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Top-down pressure on a coastal ecosystem by harbor seals

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Abstract. Historic hunting has led to severe reductions of many marine mammal species across the globe. After hunting ceased, some populations have recovered to pre-exploitation levels and may have regained their prominent position as top predator in marine ecosystems. Also, the harbor seal population in the international Wadden Sea grew at an exponential rate following a ban on seal hunting in 1960s, and the current number ~38,000 is close to the historic population size. Here we estimate the impact of the harbor seal predation on the fish community in the Wadden Sea and nearby coastal waters. Fish remains in fecal samples and published estimates on the seal's daily energy requirement were used to estimate prey selection and the magnitude of seal consumption. Estimates on prey abundance were derived from demersal fish surveys, and fish growth was estimated using a Dynamic Energy Budget model. GPS tracking provided information on where seals most likely caught their prey. Harbor seals hauling-out in the Dutch Wadden Sea fed predominantly on demersal fish, for example, flatfish species (flounder, sole, plaice, dab), but also on sandeel, cod, and whiting. Although harbor seals acquire the majority of prey further offshore in the adjacent North Sea, and only spend 14% of their diving time in the Wadden Sea, seal predation was still estimated to cause an average annual mortality of 43% of the remaining fish in the Wadden Sea and 60% in the nearby shallow coastal waters (<20 m). There were however large sources of uncertainty in the estimated impact of seals on fish, including the migration of fish between the North Sea and Wadden Sea, and catchability estimates of the fish survey sampling gear, particularly for sandeel and other pelagic fish species. Our estimate suggested a considerable top-down pressure by harbor seals on demersal fish. However, predation by seals may also alleviate density-dependent competition between the remaining fish, allowing for increased fish growth, and partly compensating for the reduction in fish numbers. This study shows that recovering coastal marine mammal populations could become an important component in the functioning of shallow coastal ecosystems.

Key words: demersal fish; diet; harbor seal; impact; intertidal; *Phoca vitulina;* predation pressure; sealing; subtidal; top-down regulation; top predator.

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INTRODUCTION

Large-scale historic whaling and sealing led to a severe global decline of many marine mammal species (Clapham et al. 1999, Baker and Clapham 2004). As a consequence, marine ecosystems may have lost important regulating forces from such top predators (Heithaus et al. 2008, Estes et al. 2016). While some marine mammal populations have not fully recovered after hunting ceased (Baylis et al. 2015), or have even continued to decline (Springer et al. 2003), others have gone through rapid increases (Brasseur et al. 2018) reaching or exceeding presumed pre-exploitation levels (Roman et al. 2015). This raises the question how such recoveries influence the food web regulation in marine ecosystems.

Harbor seals (*Phoca vitulina* ssp. *vitulina*) have been top predators in the Wadden Sea of the Netherlands, Germany, and Denmark, since its formation 7500 yr ago. Due to severe human hunting and pollution, their numbers declined from an estimated 40,000 in 1900 to approximately 4500 around 1960 (Reijnders 1992). After a ban on seal hunting, the population grew at an annual rate of 12% (Brasseur et al. 2018). Currently, the population is approaching estimated pre-1900 levels with approximately 38,000 individuals regularly hauling-out in the international Wadden Sea (Galatius et al. 2017), of which approximately 10,000 in the Dutch part of the Wadden Sea (Fig. 1).

Harbor seals require approximately 4–5 kg of fish each day, although this varies by season and the seals' size (Härkönen and Heide- Jørgensen 1991). They are considered generalist predators feeding on both demersal and pelagic fish species, but in shallow, soft-sediment regions like the southern North Sea, they mostly eat flatfish (~75%) such as flounder (*Platichtys flesus*), sole (*Solea solea*), and dab (*Limanda limanda*), but also gadoids and sandeel (*Ammodytidae*; Härkönen 1987, Tollit et al. 1997, Kavanagh et al. 2010).

The strong growth of the harbor seal population in recent decades occurred almost at the same time as the abundances of their prey in the Wadden Sea and the adjacent coastal zone of the

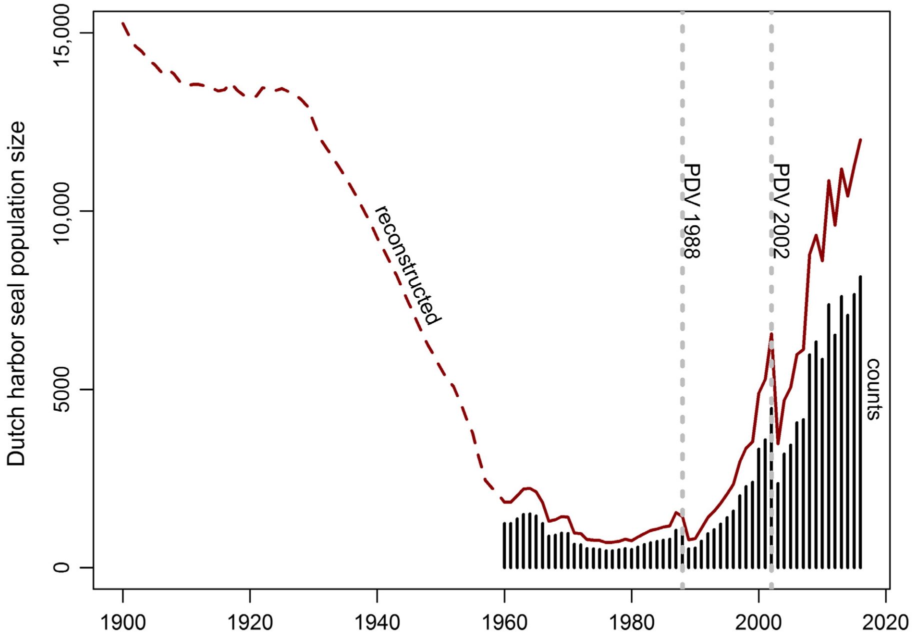

Fig. 1. Development of the harbor seal population in the Dutch Wadden Sea. The maximum numbers of seals observed during the molt survey are represented by the vertical bars (Brasseur et al. 2018). Prior to 1960, the estimated population size was reconstructed based on seal hunting statistics (Reijnders 1992), while from 1960 onwards, the population size was estimated to be 1.47 (i.e., 0.68^{-1}) times the observed counts, to correct for animals at sea at the time of the census (Ries et al. 1998). In 1988 and 2002, the population was reduced by approximately 50% due to the Phocine distemper virus (PDV).

North Sea declined (Tulp et al. 2008, 2017). Some size classes, such as >1-yr-old plaice and flounder, have almost completely disappeared from the Wadden Sea (van Keeken et al. 2007, van der Veer et al. 2011). Several hypotheses have been put forward to explain the declines in the fish biomass, for example, increasing water temperature, increased human activities, declining nutrients due to cleaner river outflows, fishery by-catch, or increased predation by birds (e.g., cormorants) and seals (Temming and Hufnagl 2015, van der Veer et al. 2016, Tulp et al. 2017).

The objective of this study is to estimate predation pressure by harbor seals on the demersal fish community in the Dutch Wadden Sea and nearby coastal North Sea. One contribution of this study is to highlight that estimates of predation pressure by top predators should ultimately be included into fish population and ecosystem models (Tyrrell et al. 2011).

METHODS

Analysis structure

We estimated the impact of seals on the local fish abundance as follows:

1. Harbor seal diet was defined based on analysis of fecal samples collected on haul-out sites in the Dutch Wadden Sea.
2. Based on estimated seal energy requirements, and energetic content of the prey in their diet, the average daily fish consumption was estimated.
3. The total daily fish consumption by all harbor seals was estimated, taking into account the size of the population in the Dutch Wadden Sea and the time spent foraging in different regions (using data from GPS tracked harbor seals).
4. Total number and biomass of prey species present in three regions (the area within the Wadden Sea barrier island (the Dutch part of the Wadden Sea), the Wadden coastal zone up to 25 m depth (Wadden coast), and offshore North Sea up to 50 km from the nearest haul-out) were estimated using data from the annual demersal fish survey (DFS) and beam trawl survey (BTS) collected in September.
5. Growth in prey biomass from September onwards was reconstructed using a dynamic energy budget (DEB) model. The model was fitted to seasonal length distribution data and accounted for daily variations in temperature.
6. The reconstructed prey numbers and biomass were subsequently reduced by the estimated daily food intake by all harbor seals.

