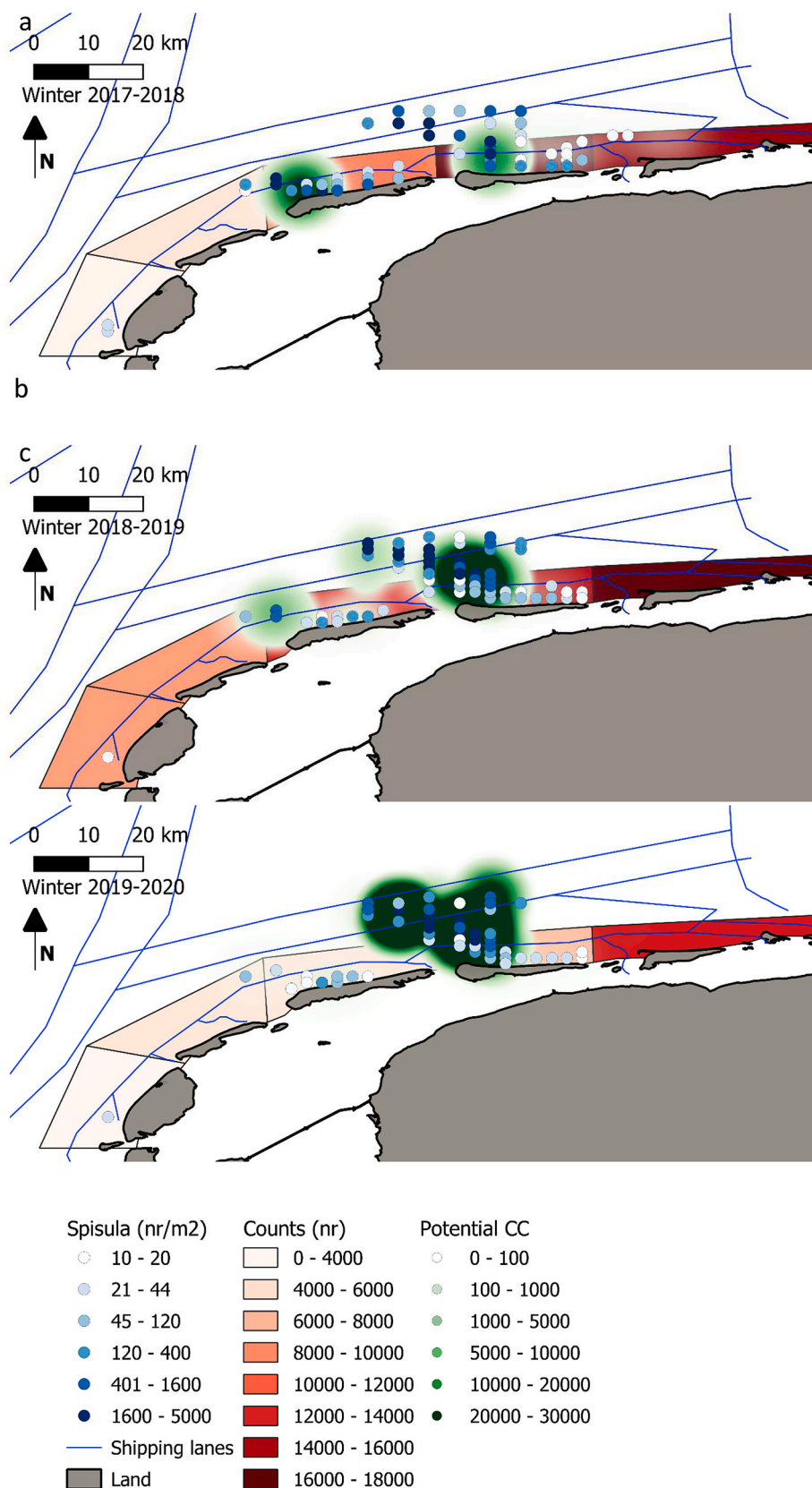
**Table 7**

Potential carrying capacity of the area based on *Spisula subtruncata* and the abiotic parameters for each disturbance scenario and each winter. Values are given in absolute numbers and as percentage different from the scenario with all sources of disturbance included.

