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Harbour seals are regaining top-down control in a

coastal ecosystem

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20 **ABSTRACT**

21 Historic hunting has led to severe reductions of many marine mammal species across the

22 globe. After hunting ceased, some populations have recovered to pre-exploitation levels,

23 and may again act as a top-down regulatory force on marine ecosystems. Also the

24 harbour seal population in the international Wadden Sea grew at an exponential rate

25 following a ban on seal hunting in 1960's, and the current number ~38,000 is close to the

26 historic population size. Here we estimate the impact of the harbour seal predation on the

27 fish community in the Wadden Sea and nearby coastal waters.

28 Fish remains in faecal samples and published estimates on the seal's daily energy

29 requirement were used to estimate prey selection and the magnitude of seal consumption.

30 Estimates on prey abundance were derived from demersal fish surveys, and fish growth

31 was estimated using a Dynamic Energy Budget model. GPS tracking provided

32 information on where seals most likely caught their prey.

33 Harbour seals from the Dutch Wadden Sea fed predominantly on demersal fish, e.g.

34 flatfish species (flounder, sole, plaice, dab), but also sandeel, cod and whiting. Total fish

35 biomass in the Wadden Sea was insufficient to sustain the estimated prey consumption of

36 the entire seal population year-round. This probably explains why seals also acquire prey

37 further offshore in the adjacent North Sea, only spending 13% of their diving time in the

38 Wadden Sea. Still, seal predation was estimated to cause an average annual mortality of

39 43% and 60% on fish in the Wadden Sea and adjacent coastal zone, respectively. There

40 were however large sources of uncertainty in the estimate, including the migration of fish

41   between the North Sea and Wadden Sea, and catchability estimates of the fish survey

42   sampling gear, particularly for sandeel and other pelagic fish species.

43   Our estimate suggested a considerable top-down control by harbour seals on demersal

44   fish. However predation by seals may also alleviate density-dependent competition

45   between the remaining fish, increasing fish growth, and partly compensating for the

46   reduction in fish numbers. This study shows that recovering coastal marine mammal

47   populations could potentially become an important component in the functioning of

48   shallow coastal systems.

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50   **Keywords**: *Phoca vitulina vitulina, predation pressure, top-down regulation, sealing,*

51   *impact, diet, demersal fish, coastal ecosystem, intertidal, top-predator, seals*

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54 **INTRODUCTION**

55 Large-scale historic whaling and sealing led to a severe global decline of many marine

56 mammal species (Clapham et al. 1999, Baker and Clapham 2004). As a consequence,

57 marine ecosystems may have lost important regulating forces from such top-predators

58 (Heithaus et al. 2008, Estes et al. 2016). While some marine mammal populations have

59 not fully recovered after hunting ceased (Baylis et al. 2015), or have even continued to

60 decline (Springer et al. 2003), others have gone through rapid increases (Brasseur et al.

61 2015, 2018) reaching or exceeding presumed pre-exploitation levels (Roman et al. 2015).

62 This raises the question how such recoveries influence the food web regulation in marine

63 ecosystems.

64 Harbour seals (*Phoca vitulina*) have been top predators in the Wadden Sea of the

65 Netherlands, Germany and Denmark, since its formation 7,500 year ago. Due to severe

66 human hunting, their numbers declined from an estimated 40,000 in 1900 to

67 approximately 4,500 around 1960 (Reijnders 1992). After a ban on seal hunting, the

68 population grew at an annual rate of 12% (Brasseur et al. 2018). Currently, the population

69 is approaching pre-1900 levels with approximately 38,000 individuals regularly hauling

70 out in the international Wadden Sea (Galatius et al. 2017), of which approximately

71 10,000 in the Dutch part of the Wadden Sea (Figure 1).

72 Harbour seals require approximately 4-5 kg of fish each day, although this varies by

73 season and the seals' size (Härkönen and Heide- Jørgensen 1991). They are considered

74 generalist predators feeding on both demersal and pelagic fish species, but in shallow,

75 soft-sediment regions like the southern North Sea, they mostly eat flatfish (~75%) such as

4

76   flounder (*Platichtys flesus*), sole (*Solea solea*), and dab (*Limanda limanda*), but also

77   gadoids, sandeel (*Ammodytidae*) (Härkönen 1987, Tollit et al. 1997, Kavanagh et al.

78   2010).