Harbor seal diet based on fecal analysis.—Between 2002 and 2009, 103 fecal samples were collected opportunistically from tidal haul-out sites throughout the Dutch Wadden Sea. Most samples were collected near Texel in the west (i.e., Noorderhaaks and Steenplaat) and near Schiermonnikoog in the east (i.e., Simonszand; Fig. 2a). After collection, samples were frozen (−20°C) until further processing. For the analysis, samples were placed in a meshed (120 μm) bag and washed in a laundry washing machine at 70°C, including a prewashing cycle using a biological detergent (Biotex, Unilever). Samples were then dried. Recognisable fish remains (otoliths and bones) were analyzed and measured with a Zeiss camera stereoscope (Stereo Discovery.V8 Achromat S, 0.63 × FWD 115 mm). These hard parts were identified using available reference guides (Härkönen 1986, Watt et al. 1997) and compared to a reference collection containing fish remains from known North Sea fish species (held by WMR). For this study, only otoliths were used and each otolith was treated as one-half fish. Otoliths were measured using Axiovision software (AxioVs 40 v.4.7 and 4.8, Carl Zeiss Microscopy GmbH, Jena, Germany) and assigned to a wear class. The species-specific correction for wear was derived from Leopold et al. (2001). For species where such corrections were unavailable, corrections for species with comparable otoliths were used. Both otolith length and width were used to infer fish length based on known otolith length to fish length regressions (Härkönen 1986, Watt et al. 1997, Leopold et al. 2001). Fish weights were inferred using known fish length to weight regressions (Robinson et al. 2010, and WMR, *unpublished data*). Given the potential spatial and temporal bias in the collected fecal samples, the observed proportions of the different fish species in the harbor seals diet were not used to estimate the species-specific impact of harbor seal predation. The information was merely used to identify the ten most important species in the diet based on calculated contributions by fresh mass to the seal diet, and to define the size range of prey eaten. These ten

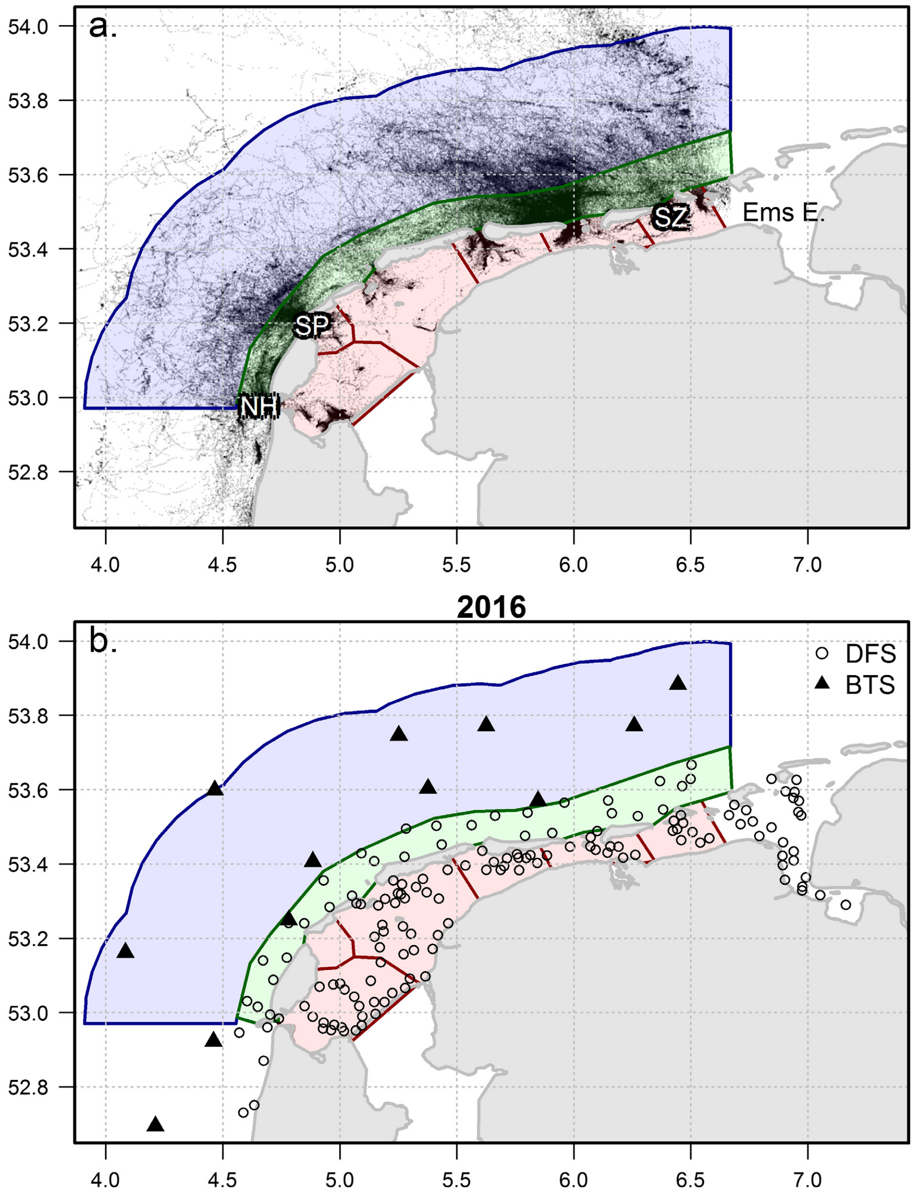

Fig. 2. (a) Distribution of harbor seals, and abbreviations of some fecal sampling locations. Data from the 149 tracked harbor seals making trips from haul-out sites located in the Wadden Sea. Trips of seals making trips from haul-out sites located in the Ems Estuary (Ems E.) were excluded. Most fecal samples were collected on the Noorderhaaks (NH), Steenplaat (SP), and Simonszand (SZ). (b) Fish survey areas along the North Sea coasts of The Netherlands (adapted from Tulp et al. 2016). Harbor seal fish consumption was assessed in three zones: the Wadden Sea (shaded pink—corresponding to ICES areas 610, 612, 616–619), Wadden coast (shaded lime green—ICES area 404), and a North Sea offshore zone up to 50 km away from the seal haul-out sites located in the Dutch Wadden Sea (shaded blue). The points represent fish survey locations from 2016.

species determined the prey base used for further calculations.

Harbor seal average daily food requirement.—Harbor seals require energy for maintenance and growth (Markussen et al. 1990), reproduction (i.e., fetal growth, lactation, mating), molt, and activities such as locomotion. Juvenile phocid seals require on average 1.4 times more energy per kg body weight for maintenance and growth than adults (Innes et al. 1987) but have a lower overall energy requirement because they are smaller in size and do not take part in reproduction. In a study on captive harbor seals (four adult males, one subadult male, and one adult female) which were fed ad libitum, the gross energy intake was estimated to be 6071 kcal/day (Rosen and Renouf 1998). These estimates were close to the estimates for adult males used by Härkönen and Heide-Jørgensen (1991) (i.e., 5890 kcal/day). When taking the local population structure into account, Härkönen and Heide- Jørgensen (1991) estimated that on average harbor seals in the Skagerrak (Sweden) have an ingested energy requirement (ER) of 4680 kcal per day.

To meet this energy requirement, Härkönen and Heide- Jørgensen (1991) estimated that harbor seals should consume 4.1 kg of flatfish each day in the Skagerrak. The energy densities of their prey, and hence also the seals' food intake, vary between prey species and seasons (Pedersen and Hislop 2001). The energy density of fish is often highest just after the growth season, prior to the winter, which is subsequently devoted to maintenance and reproduction (Dawson and Grimm 1980). Whenever possible, we used caloric densities from late summer or early winter (see Appendix S2: Table S2). The average daily consumption C (in kg) per seal was estimated based on the energy required (ER) and species-specific caloric densities (ED in kcal/g), weighted by the relative occurrence of prey W_i in the harbor seal diet:

$$C = \frac{\mathrm{ER}}{\sum_{i=1}^{n} W_i \mathrm{ED}_i} \quad (1)$$

Total fish consumption and distribution of foraging effort.—To estimate the total fish consumption by harbor seals in the Wadden Sea and nearby waters, information is needed on how many seals there are, and where they acquire their food. Harbor seal count data were collected annually in the Dutch Wadden Sea using aerial surveys since the 1960s (Reijnders 1992, Brasseur et al. 2018). This study assumed that 32% of seals were in the water during the survey (based on a previously estimated haul-out probability of 68%; Ries et al. 1998), and this was used to derive population size from the survey counts.