Disturbance scenario	2017–2018	2018–2019	2019–2020
No disturbance	28200 (+42)	853428 (+104)	2013834 (+95)
All fleets	19833	417822	1033707
No Shrimp fishing	25643 (+29)	452840 (+8)	1048902 (+2)
No Ensis and spisula fishing	19924 (+0)	422650 (+1)	1035170 (+0)
No Other Fishing	20256 (+2)	435996 (+4)	1036973 (+0)
No Cargo shipping	20070 (+1)	768836 (+84)	1922064 (+86)
No Dredging	19993 (+1)	425063 (+2)	1035536 (+0)
No Recreation	20054 (+1)	423307 (+1)	1035882 (+0)
No Rest category	20500 (+3)	449709 (+8)	1043179 (+1)

but the time needed to get the prey, and thus the maximum calories per dive, is limiting a net positive energy gain, corroborating other studies on diving ducks (De Leeuw, 1997; Fox, 2003; Rizzolo et al., 2005). We assume ducks can spend a maximum of 80% of 24 h foraging. Daylight would not be needed for foraging at the seafloor with no visibility and scoters remained present at night in waters overlying a large *Spisula* bank in the current study area (Dirksen et al., 2005), suggesting that feeding can continue in darkness. More fieldwork on this is obviously needed because if foraging time is limited to daylight this would have repercussions for the time budget and the effect of disturbance. If we assume that scoters can take more than 3 prey items per dive ducks can sustain themselves for a larger parameter space, yet the shape of the

relationship and the threshold remain. The general negative relationship between density and size of prey will also play an important role in the number of items taken per dive. Generally, disturbance with its twofold effect on birds affects the time available negatively. Also, the time being disturbed (set to 1 h based on Krijgsveld et al. (2008)) affects the time for foraging. Each 15-min increase of time being disturbed reduces the depth for which a bird can sustain itself by 3 m (parameter settings identical to those used in the first section of the results, current = 0.5 ms<sup>-1</sup> and disturbance = 3 h/24 h). Consequently, also the parameter ranges for depth, current and disturbance for which a bird can sustain itself will change with different assumptions on the duration of being disturbed (results not shown). When conditions are less favourable, for example with increased current velocity and/or depth, or at lower food availability, disturbance increasingly hampers meeting energy demands and can be detrimental to fitness (Goss-Custard et al., 2006; Nolet et al., 2016). Knowledge of when disturbance is critical can be used to protect birds (e.g., Goss-Custard et al. (2006)) but also to repel birds (e.g., Nolet et al. (2016)). However, accurate threshold values for a certain location cannot be given. This is mainly due to rather unpredictable and irregular food availability due to stochastic recruitment of many bivalve populations (Armonies, 2001; Baptist and Leopold, 2009; Cardoso, Witte, and van der Veer, 2007; Troost et al., 2021; Strasser et al., 2003), fluctuations in weather conditions, which also plays a role in the energy balance and uncertainty of parameter values with little empirical support. Individual variation between birds can lower critical disturbance thresholds (Goss-Custard et al., 2006). This implies that from a conservation perspective management should aim for minimum disturbance in the vicinity of *Spisula* beds based on a precautionary principle rather



**Fig. 8.** Location of the potential carrying capacity hotspots (in green, in numbers of birds per grid cell) for the three winters along the coast and the *Spisula subtruncata* density from the benthos survey (only locations with  $>10 \text{ nr m}^{-2}$  are shown; summed over the size-classes). All sources of disturbance are included. Note that for illustration purposes as maximum value for potential carrying capacity for winter 2017–2018 (a) 9000 was used, while for the winters 2018–2019 (b) and 2019–2020 (c) 100,000 was used. Count area colour indicates the number of birds observed per winter. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

than threshold values. Moreover, such management should be flexible because bivalve bed locations vary in time and space (Troost et al., 2021).

#### 4.2. Model comparison

The model presented here is deterministic, modelling bird energetics in a mechanistic manner, without behaviour or movement, such as was done in an individual-based model (IBM) by Kaiser (2002). SCOTERS is in that sense more basic than an IBM, but does not require assumptions on the whole population and predictions of drivers of migration. We can therefore predict the potential carrying capacity, regardless of the population status and provide other and complementary information to an IBM (Kaiser, 2002) or statistical model (Schwemmer et al., 2019). Population models have been used to study effects of competition for resources or space between humans and birds (Hentati-Sundberg et al., 2021; Koehn et al., 2021), but too little is known about the common scoter to develop such a model.

#### 4.3. Relation to observations

Our model provides an energetic underpinning of why areas are or are not potential hotspots based on foraging (excluding behaviour as a possible explanation for absence). This also defines one of the difficulties of comparing the model results with observations. There is an overlap between where the model predicts scoters and where scoters were observed (Fig. 8). There are also observations of scoters in parts of the study area where there was no *Spisula* present and thus no predicted carrying capacity for the three winters studied. Birds have been observed in areas without apparent food which could be related to calm, low current velocity conditions, or areas with little disturbance (Heesen, 2011; Leopold et al., 1995) that may provide undisturbed, sheltered resting places instead of functioning as foraging area, despite the strong observational relationship between scoters and *Spisula* beds (Baptist and Leopold, 2009).