79   The strong growth of the harbour seal population in recent decades occurred almost at the

80   same time as the abundances of their prey in the Wadden Sea and the adjacent coastal

81   zone of the North Sea declined (Tulp et al. 2008, 2017). Some size classes, such as >1

82   year old plaice and flounder, have almost completely disappeared from the Wadden Sea

83   (van Keeken et al. 2007, van der Veer et al. 2011). Several hypotheses have been put

84   forward to explain the declines in the fish biomass, e.g. increasing water temperature,

85   increased human activities, declining nutrients due to cleaner river outflows, fishery

86   bycatch or increased predation by birds (e.g. cormorants) and seals (Temming and

87   Hufnagl 2015, van der Veer et al. 2016, Tulp et al. 2017).

88   The objective of this study is to estimate the role of predation pressure by harbour seals

89   on the demersal fish community in the Dutch Wadden Sea and nearby coastal North Sea.

90   The specific value of this study is that such estimates of predation pressure can

91   subsequently be included as an additional source of mortality into fish population models

92   (Tyrrell et al. 2011). More generally, this study may shed light on how marine coastal

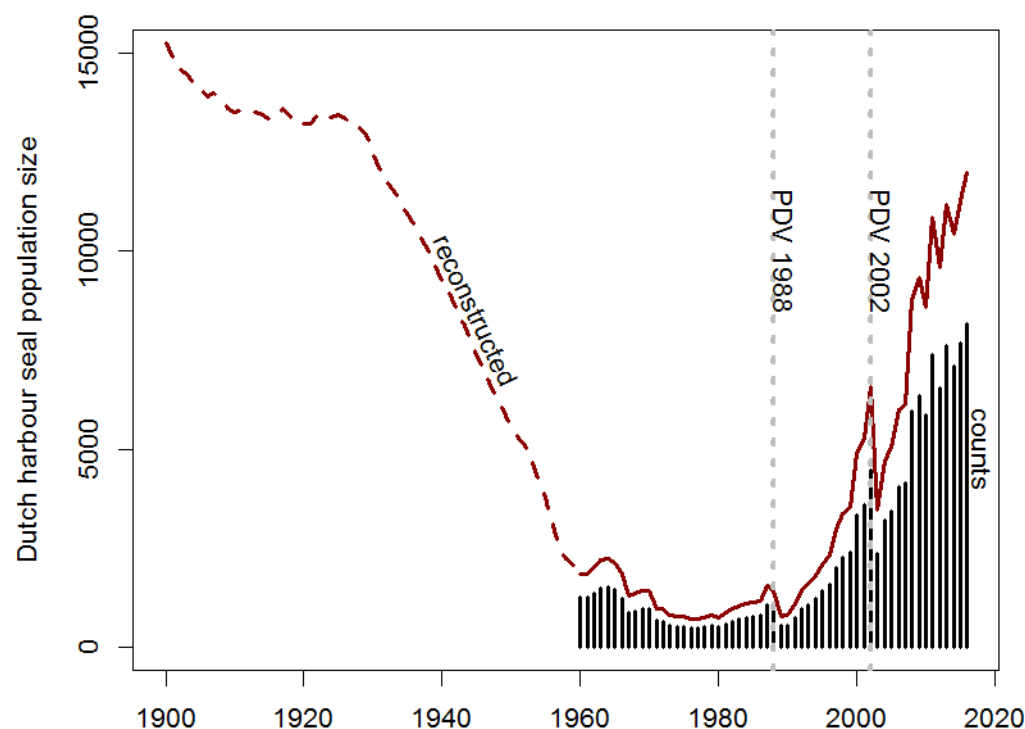93   ecosystems function under the presence of large numbers of marine top-predators.

Figure 1. Development of the harbour seal population in the Dutch Wadden Sea. The maximum numbers of seals observed during the moult 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).

METHODS

Analysis structure

6

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

107   1. Harbour seal diet was defined based on analysis of faecal samples collected on

108   haul-out sites in the Dutch Wadden Sea.

109   2. Based on estimated seal energy requirements, and energetic content of the prey in

110   their diet, the average daily fish consumption was estimated.

111   3. The total daily fish consumption by all harbour seals was estimated, taking into

112   account the size of the population in the Dutch Wadden Sea and the time spent

113   foraging in different regions (using data from GPS tracked harbour seals).

114   4. Total number and biomass of prey species present in three regions (Wadden Sea,

115   Wadden coastal zone up to 25 m depth ('Wadden coast') and offshore North Sea

116   up to 50 km from the nearest haul-out) were estimated using data from the annual

117   demersal fish survey (DFS) and beam trawl survey (BTS) collected in September

118   5. Growth in prey biomass from September onwards was reconstructed using a

119   dynamic energy budget (DEB) model. The model was fitted to seasonal length

120   distribution data, and accounted for daily variations in temperature.

121   6. The reconstructed prey numbers and biomass were subsequently reduced by the

122   estimated daily food intake by all harbour seals.