To study the seals' distribution at sea, we relied on data from animal-borne GPS data loggers collected in a series of research projects. In total, 225 harbor seals were tracked in the Netherlands between 2007 and 2015, with most (142 individuals) tracked from the Ems estuary (tagged between 2009 and 2011). Harbor seals were caught on haul-out sites with a large seine net, fitted with Fastloc GPS data loggers glued to the fur of the neck using epoxy, and released directly on location. Loggers fell off as hair weakened during the annual molt (July–August), if they did not dislodge before-hand. The GPS data loggers also contained depth and submergence sensors: These were used to determine the activity of the seal: diving (deeper than 1.5 m for at least 8 s), at surface (no dives for 180 s) or hauled out (start is continuously dry for at least 600, end is wet for at least 40 s). Dive records included a description of the dive-profile at 23 points of the dive, but also summary data on maximum dive depth, dive duration, and surface interval duration. All data were logged and transmitted when in contact with a GSM (mobile phone) base.

The seal location data from the GPS loggers were classified into trips, where the start and end time of each trip was defined by the haul-out data from the loggers. The seal's location during the haul-out event was linked to the nearest known haul-out site (based on the location of groups of seals observed during the aerial survey). Only locations from trips starting at haul-out sites in the Dutch Wadden Sea, excluding the Ems estuary (see Fig. 2), were used. The Ems estuary was excluded from the analysis, because this area is used by seals hauling-out on both the Dutch and German side, but the required counts at the level of haul-out sites were only available to us for the Dutch section.

The seal GPS location data were used to estimate the fraction of time spent at sea within three zones: that is, the Wadden Sea, the adjacent coastal zone up to the 25 m depth contour (Wadden coast) and the offshore area between the 25 m depth contour up to 50 km distance from haul-out sites (Fig. 2). To estimate foraging effort in each region, the proportion of dive time (i.e., time spent below 1.5 m depth) in each region was used as a proxy. Some dive time may not relate to foraging, but because seals were not equipped with accelerometer or video sensors, we were unable to define when and where seals caught their prey.

Estimation of total number of biomass prey species present in Wadden Sea and nearby waters.—Data from two fish surveys were used: the demersal fish survey (DFS) and the Dutch beam trawl survey (BTS; see Fig. 2b for distribution of sample locations, see Appendix S2: Table S1 describing the gear characteristics). The DFS has been conducted annually in September–October since 1970. The DFS covers the Wadden Sea and coastal waters (up to 25 m depth) from the southern border of the Netherlands to Esbjerg in Denmark (van Beek et al. 1989). A bottom trawl with a smaller width (i.e., 3 m) was used in the Wadden Sea, to navigate the often-narrow gullies, while a larger, more robust bottom trawl (width, 6 m) was used in the more exposed adjacent waters. Although the size of the beam differed, both gears were rigged similarly (Tulp et al. 2008). In the Wadden Sea, fishing was restricted to the tidal channels and gullies deeper than 2 m. By fishing at low speed (2–3 knots) and using a fine meshed cod end (20 mm), larger sized fish (>15 cm) were relatively underrepresented in the surveys. The gear used is suitable for demersal species, but suboptimal for pelagic species such as herring and sprat. Totals of 110–120 hauls in the Wadden Sea and 30 hauls in the adjacent coastal zone were taken annually, unless adverse weather conditions limited sampling. During each haul, the position, date, time of day, and depth were recorded. Fish species were identified and measured to the nearest cm. Local fish densities (n/10,000 m^2) were calculated from fish counts per haul using the distance covered during the haul and the beam width to calculate the swept area.

The Dutch BTS covers the central North Sea and is designed to sample the older flatfish species (i.e., ≥1-yr old). Compared to the DFS, the BTS is carried out with a larger beam trawl (8 m), a higher speed (4 knots), and a larger mesh size of 120 mm, with 40 mm stretched mesh cod end (Rogers et al. 1998). Only data from quarter 3 were used.

During most fish surveys, only a fraction of the fish present in the path of the net will be caught (i.e., imperfect catchability), and this depends on the vertical distribution of fish in the water column and gear efficiency. Gear efficiency depends on a number of factors, such as the gear-type used (e.g., mesh size, net configuration), fishing speed, water clarity, and fish length, behavior, and species (Dickson 1993). Using existing studies (e.g., Kuipers 1975, Reiss et al. 2006), estimates for the catching efficiencies were derived (See Appendix S1).

To determine the catching efficiency of the BTS, the catching efficiency for the DFS in the Wadden coast was used as a reference, and the DFS catchability was subsequently corrected by comparing length-specific numbers per unit of effort between the DFS and other surveys (see Appendix S1). Given the lack of catchability estimates for any of the other demersal fish species, we assumed them to be similar to plaice.

Fish growth based on dynamic energy budget models.—The seal consumption was calculated in kg/day. To convert this into the *number* of fish caught each day, it was necessary to know the average weight of fish. Fish growth is species specific and depends on fish size, ambient temperature, and food conditions, and therefore, seasonal changes in weight need to be taken into account. These aspects can be parameterized in a Dynamic Energy Budget (DEB) model (Sousa et al. 2010). Here, DEB models were used for five important prey species (61% of total weight in their diet), for which DEB parameters were readily available, namely flounder, plaice, dab, sole, and bull-rout. DEB model specification and parameters were based on van der Veer et al. (2009), Freitas et al. (2010), and Teal et al. (2012). The volumetric daily growth (in gram) was defined as

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \frac{(\kappa f\{p_{\mathrm{Am}}\}\mathrm{Fr})V^{\frac{2}{3}} - [p_{\mathrm{M}}]\exp\left(\frac{T_{\mathrm{A}}}{T_{\mathrm{ref}}} - \frac{T_{\mathrm{A}}}{T}\right)V}{\kappa f[E_{\mathrm{m}}] + [E_{\mathrm{G}}]} \quad (2)$$

V is the weight of the individual fish (in gram) and T is ambient water temperature (in K, derived from website http://live.waterbase.nl, station Den Helder veersteiger, 52.96328° N, 4.77805° E). κ is the fraction of utilized energy spent on maintenance plus growth, f is a multiplication factor for food availability ($f = 1$, ad libitum), and $\{p_{\mathrm{Am}}\}$ is maximum surface area specific assimilation rate (in $\mathrm{J{\cdot}cm^{-2}{\cdot}d^{-1}}$). $[p_{\mathrm{M}}]$ is the volume-specific maintenance cost, which is based on field data and hence also includes the cost for feeding and activity (e.g., swimming; van der Veer et al. 2009). T_A is Arrhenius temperature (in K), T_{ref} is the reference temperature at which the assimilation rate is known, $[E_m]$ is the maximum equilibrium reserve density that occurs at maximum food density (J/cm^3), and $[E_G]$ is the energetic growth costs per unit of growth in structural body volume (J/cm^3; Van Der Meer 2006, van der Veer et al. 2009). Fr is the metabolic and digestive enzyme fraction that is in its active state, which is temperature dependent (see Eq. 2 in van der Veer et al. 2009). Here for all species Fr was based on plaice, given the lack of the necessary parameters for the others species.

Preliminary runs of our DEB models suggested that the reduced growth in late summer (also observed in van der Veer et al. 2016) and winter could not be explained by low temperature alone (Appendix S2: Fig. S2). To parameterize the DEB model in order to account for additional seasonal variability in growth, field data on seasonal variation in fish length were used. The fish length data were collected during fish surveys of the National Programme Sea and Coastal Research (van der Veer et al. 2016). Sampling took place in the western Wadden Sea in 2009 and 2010 during most months, except for the winter months (December–February), and covered both the intertidal areas (using 2-m beam trawl towed from a rubber dinghy) and subtidal areas (using a 3-m beam trawl towed by the 20 m, low draft vessel RV *Navicula*). Sampling took place during daytime and was centered around high tide (i.e., 3 h before and after high tide). See van der Veer et al. 2016, for more details.