The absence of common scoters in areas in which prey availability is deemed sufficient does also occur (Degraer et al., 1999; Fijn et al., 2017). Such absence can be due to more profitable circumstances elsewhere along the west-European coastline, which is not considered in the model. In addition, the bird survey covered a smaller area than the model grid used, staying parallel to the coast at a closer range leaving the large *Spisula* bed north of Ameland partly uncovered. It is unclear if birds cross the cargo shipping lane to forage on the *Spisula subtruncata* bed in between the eastbound and westbound shipping lanes, but large flocks have never been noticed here. The overall population status also has an influence on scoter presence in a selected area. The January counts that should be representative of overwintering scoter presence indicate a pattern with high numbers in winter 2017–2018 (62,000) and winter 2018–2019 (50,000), but low numbers in winter 2019–2020 (25,000) (Lilipaly et al., 2018, 2019; Sluijter et al., 2021). This contrasts the pattern in potential carrying capacity, with low numbers for winter 2017–2018 and high numbers in the two winters thereafter for which high densities of *Spisula* are present. Scoters typically winter in large flocks and if such a flock, for some reason, switches from one area to the next, the first area no longer has birds, but might still have food. When the population as a whole is low, the number of flocks might decrease. Seasonal migration may also play a part here, as scoters may change locations while transiting from their northern breeding areas to wintering in the south, or vice versa.

We limited our application to *Spisula subtruncata* as prey, even though scoters are known to feed on *Ensis leei* (Kottsieper et al., 2019; Tulp et al., 2010) and other shellfish (Fijn et al., 2017; Fox, 2003; Kaiser et al., 2006; Van Steen, 1978). In this particular area, north of the Dutch Wadden Sea islands, high densities of scoters have been observed over *Spisula subtruncata* beds. Running the model based on *Ensis leei* (data from the same benthos survey) resulted in a potential carrying capacity

of 515 (2017–2018), or 1602 (2018–2019) when all disturbance sources are included. Only for winter 2019–2020 the predicted potential carrying capacity based on *Ensis leei* is much higher (16,418 birds). Still, compared to the results based on *Spisula subtruncata* this is only a fraction of the estimated carrying capacity for that winter. A further increase in *Ensis leei* density, and a decrease in *Spisula subtruncata* density could lead to a diet shift (Houziaux et al., 2012) and a spatial shift within the area, with potential differences in effects of disturbance types.

#### 4.4. Other shipping

Of interest is the effect of ‘other fishing’ and the ‘rest category’ in winter 2018–2019, for which there is a larger effect on the potential carrying capacity than in the other two winters (Table 7), and an increase in disturbance itself (Table 1). Also, the overall disturbance is highest for winter 2018–2019 compared to the other two winters. That particular winter, in January, the cargo vessel MSCZoe lost over 200 containers in the area northwest of the island of Ameland (Herman et al., 2021). In response to the loss of cargo clean-up actions were undertaken, by small vessels such as fishing vessels, recreational or government vessels and by larger salvage vessels. This led to increased shipping activity from several vessel types, although we cannot establish if a vessel was salvaging debris from the MSCZoe based on the anonymous AIS data available. There is a possibility that the increase in vessel impact during 2018–2019 as predicted by the model was due to salvaging actions. If so, then this suggests an additional, indirect ecological effect of the MSCZoe container spill on protected species that are vulnerable to shipping disturbance, such as the common scoter.

There was only a limited effect of dredging for the potential carrying capacity, despite a 10% decrease in mean disturbance when the dredging fleet is excluded (Table 1). However, due to expected sea level rise in the future, this impact might increase as more sand is needed for coastal protection. Locations for both sand extraction and coastal nourishment may then be informed by the locality of *Spisula* beds, not only to avoid removal or burial of prey but also to limit disturbance during winter.

## 5. Conclusion

Common scoters are time rather than food limited in their conflict with humans in Dutch coastal waters due to disturbance. Managing this conflict should focus on spatial flexibility and the timely protection of *Spisula* or other food sources to guide measures such as local disturbance reduction to protect this species. It is therefore paramount that spatial and temporal flexibility is incorporated into marine spatial planning.

#### Author contribution

KW parameterized the model, performed all analysis and wrote the manuscript. AB created the model and revised the manuscript. DB programmed the model. JC provided benthos data and knowledge, and revised the manuscript. SG created the disturbance input for the model. ML conceived the idea and model application, and revised the manuscript.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.



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