123

124   *1. Harbour seal diet based on faecal analysis*

125   Between 2002 and 2009, 103 faecal samples were collected opportunistically from tidal

126   haul-out sites throughout the Dutch Wadden Sea. Most samples were collected near

127   Texel in the west (i.e. 'Noorderhaaks' and 'Steenplaat') and near Schiermonnikoog in the

7

128   east (i.e. 'Simonszand') (Figure 2a). After collection, samples were frozen (-20°C) until

129   further processing. For the analysis, samples were placed in a meshed (120μm) bag and

130   washed in a laundry washing machine at 70°C, including a prewashing cycle using a

131   biological detergent (Biotex, Unilever). Samples were then dried. Recognisable fish

132   remains (otoliths and bones) were picked out using a binocular microscope. These hard

133   parts were identified using available reference guides (Härkönen 1986, Watt et al. 1997)

134   and compared to a reference collection. For this study only otoliths were used. Otoliths

135   were measured using digital callipers (to 0.1 mm), and assigned to a wear class. After

136   correction for wear (Leopold 2015), both otolith length and width were used to infer fish

137   length based on known otolith length - fish length regressions (Härkönen 1986, Watt et

138   al. 1997, Leopold et al. 2001). Fish weights were inferred using known fish length –

139   weight regressions ((Robinson et al. 2010) and WMR unpublished data). The ten most

140   important species in the diet were identified based on calculated contributions by fresh

141   mass to the seal diet.

142

143   *2.   Harbour seal average daily food requirement*

144   Harbour seals require energy for maintenance and growth (Markussen et al. 1990),

145   reproduction (i.e. foetal growth, lactation, mating), moult, and activities such as

146   locomotion. Juvenile phocid seals require on average 1.4 times more energy per kg body

147   weight for maintenance and growth than adults (Innes et al. 1987), but have a lower

148   overall energy requirement because they are smaller in size and do not take part in

149   reproduction. A study on captive harbour seals (four adult males, one sub adult male and

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150   1 adult female) which were fed ad libitum, the gross energy intake was estimated to be

151   6071 kcal/day (Rosen and Renouf 1998). These estimates were close to the estimates for

152   adult males used by (Härkönen and Heide- Jørgensen 1991, i.e. 5890 kcal/day). When

153   taking the local population structure into account, Härkönen & Heide- Jørgensen (1991)

154   estimated that on average harbour seals in the Skagerrak (Sweden) have an ingested

155   energy requirement (*ER*) of 4680 kcal per day.

156   To meet this energy requirement, Härkönen & Heide- Jørgensen (1991) estimated that

157   harbour seals should consume 4.1 kg of flatfish each day in the Skagerrak. The energy

158   densities of their prey, and hence also the seals' food intake varies between prey species

159   and seasons (Pedersen and Hislop 2001). The energy density of fish is often highest just

160   after the growth season, prior to the winter, which is subsequently devoted to

161   maintenance and reproduction (Dawson and Grimm 1980). Whenever possible, we used

162   caloric densities from late summer, early winter (see Table 1). The average daily

163   consumption *C* (in kg) per seal, was estimated based on the energy required (ER) and

164   species-specific caloric densities (*ED* in kcal/g), weighted by the relative occurrence of

165   prey W_i in the harbour seal diet:

166     $$C = \frac{ER}{\sum_{i=1}^{n} W_i ED_i} \quad \text{eq. 1}$$

167   *3. Total fish consumption and distribution of foraging effort*

168   To estimate the total fish consumption by harbour seals in the Wadden Sea and nearby

169   waters, information is needed on how many seals there are, and where they acquire their

170   food. Harbour seal count data were collected annually in the Dutch Wadden Sea using

171   aerial surveys since the 1960s (Brasseur et al. 2018). To correct for the number of seals in

172   the water during the aerial survey counts, this studied assumed a haul-out probability of

173   68% (Ries et al. 1998).

174   To study the seals' distribution at sea, we relied on data from animal-borne GPS data

175   loggers collected in a series of research projects. In total, 225 harbour seals were tracked

176   in the Netherlands between 2007 and 2015, with most (142 individuals) tracked from the

177   Ems estuary (tagged between 2009 and 2011). Harbour seals were caught on haul-out

178   sites with a large seine net, fitted with Fastloc GPS data loggers glued to the fur of the

179   neck using epoxy, and released directly on location. Loggers fell off as hair weakened

180   during the annual moult (July-August), if they did not dislodge before-hand. The GPS

181   data loggers also contained depth and submergence sensors: These were used to

182   determine the activity of the seal: "diving" (deeper than 1.5 m for at least 8 s), "at

183   surface" (no dives for 180 s) or "hauled out" (start = continuously dry for at least 600,

184   end = wet for at least 40 s). Dive records included a description of the dive-profile at 23

185   points of the dive, but also summary data on maximum dive depth, dive duration, and

186   surface interval duration. All data were stored on-board and transmitted, when in contact

187   with a GSM base.