The DEB model was fitted to monthly mean length estimates of 0- and 1-yr-old fish (Fig. 6, Appendix S2: Fig. S3a–e). While all parameters were fixed (see van der Veer et al. 2009, Freitas et al. 2010, Teal et al. 2012), the food availability parameter f was estimated, and allowed to vary between summer (f_{summer}) and winter (f_{winter}), and also, the onset of summer (t_{summer}) and winter (t_{winter}) was estimated (based on least-squares in R-function optim).

Taking the size distribution, ambient water temperature, and estimated food availability into account, the final parameterized DEB models for the five species were used to estimate average daily growth and assumed to be representative for all prey species, including the one for which DEB parameters were lacking. The initial size distribution was based on the abundance and size distribution of each species measured during the DFS surveys in September surveys (Tulp et al. 2017). This procedure allowed for the estimation of total biomass and the reconstruction of biomass growth for all harbor seal prey species.

Reducing fish numbers and biomass by harbor seal consumption.—After correcting for catchability, the DFS and BTS provide an estimate of both biomass B and total number of fish N present in each region j in September ($t = 0$). Each day, the biomass can increase as a result of fish growth (defined by the variable v). The fish growth was predicted by the DEB model, taking water temperature, seasonal variation in food density, and initial length distribution of fish caught during the survey into account (see also Eq. 2). This biomass was reduced by seal predation. We assumed that intake rate of seals increased linearly with food density (type I functional response); that is, the time spent foraging in areas with higher food density leads to a higher intake and hence a larger reduction in fish biomass. Therefore, the proportion of dive time p in each region j was weighted by food density $\mathrm{N}_{t-1,j}A_j^{-1}$ (where A_j is the area of the region j), to arrive at the proportional intake $\frac{p_j\mathrm{N}_{t-1,j}A_j^{-1}}{\sum_j p_j\mathrm{N}_{t-1,j}A_j^{-1}}$. This was subsequently multiplied by the total number of seals S and average daily consumption (C).

$$B_{t,j} = v_t B_{t-1,j} - \frac{p_j\mathrm{N}_{t-1,j}A_j^{-1}}{\sum_j p_j\mathrm{N}_{t-1,j}A_j^{-1}} SC \tag{3}$$

Similarly,

$$\mathrm{N}_{t,j} = \mathrm{N}_{t-1,j} - \frac{p_j\mathrm{N}_{t-1,j}A_j^{-1}}{\sum_j p_j\mathrm{N}_{t-1,j}A_j^{-1}} SC\left(\frac{B_{t-1}}{\mathrm{N}_{t-1}}\right)^{-1} \tag{4}$$

also changes in the number of prey fish N were estimated (Eq. 4). While biomass can increase continuously due to growth (v_t), the number of fish only increases once each year as a result of recruitment, which was assumed to occur in September, around the time of the survey. To estimate the daily food requirement in numbers, the average daily food intake (in kg) was divided by the average weight of the remaining fish (i.e., B_{t-1}/N_{t-1}).

Estimating the uncertainty in the estimated impact of seal predation on fish numbers and biomass is challenging, because it is the result of a propagation in errors of many parameters, for which the uncertainties are often unknown. One of the largest source of uncertainty is the poorly known fish survey catching efficiency, which was caused by the uncertainty in the proportion of lateral escape, avoidance of the approaching vessel, escape underneath, and for the BTS, also the translation from the DFS to BTS catchability based on length-specific catch ratios (Appendix S1). Each step in this chain produces a (length-specific) selectivity curve quantified by parameters and corresponding uncertainties. We repeatedly sampled (500 times) from these parameter distributions, to estimate how uncertainty in the catchability propagates into the estimated effect of seal predation (Eqs. 3 and 4). Species-specific effects on catchability were not taken into account.

RESULTS

Seal diet and daily consumption

Of the 103 fecal samples, 79 contained otoliths (n = 2168). Of these, 36 samples were collected in September, 17 in August, and the rest in November (8), March (5), April (5), January (3), October (2), December (2), and July (1). Samples were collected between 1999 and 2009, with most samples from 2005 (29), 2007 (26), and 2002 (10). The 10 most represented fish species (based on estimated fresh weight) were flounder (39% of the total estimated weight), sandeel (17%), sole (14%), five-bearded rockling (5.1%), whiting (4.6%), plaice (4.4%), cod (4.3%), common dragonet (2.1%), dab (2%), and bull-rout (2%; Fig. 3). Together, these prey species represent 95% of the

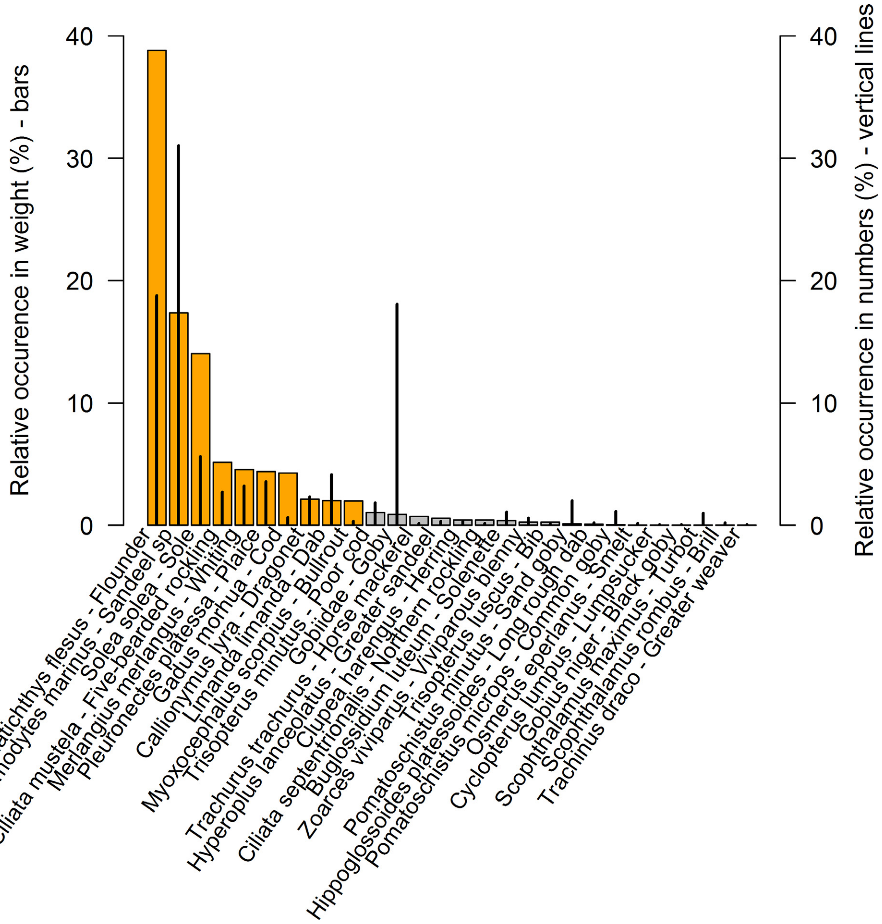

Fig. 3. The percentage by estimated fresh weight (bars, left axis) and number of otoliths (vertical lines, right axis) of each fish species found in harbor seal scat samples collected in the Dutch Wadden Sea. The 10 most important prey species (95% of biomass in the diet) are indicated using orange vertical bars.

seals' diet. Estimated fish lengths in the fecal samples were mostly <25 cm, with a peak between 10 and 20 cm (Fig. 4).

The estimated average energetic content of the fish consumed (weighted by their relative occurrence in the diet, see Fig. 3) was 1.007 kcal/kg (Appendix S2: Table S2). Assuming a daily energetic requirement of 4680 kcal per seal per day (Härkönen and Heide- Jørgensen 1991), this amounts to approximately 4.6 kg per day per individual.