188   The seal location data from the GPS loggers were classified into trips, where the start and

189   end time of each trip was defined by the haul-out data from the loggers. The seal's haul-

190   out location was linked to the nearest known haul-out site (based on aerial survey data).

191   Only locations from trips starting at haul-out sites in the defined study area (i.e. the Dutch

192   Wadden Sea, see Figure 2) were used. Location data from seals making trips from haul-

193   out sites located within the Ems estuary were excluded, since they were over-represented

194   in the sample, and inclusion would result in an over-estimate of the time harbour seals

195   spent within the Wadden Sea. The seal GPS location data were used to estimate the

196   fraction of time spent at sea, within three zones: i.e. the Wadden Sea, the adjacent coastal

197   zone up to the 25 m depth contour ('Wadden coast') and the offshore area between the 25

198   m depth contour up to 50 km distance from haul-out sites (Figure 2). The proportion of

199   time spent 'foraging' within the different regions was estimated by calculating the dive

200   time (i.e. time spent below 1.5 m depth) in each region, as fraction of total dive time. It

201   was not possible to identify feeding dives from other dives (e.g. resting or transiting),

202   because Wadden Sea and nearby waters are shallow (max 30 m), and the bottom is

203   always within reach.

204

205   *4. **Estimation of total number of biomass prey species present in Wadden Sea and***

206   *nearby waters*

207   Data were available from four fish surveys; the demersal fish survey (DFS), the Dutch

208   beam trawl survey (BTS), the international bottom trawl survey (IBTS) and the sole net

209   survey (SNS) (see Figure 2b for distribution of sample locations, see Appendix 2: Table

210   S1 describing the gear characteristics). The DFS has been conducted annually in

211   September-October since 1970. The DFS covers the Wadden Sea and coastal waters (up

212   to 25 m depth) from the southern border of the Netherlands to Esbjerg (van Beek et al.

213   1989). A smaller beam size (3 m) was used in the Wadden Sea, to navigate the often-

214   narrow gullies, while a larger, more robust beam (6 m) was used in the more exposed

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215   adjacent waters. Both gears were rigged similarly, only the size of the beam differed: the

216   trawls were rigged with one tickler chain, a bobbin rope, and a fine-meshed cod-end (20

217   mm). In the Wadden Sea, fishing was restricted to the tidal channels and gullies deeper

218   than 2 m because of the draught of the research vessel. By fishing at low speed (2–3

219   knots) and using a fine meshed cod end (20 mm), larger sized fish (>15 cm) were

220   relatively underrepresented in the surveys. The gear used is suitable for demersal species,

221   but suboptimal for pelagic species such as herring and sprat. Totals of 110-120 hauls in

222   the Wadden Sea and 30 hauls in the adjacent coastal zone were taken annually, unless

223   adverse weather conditions limited sampling. During each haul the position, date, time of

224   day and depth were recorded. Fish species were identified and measured to the nearest

225   cm. Local fish densities (n/10,000 m^2) were calculated from fish counts per haul using the

226   travelled distance during the haul and the beam width to calculate the swept area.

227   The Dutch BTS covers the central North Sea, and is designed to sample the older flatfish

228   species (i.e. ≥1 year old). Compared to the DFS, the BTS is carried out with a larger

229   beam trawl (8 m), a higher speed (4 knots) and a larger mesh size of 120 mm, with 40

230   mm stretched mesh cod end (Rogers et al. 1998). Another fish survey in the region is the

231   IBTS (Heessen and Daan 1996). Its aim is to obtain recruitment-indices for species, like

232   cod, haddock, whiting, Norway pout, mackerel, saithe, herring and sprat, but catchability

233   of flatfish species is very low. The SNS focuses on 1-4 year old sole (van Keeken et al.

234   2007), but fishing only takes place at pre-defined transects parallel or perpendicular to the

235   coast. Because of the above mentioned limitations, this study only uses the DFS for the

236   Wadden Sea and nearby coastal zone, and the BTS for regions further offshore regions

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237   (up to 50 km from the nearest Wadden Sea seal haul-out site). Only data from quarter 3

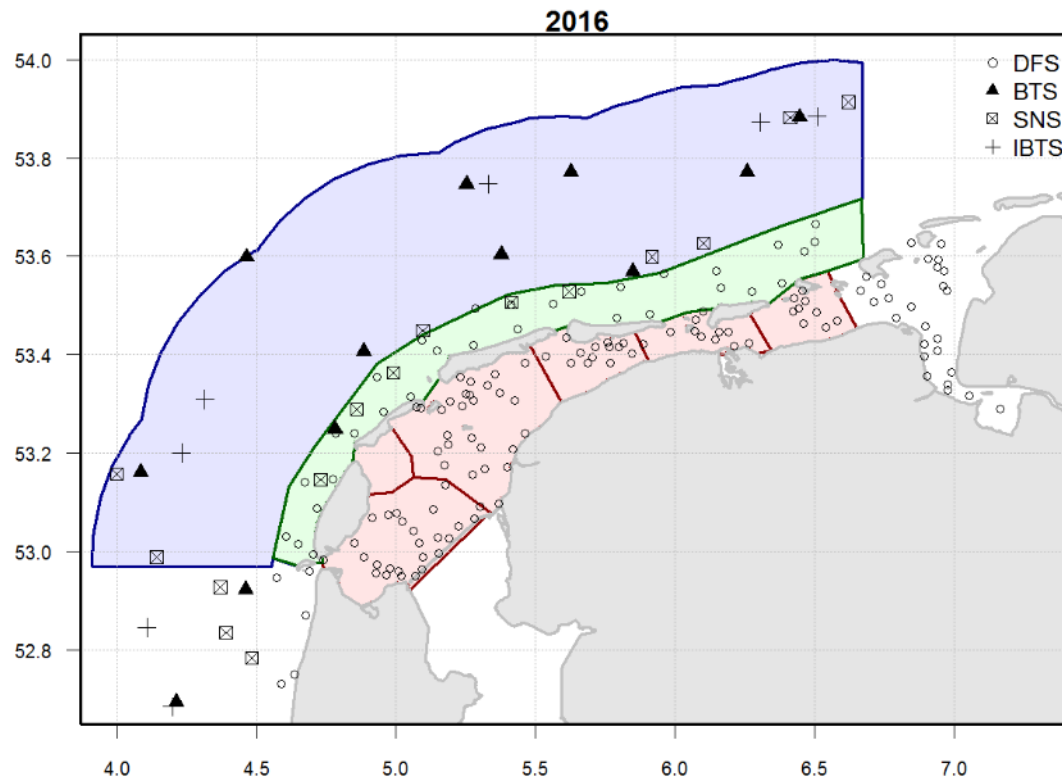238   were used.

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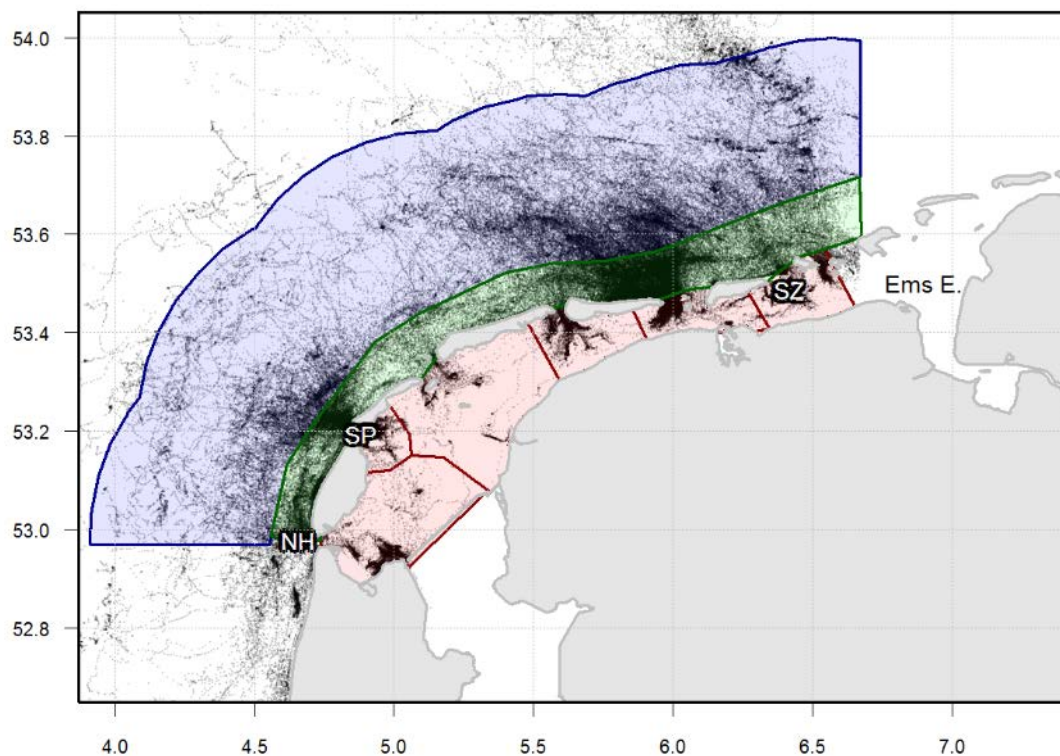
Figure 2 a. Top figure: Distribution of harbour seals, and abbreviations of some faecal

sampling locations. Data from the 149 tracked harbour seals making trips from haul-out

sites located in the Wadden Sea. Trips of seals making trips from haul-out sites located

the Ems Estuary (Ems. E), were excluded. Most faecal samples were collected on the