Fish abundance

The biomass of the 10 most important species consumed by harbor seals in the Dutch Wadden Sea (i.e., plaice, sole, dab, flounder, sandeel, whiting, cod, five-bearded rockling, common dragonet, and bull-rout) is shown in Fig. 5 (and Appendix S2: Fig. S4). Up to the mid-1980s, the fish biomass increased in both the Wadden Sea and adjacent coastal zone, but declined after that. In the most recent year (2016), the Wadden Sea contained on average 535 kg/km^2 (corrected for

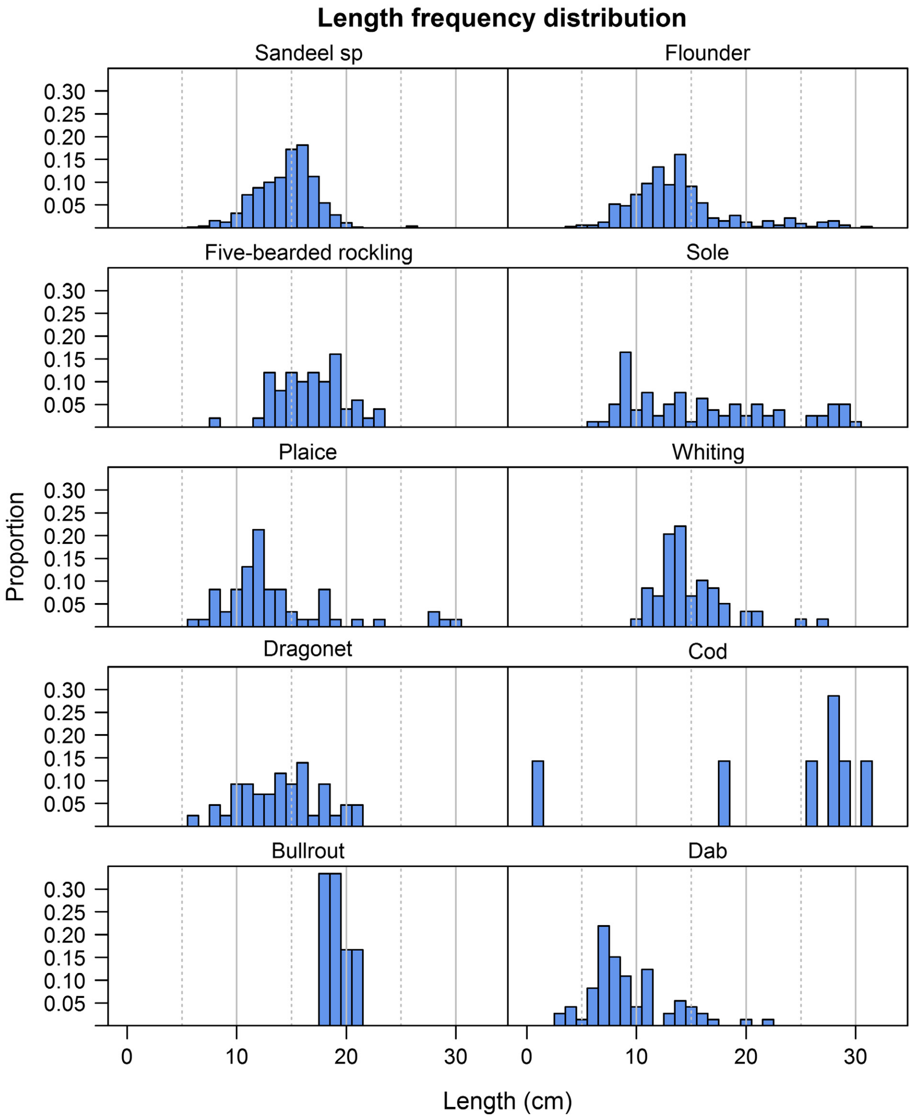

Fig. 4. Length distribution of the 10 most common fish species found in scat samples of harbor seals, collected 1999–2009.

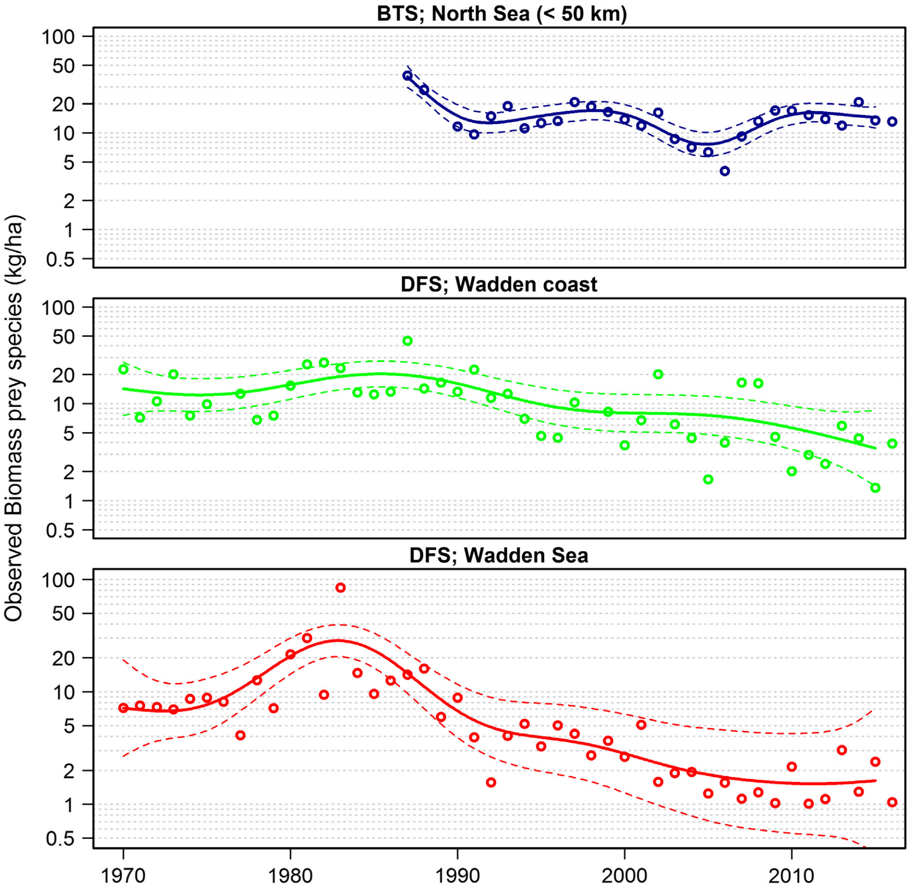

Fig. 5. Trend in biomass (in kg/ha) of the 10 most important harbor seal prey species (based on scat samples), for the beam trawl survey (BTS) in the offshore zone, the demersal fish survey (DFS) in the coastal zone bordering the Wadden Sea (Wadden coast), and the DFS in the Wadden Sea (See also Fig. 2). The solid line represents a generalized additive model where prey biomass density was modeled as a smooth function of year (assuming a quasi-binomial error distribution). Dashed lines represent 95% confidence intervals (Wood 2017). Note the log-scale on the *y*-axis.

catchability) and the adjacent coastal zone (Fig. 2) held 2104 kg/km^2. The total area of these two zones is 2088 and 1707 km^2, respectively. Hence, the average biomass observed in 2016 was 1117 tons for the Wadden Sea and 3592 tons for the adjacent coastal zone. In the Wadden Sea in the most recent 5-yr period (2012–2016), the most abundant prey species were plaice (59%) and flounder (14%). In the coastal zone, the most abundant prey species in the same period were dab (40%), whiting (30%), and plaice (11%; Appendix S2: Fig. S4).