'Noorderhaaks' (NH), 'Steenplaat' (SP) and 'Simonszand' (SZ).

b. Bottom figure: Fish survey areas along the North Sea coasts of The Netherlands

(adapted from Tulp et al. 2016). Harbour 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 50km away from the seal haul-out sites located in the Dutch Wadden sea (shaded

blue). The points represent fish survey locations from 2016.

253

254   In most fish surveys, a variable fraction of the fish present in the path of the net will be

255   caught (i.e. incomplete catchability), which depends on the vertical distribution of fish in

256   the water column and gear efficiency. Gear efficiency depends on a number of factors,

257   such as the gear-type used (e.g. mesh size, net configuration), fishing speed, fish length,

258   fish behaviour, water clarity and fish species (Dickson 1993). Catchability estimates of

259   the DFS are unavailable for demersal species, but Kuipers (1975) attempted to unravel

260   how several processes influence the catching efficiency for plaice. The data provided in

261   (Kuipers 1975) were used to re-estimate the catching efficiency functions based on more

262   up-to-date statistical techniques. In addition, we also accounted for escape underneath the

263   net based on (Reiss et al. 2006). See Appendix S1 for a detailed description of the

264   analysis and results. For the 3m beam trawl used by the DFS, we arrived at an overall

265   catching efficiency which closely corresponds to the efficiency provided by Bergman *et*

266   *al.* (1989).

267   To determine the catching efficiency of the BTS, SNS and IBTS, the catching efficiency

268   for the DFS in the Wadden coast was used as a reference, and the DFS catchability was

269   subsequently corrected by comparing length-specific numbers per unit of effort between

270   the DFS and other surveys (see Appendix S1). Given the lack of catchability estimates

271   for any of the other demersal fish species, we assumed them to be similar to plaice.

272

273   **5.   *Fish growth based on Dynamic Energy Budget models***

15

274   The seal consumption was calculated in kg/day. To convert this into the *number* of fish

275   caught each day, it was necessary to know the average weight of fish. Since fish grow,

276   seasonal changes in weight need to be taken into account. Growth is species specific, and

277   depends on fish size, ambient temperature, and food conditions. These aspects can be

278   parameterized in a Dynamic Energy Budget (DEB) model (Sousa et al. 2010). Here, DEB

279   models were used for the five important prey species, for which DEB parameters were

280   readily available, namely flounder, plaice, dab, sole and bull-rout. DEB model

281   specification and parameters were based on (van der Veer et al. 2009, Freitas et al. 2010,

282   Teal et al. 2012). The volumetric daily growth (in gram) was defined as

283
$$\frac{dV}{dt} = \frac{(\kappa f\{p_{Am}\}Fr)V^{\frac{2}{3}} - [p_M]\exp\left(\frac{T_A}{T\mathrm{ref}} - \frac{T_A}{T}\right)V}{\kappa f[E_m] + [E_G]}, \quad \mathrm{eq.}\,2$$

284   *V* is the weight of the individual fish (in gram) and *T* is ambient water temperature (in K).

285   κ is the fraction of utilized energy spent on maintenance plus growth, *f* is a multiplication

286   factor for food availability (*f*=1, ad libitum) and $\{p_{Am}\}$ is maximum surface area specific

287   assimilation rate (in J cm^{-2}d^{-1}). $[p_M]$is the volume-specific maintenance cost, which is

288   based on field data and hence also includes the cost for feeding and activity (e.g.

289   swimming) (van der Veer et al. 2009). T_A is Arrhenius temperature (in K), T_{ref} is the

290   reference temperature at which the assimilation rate is known, $[E_m]$ is the maximum

291   storage density (J cm^{-3}), and $[E_G]$ and is the volume-specific costs of structure (J cm^{-3}).

292   *Fr* is the enzyme fraction that is in its active state, which is temperature dependent (see

293   eq. 2 in (van der Veer et al. 2009)). Here for all species *Fr* was based on plaice, given the

294   lack of the necessary parameters for the others species.

16

295   Preliminary runs of our DEB models suggested that the reduced growth in late summer

296   (also observed in van der Veer et al. 2016) and winter could not be explained by low

297   temperature alone (Appendix S2: Figure S2). To parameterize the DEB model in order to

298   account for additional seasonal variability in growth, field data on seasonal variation in

299   fish length were used. The fish length data were collected during fish surveys of the

300   National Programme Sea and Coastal Research (van der Veer et al. 2016). Sampling took

301   place in the western Wadden Sea in 2009 and 2010 during most months, except for the

302   winter months (December to February), and covered both the intertidal areas (using 2-m

303   beam trawl towed from a rubber dinghy) and subtidal areas (using a 3-m beam trawl

304   towed by the 20m, low draft vessel *RV Navicula*). Sampling took place during day-time,

305   and was centred around high tide (i.e. 3 hours before and after high tide). See (Freitas et

306   al. 2016) for more details.

307   The DEB model was fitted to monthly mean length estimates of 0- and 1-year old fish

308   (Figure 6, Appendix S2: Figure S3a-e).While all parameters were fixed (see, van der

309   Veer et al. 2009, Freitas et al. 2010, Teal et al. 2012), the food availability parameter f

310   was estimated, and allowed to vary between summer (f_{summer}) and winter (f_{winter}), and also

311   the onset of summer (t_{summer}) and winter (t_{winter}) was estimated (based on least-squares in

312   R-function 'optim').

313   The final parameterized DEB models for the five species were used to estimate the

314   average daily growth, taking the size distribution, ambient water temperature and

315   estimated food availability into account. The initial size distribution was based on the

316   abundance and size distribution of each species measured during the DFS surveys in

17

317   September surveys (Tulp et al. 2017). Temperature data were obtained from the website

318   http://live.waterbase.nl, for the station "Den Helder veersteiger" (52.96328 ° N, 4.77805 °

319   E). This procedure allowed for the estimation of total biomass and the reconstruction of

320   biomass growth.

321

322   **6.   Reducing fish numbers and biomass by harbour seal consumption**

323   During the survey in September (t=0), after correcting for catchability, the DFS and BTS

324   provide an estimate of both biomass B and total number of fish N present in each region j.

325   Each day, the biomass can increase as a result of fish growth (defined by the variable v).

326   The fish growth was predicted by the DEB model, which took the water temperature,

327   seasonal variation in food density and initial length distribution of fish caught during the

328   survey into account (see also eq. 2). The biomass can also be reduced by seal predation.

329   Particularly after the moult, in September, harbour seals are presumed to feed intensively

330   to replenish losses in condition experienced during the reproduction and moult-period,

331   and build up a fat layer for the winter (Kastelein et al. 2005).

332   We assumed that intake rate increases linearly with food density (type I functional

333   response), i.e. the time spent foraging in areas with higher food density leads to a higher

334   intake, and hence a larger reduction in biomass. Therefore, the proportion of dive time p

335   in each region j, was weighted by food density $N_{t-1,j}A_j^{-1}$ (where A_j is the area of the

336   region j), to arrive at the proportional intake $\frac{p_j N_{t-1,j} A_j^{-1}}{\sum_j p_j N_{t-1,j} A_j^{-1}}$. This was subsequently

337   multiplied by the total number of seals S, and average daily consumption (C).

18

338
$$B_{t,j} = v_t B_{t-1,j} - \frac{p_j N_{t-1,j} A_j^{-1}}{\sum_j p_j N_{t-1,j} A_j^{-1}} SC, \qquad \text{eq. 3}$$

339
$$N_{t,j} = N_{t-1,j} - \frac{p_j N_{t-1,j} A_j^{-1}}{\sum_j p_j N_{t-1,j} A_j^{-1}} SC \left(\frac{B_{t-1}}{N_{t-1}}\right)^{-1} \quad \text{eq. 4}$$

340 Similarly, the changes in numbers of prey fish N were estimated, with the main difference

341 that fish numbers only increased due to recruitment. Here, 0-year old fish were assumed

342 to 'recruit' in September, around the time of the survey. To estimate the daily food

343 requirement in numbers, the average daily food intake (in kg) was divided by the average

344 weight of the remaining fish (i.e. B_{t-1}/N_{t-1}).

345 The uncertainty in the estimated impact of seal predation on fish numbers and biomass is

346 influenced by a large number of parameters, for which the uncertainties are often

347 unknown. One of the largest uncertainties is expected to occur in the catchability; e.g. a

348 change in catchability from 20% to 10% would lead to a doubling of the number of fish

349 present. The uncertainty in our catchability estimate was caused by the uncertainty in the

350 proportion of lateral escape, avoidance of the approaching vessel, escape underneath, and

351 for the BTS, also the translation from the DFS- to BTS- catchability based on length-

352 specific catch ratios (Appendix S1). Each step in this chain produces a (length-specific)

353 selectivity curve quantified by parameters and corresponding uncertainties. We

354 repeatedly sampled (500 times) from these parameter distributions, to estimates how

355 uncertainty in the catchability propagates into the estimated effect of seal predation (eq. 3

356 and 4). Species-specific effects on catchability were not taken into account.