Fish growth

The biomass of demersal fish in the Wadden Sea and nearby waters shows large seasonal variability. Most 0-yr-old fish (e.g., plaice, sole, and flounder) settle in early spring (March/April). These 0-yr-olds can be highly abundant, but their total biomass is still low. They grow during spring and summer, and once they exceed ~5 cm (around June–July; Fig. 6; Appendix S2: Fig. S3a–e), they can be caught by DFS-type gear. From September onwards, the observed growth of 0-yr-old plaice and flounder was substantially reduced, despite the high-water temperature which should result in large growth according to the DEB model (Fig. 6). The following spring (March/April) they (now 1-yr-olds) start to grow again, despite low water temperature (Fig. 6; Appendix S2: Fig. S3a–e), suggesting food availability is sufficient. They continue to grow up to the late

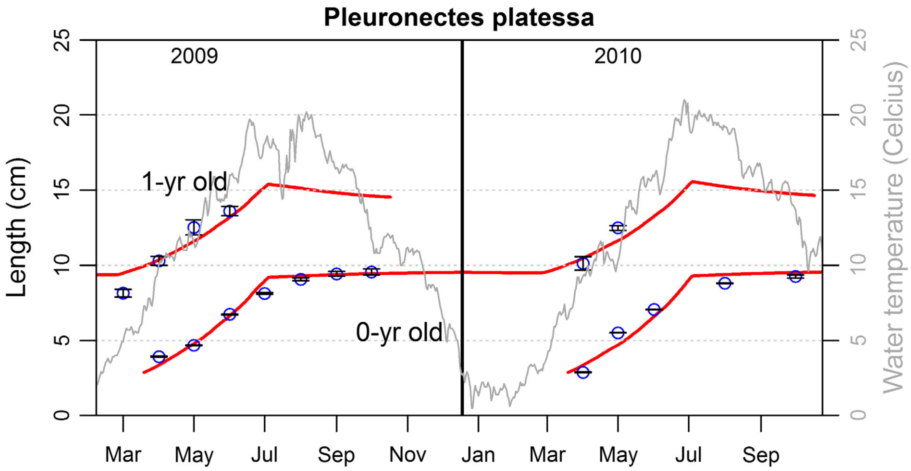

Fig. 6. Observed length (circles and standard error bars) and predicted length (solid red line) of 0- and 1-yr-old plaice. Gray line indicates water temperature. Predicted growth (solid lines) is based on DEB model where food intake parameter *f* was allowed to vary between the winter months ($f = 0.11$) and other times of the years ($f = 0.66$).

summer and fall. The predicted decline in length during the winter months is an artifact of the model: Since length is defined as a function of volume $V^{1/3}$, a decrease in volume will lead to an apparent decrease in length.

Harbor seal spatial distribution and foraging activity

Although harbor seals are often observed on the sandbanks located within the Wadden Sea, at any time, they only spend on average 17% of their time on land (Appendix S2: Fig. S1). Of the remaining 83% of their time, harbor seals spend on average 26% within the Wadden Sea, 28% in the adjacent coastal zone and the remaining time, 46% further offshore (Fig. 2; Appendix S2: Fig. S1). There are, however, large seasonal variations. During summer months (April–September), seals spend more time on land (20–23%), and the least amount of time outside the study region (i.e., beyond the 50 km buffer). During the winter months, seals spend most time further offshore beyond the 20 m depth line, outside the Wadden Sea and Wadden coast zone (Appendix S2: Fig. S1).

The time spent in each zone is not necessarily a good proxy for foraging, as seals also perform other activities at sea (like resting or transiting). When considering the total dive time (<1.5 m depth) in each zone, only 14% of their dive time is spent within the Wadden Sea (substantially less than the total time spent there), 31% in the Wadden coastal zone, and 46% in the remaining areas further offshore. Particularly during the winter months January–March, they spend most time diving further offshore and only spend 26–37% of their dive time in the Wadden Sea and Wadden coastal zone (Appendix S2: Fig. S1).

Consumption estimates

The total number of seals counted in the Dutch Wadden Sea in 2016 was 8160 (Galatius et al. 2017), of which 7004 individuals occurred in our study region (i.e., excluding Ems estuary). Assuming a 0.68 haul-out probability during low tide in summer when the Dutch aerial surveys are conducted (Ries et al. 1998), 10,300 were estimated to be present. Based on the estimated 4.6 kg of fish consumed per seal per day, these 10,300 harbor seals in the study region consumed approximately 48,000 kg of fish per day, and 17,500 tons of fish that year. This total estimated fish consumption by seals for one complete annual cycle is substantially larger than the estimated fish standing stock biomass observed in the Wadden Sea (~1100 tons) and adjacent coastal zone (~3600 tons) at the time of the survey.

As the observed average fish growth (based on flounder, plaice, dab, sole, and bull-rout) was low during the winter months, harbor seals were expected to have the largest impact on the fish population during this period (Fig. 7). During

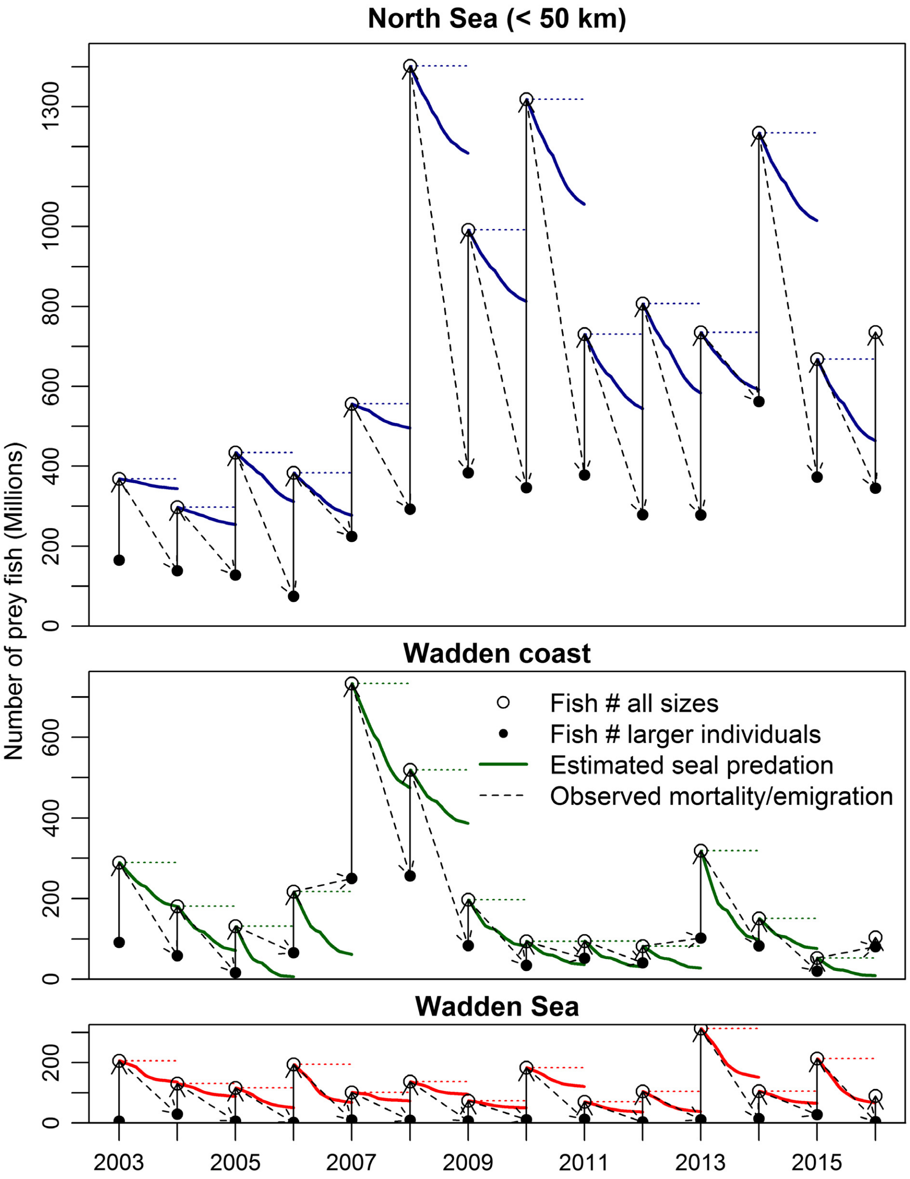

Fig. 7. The estimated effect of seal predation on the number of prey fish for the Wadden Sea (red lines), Wadden coast (green lines), and remaining areas up to 50 km from the haul-outs (blue lines, and see regions in Fig. 2). The fish survey in September (i.e., BTS for the North Sea areas within 50 km of the nearest haul-out, and DFS for the Wadden coast and Wadden Sea) is the starting point (open circle, representing all size classes), after which numbers decline due to seal predation. In the subsequent survey in September the following year, the number of remaining individuals (black dot, representing larger individuals, >13.5 cm, presumed 1+ yr-olds) has declined, but is again supplemented with new recruits. In the Wadden Sea, nearly all larger individuals (black dots) seemed to have disappeared (either they died or moved elsewhere).

the more productive spring and summer months, seals will continue to have an impact on prey numbers; however, prey biomass continues to increase due to growth. Fig. 7 also shows the decline in numbers of fish (all ages) observed in a specific year, and the number of larger individuals (attempting to exclude 0-yr-olds) the following year. While seal predation is estimated to be a major contributor to the apparent annual fish mortality, for most years the fish mortality (or emigration) exceeds the estimated mortality caused by seals (the difference between solid colored lines, with seal predation, and the dotted lines in Fig. 7). For the Wadden coast, the estimated impact of seals is highest, and for several years, the estimated mortality caused by seals exceeds the observed decline in prey numbers from one year to the next. Based on all years combined (2003–2016), the average estimated mortalities for the different zones are 43% (SD = 13%) for the Wadden Sea, 60% (SD = 19%) for the Wadden coast, and 20% (SD = 7%) for the North Sea zone further offshore. Similar reductions were estimated for the biomass of the seals' prey (Appendix S2: Fig. S5), but mostly during the winter months when fish growth is low. During the productive summer months, the increase in biomass outpaced the seal predation.

The estimated impact of seal predation contained a large number of uncertainties. One of the largest source of uncertainty was the uncertainty in the catchability estimate (Fig. 8). For example, we estimated that seal predation in the Wadden Sea in 2016 would lead to an estimated reduction of prey species varying between 5% and 75% (i.e., 95% CI). This implies that the estimated impact of seal predation could be either substantially larger or smaller than our mean estimate.

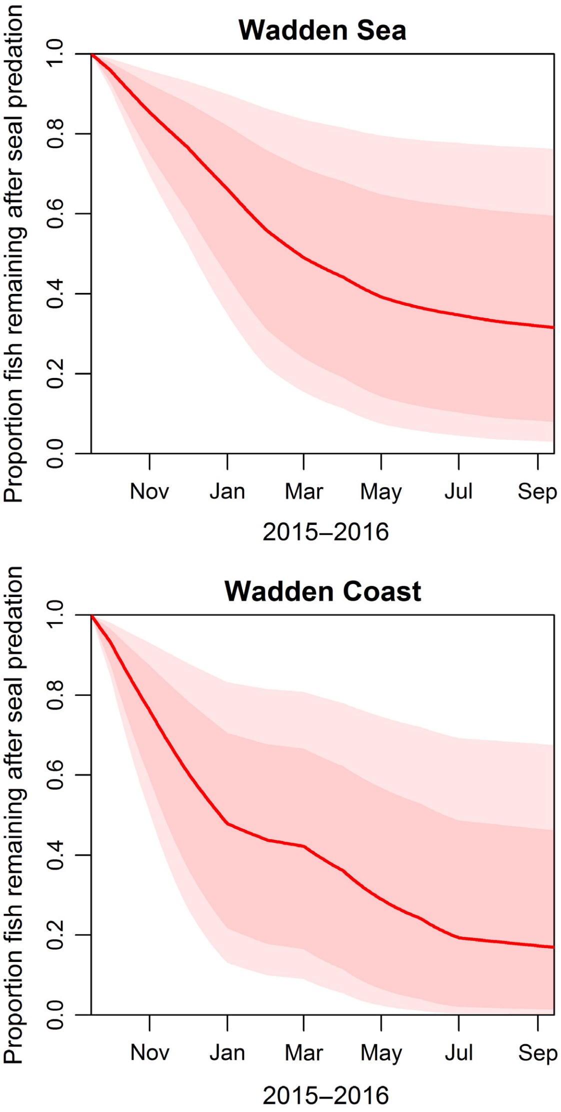

Fig. 8. Uncertainty in the effect of the estimated impact of seals on fish numbers in the Wadden Sea (top) and Wadden coast (bottom). The solid red line represents the mean estimated impact, the darker pink area the ±SE, and the light pink shaded area reflects the 95% confidence intervals.

Discussion

The impact of seals on fish biomass in the Wadden Sea and adjacent coastal zone

For the demersal fish species remaining in the Wadden Sea and nearby shallow coastal zone (<25 m depth) from September onwards, we estimated that harbor seal predation would impose an annual mortality of approximately 50%. There are however large sources of uncertainty which are described in the following section. This high estimated predation pressure can be explained by the relatively large estimated annual fish consumption by harbor seals (i.e., ~17,500 tons between September 2015 and 2016) compared to the recent low prey fish standing stock biomass observed in the Dutch Wadden Sea (1100 tons) and adjacent Wadden coastal zone (3600 tons). While during the productive summer months fish biomass production should outpace seal predation (Appendix S2: Fig. S1), this is unlikely to be the case during the colder winter months, when fish growth (i.e., biomass production) is limited. Particularly during those colder periods seals may be able to deplete prey resources locally, and this could be one explanation why harbor seals only spend ~14% of their diving time in the Wadden Sea, and extensively feed further offshore, particularly during the winter months (Appendix S2: Fig. S1).

Although the total demersal fish biomass in the Wadden Sea and nearby waters has decreased in the last two decades and the size of the harbor seal population has strongly increased, there are two reasons why it is unlikely that seals are the single cause of the decline in the fish populations in the Wadden Sea. First, the decline in fish stocks in the Wadden Sea and coastal waters started in the mid-80s, when the seal population was not recovered and numbers were still low. The decrease in fish biomass from the mid-1980s was therefore most probably related to a combination of a decrease in nutrient loadings (Støttrup et al. 2017) and increase in water temperature (Teal et al. 2012). Second, the decline in demersal fish biomass (and fish numbers) in and near the Wadden Sea was observed for all age-classes, including the 0-yr-olds (Tulp et al. 2008, Støttrup et al. 2017). Since harbor seals seem to predominantly feed on fish >10 cm (Fig. 4), we expect the predation pressure by seals on small (<10 cm) 0-yr-olds prior to the survey in September to be rather low. Therefore, bottom-up processes (e.g., low nutrient loadings) in combination with mortality by birds or by-catch in the shrimp fishery are a more likely explanation for the observed decline in 0-yr-old fish biomass. However, during the winter months following the survey, seals could impose a considerable predation pressure on the remaining prey. Hence, given the low fish density and high seal numbers it is likely that seals are currently applying top-down pressure on fish occurring in the Wadden Sea and nearby shallow waters, especially on those fish species found in high numbers in their diet and who predominantly occur in these shallow waters, like flounder.

These results are in line with some studies that suggest that the predation pressure by marine mammals could alter the abundances of prey species. For examples, gray seals (*Halichoerus grypus*) may have impaired the recovery of overexploited northwest Atlantic cod stocks (Trzcinski et al. 2006, Cook and Trijoulet 2016). Benoît et al. (2011) estimated that in the Gulf of St. Lawrence (East Canada), gray seal predation constitute 20–50% of natural mortality of some demersal fish species. In contrast, other studies elsewhere have demonstrated low impacts by seals on fish communities (Houle et al. 2016). Such differences between observed impacts undoubtedly relate to the sizes of seal and fish stocks, the relative importance of other ecosystem components (e.g., commercial fishery and predation by fish like cod and whiting; Temming and Hufnagl 2015), stock replenishment rates, and the spatial scale at which the comparison between seal consumption and fish stock size is made. Here, this comparison is made for the area in the direct vicinity of the haul-out sites from which seals forage, and hence, resource depletion is more likely to occur. Such local depletion has been observed in several colonial central-place foraging species and is known as Ashmole's halo (Gaston et al. 2007).

Sources of uncertainty

One main source of uncertainty was the lack of experimentally derived catchability estimates (Fraser et al. 2007) for the DFS gear. Instead, we attempted to estimate catchability based on experiments for plaice, which used different fishing gear (Kuipers 1975). Plaice only constitute 4.4% of the seals diet and the catchability of other species might be very different from plaice. For example, sandeel is the second most important prey item observed in the seal diet, but they are not caught optimally by the used gears, because of their pelagic and burial phase, and their thin elongated shape. Surveys specifically designed for sandeel use different gear that dislodges them from the substrate and consequently catch higher numbers (Tien et al. 2017). Also, other pelagic species (e.g., herring, sprat) are poorly sampled by a demersal beam trawl gear (Couperus et al. 2016). Although only two of the sampled scats contained herring (max 5%), only five samples were collected between December and February. Harbor seals may feed more on pelagic fish species (e.g., herring, sprat) during these winter months (de la Vega et al. 2016). This could imply that the consumption of demersal prey, and impact of seals on the demersal fish community, might be overestimated.

Another source of uncertainty is where seals capture their prey. In this study, the prey removal in each region was defined as the product between prey density and dive time in the different regions. Clearly, some dive time is not related to foraging, and the amount of non-foraging dives may differ between the regions, and even between seasons. In addition, the distribution of their prey is not static. While we accounted for changes in prey density due to seal predation, relative changes in fish distribution were not taken into account. For example, several studies have suggested an offshore movement of fish toward deeper (warmer) waters during the winter months (de Veen 1978, Teal et al. 2012, van der Veer et al. 2016). This also seems to be reflected in the movement of seals that tend to forage further offshore during the winter (Aarts et al. 2016). In addition, also other sources of mortality (e.g., predation by cormorants or by-catch in the shrimp fishery [Leopold et al. 1998, Glorius et al. 2015]) could locally lower fish density. This would lead to lower intake rates by seals, possibly over-estimating the effect of seal predation in the Wadden Sea.

However, regardless of where exactly seals capture their prey, all living seals ultimately need to acquire sufficient prey to meet the energy demands (Härkönen and Heide- Jørgensen 1991). Since foraging sites within and close to the Wadden Sea require less traveling, they are more beneficial. Therefore, if prey quality and catchability is equal in the different regions, which might not necessarily be the case, the highest reduction in food density is expected to occur near the colony.

Other predators in the Wadden Sea

In order to evaluate the relative importance of top-down regulation by harbor seals, we need to consider other sources of mortality, such as predation by other marine mammals, piscivorous birds, predatory fish, and commercial fishery (Zijlstra and Van Eerden 1995, Leopold et al. 1998, Arnett and Whelan 2001, Glorius et al. 2015, van Kooten et al. 2015, Hansson et al. 2017). This is challenging though, since they target different size classes, and the estimated removals are based on different methodologies.

Gray seal numbers in the Wadden Sea have grown exponentially after 1990 (Brasseur et al. 2015), with a maximum of 4045 counted in the Dutch section of the Wadden Sea during the molt in 2017 (Brasseur et al. 2017). Although gray seals in the North Sea primarily feed on sandeel, they also feed on other benthic prey species (Brown et al. 2012). While gray seals may visit areas >100 km offshore, presumably to feed on sandeel grounds, they also spend a large amount of time in coastal waters near the Wadden Sea, overlapping with harbor seal distribution.

In addition to gray and harbor seals, 30,000–80,000 harbor porpoises are estimated to reside in the Dutch section of the North Sea (Geelhoed et al. 2013). Only a small part of this population uses the Wadden Sea and nearby coastal zone. In Denmark and Germany, harbor porpoises are present near the Wadden Sea throughout the summer season and are known to feed on 0-yr-old flatfish species (Gilles 2008). However, stomachs of stranded harbor porpoises from the Dutch coast mainly contained whiting, sandeel, and gobies and only a small proportion of flatfish (Leopold 2015).

Several birds like cormorants and divers also feed on demersal fish species. Cormorants are abundant and specialize mainly on 0-group flatfish, for example, plaice, dab, and flounder (Leopold et al. 1998). Currently, approximately 25,000 cormorants overwinter and breed in the Netherlands, of which half breed near the Wadden Sea (www.sovon.nl). Cormorants require approximately 460–500 g of fish per day (Zijlstra and Van Eerden 1995, Leopold et al. 1998). Assuming these cormorants feed continuously within and near the Wadden Sea, this equates to a prey requirement of approximately 2300 tons per year.

In addition to the natural sources of mortality, mortality due to commercial fisheries should also be considered. When considering the whole North Sea, the total catch by the commercial fishery exceeds by far the consumption by marine top predators (Engelhard et al. 2013). This pattern is also evident in other regions, like the Baltic (Hansson et al. 2017). However, locally near the coast with high densities of central-place foraging predators, the impact of these predators may exceed that of fishing (Hansson et al. 2017). In the Dutch coastal zone, the fisheries specifically targeting demersal fish species are rather small compared to the other predators (i.e., landing 723 tons, including 99 tons in the Wadden Sea; van Kooten et al. 2015). However, the fishery targeting shrimp, by far the most important fishery in and around the Wadden Sea, does by-catch demersal fish species, with plaice being the most numerous one. In the Dutch Wadden Sea alone, shrimp fisheries catch an estimated 99 million 0- and 1-yr-old plaice, mostly during the summer months (adapted from Glorius et al. 2015). The total number of plaice (corrected for catchability) present during the DFS in September was estimated at 89 million. This suggests that prior to the DFS and predation by seals, a large proportion of the 0-yr-old plaice was already caught by the shrimp fishery.

Although the population size, food requirement, and target species differ between marine predators and fishery, they can collectively impose a considerable predation pressure on the demersal fish communities of the Wadden Sea and nearby coastal waters. Recent simulations for a North Sea ecosystem not only suggest that top-down fishing pressure can be of tremendous importance for the dynamics of fish populations. Such top-down effects may even cascade down to lower tropic levels, like plankton (Lynam et al. 2017).

Are harbor seals food-limited?

Since harbor seals are central-place foragers, some depletion near the colonies is likely to occur. Also elsewhere (e.g., the Skagerrak in Danish and Swedish waters) such density-dependent reductions in prey availability near seal haul-outs seem to occur, which was assumed to have led to a reduction in seal somatic growth (Harding et al. 2018). However, harbor seals hauling-out in the Wadden Sea also forage well beyond the coastal zone (Fig. 2), where prey density is higher (Fig. 5) and the estimated depletion is substantially lower (Fig. 7). In recent years, harbor seals appear to be using the west coast of the Netherlands more frequently (Aarts et al. 2013), which suggests that more distant areas have become more attractive foraging locations than previously. Although the harbor seal population in the Dutch part of the Wadden Sea is still increasing (but at a slower rate than before), in other regions, like Denmark, the population seems to have reached a plateau (Brasseur et al. 2018). Given the estimated impact of harbor seals on the fish community, it is likely that the slowing down in the population growth is at least partly the result of food limitation.

Density-dependent processes and possible interactions between seals and fishery

While seals can impose a considerable mortality on individual fish, it is still debatable whether seals have an overall impact on fish biomass. This ultimately depends on whether seal predation keeps the fish numbers well below the level where intra- or inter-specific competition for food will occur. Lorenzen and Enberg (2002) reported density-dependent growth (DD-growth) reduction in 9 out of 16 marine fish populations studied. DD-growth is assumed to mainly occur in the early life of a cohort (Anderson et al. 2017) and has been reported frequently in species that concentrate during their juvenile phase in shallow coastal waters (Beverton 1995). For instance, DD-growth has been observed in juvenile plaice and sole in years of exceptionally large year classes (Rijnsdorp and Van Leeuwen 1996). The observed reduction in growth of 0-group fish species (e.g., plaice and flounder) corroborates that in summer food becomes a limiting factor in the Wadden Sea.

The density-dependent reduction in juvenile growth may have been a regular phenomenon prior to the period of eutrophication of the coastal waters (Bolle et al. 2004). Productivity in the coastal waters has decreased recently supposedly in response to the decrease in nutrient inputs (Philippart et al. 2007, Støttrup et al. 2017), lowering the biomass at which density-dependent competition for food will occur. Whether the increased predation pressure from seals is sufficient to suppress the fish biomass below a critical level where resource competition starts to slow down growth requires further study.

Another aspect that would require further study is whether seals compete with other predators, like the commercial fishery. When both marine mammals and fishery target the same (over-exploited) fish species, the additional mortality imposed by seal predation may hamper the recovery of some commercially important target species, as was suggested for cod in the west Atlantic (e.g., Trzcinski et al. 2006, Cook et al. 2015, Cook and Trijoulet 2016). However, if marine mammals and fishery target different species or size classes, this could give rise to both positive and negative feedback loops (Yodzis and Innes 1992), and the competition between marine mammals and fishery might be less obvious (Morissette et al. 2012, Houle et al. 2016).

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