357

19

358 **RESULTS**

359 *Seal diet and daily consumption*

360 In total, 79 faecal samples contained otoliths (n= 2168). Of these, 36 samples were

361 collected in September, 17 in August, and the rest in November (8), March (5), April (5),

362 January (3), October (2), December (2) and July (1). Samples were collected between

363 1999 and 2009, with most samples from 2005 (29), 2007 (26) and 2002 (10). The 10

364 most represented fish species (based on estimated fresh weight) were flounder (39% of

365 the total estimated weight), sandeel (17%), sole (14%), five-bearded rockling (5.1%),

366 whiting (4.6%), plaice (4.4%), cod (4.3%), dragonet (2.1%), dab (2%) and bull-rout (2%)

367 (Figure 3). Together, these prey represent 95% of the diet.

20

368
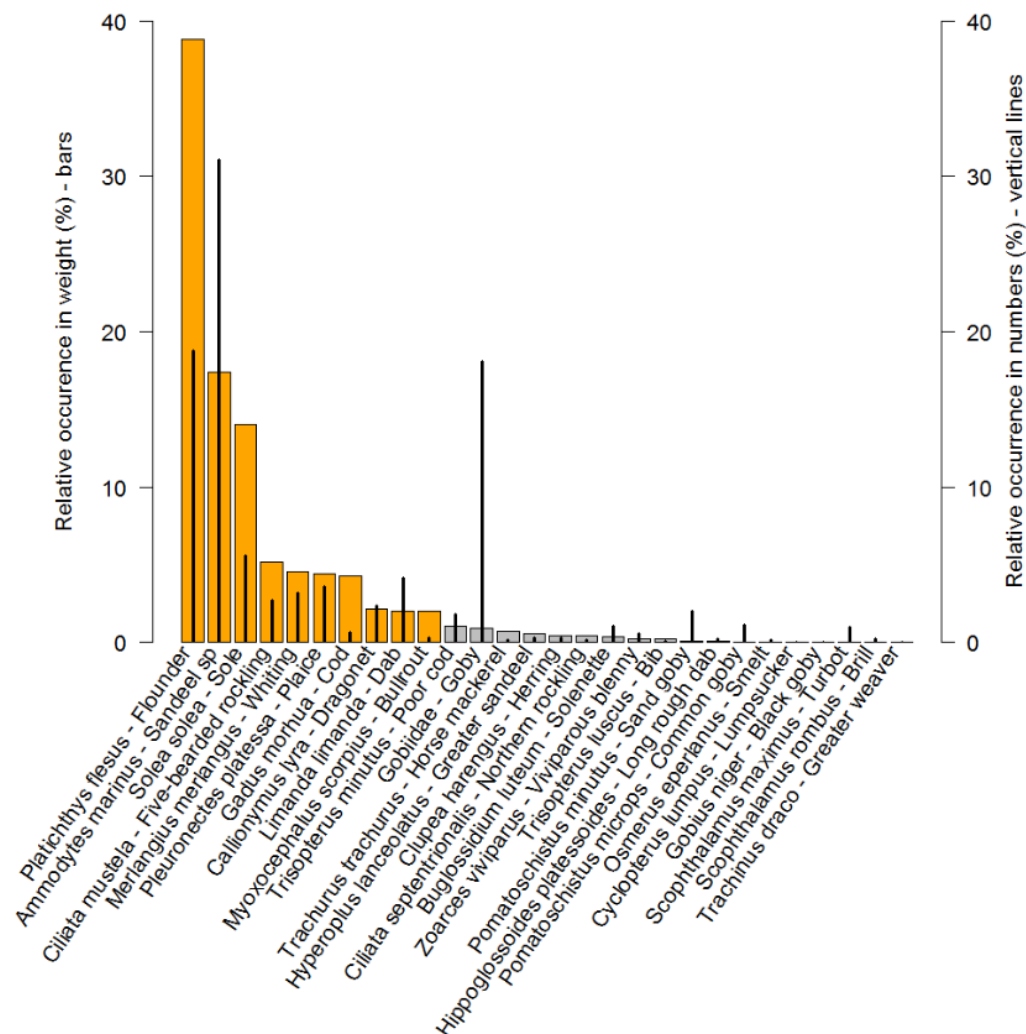
Figure 3. The percentage by estimated fresh weight (bars, left axis) and number of

otoliths (vertical lines, right axis) of each fish species found in harbour 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.

373

Estimated fish lengths in the faecal samples were mostly <25 cm, with a peak between 10

and 20 cm (Figure 4).

21

Length frequency distribution

376
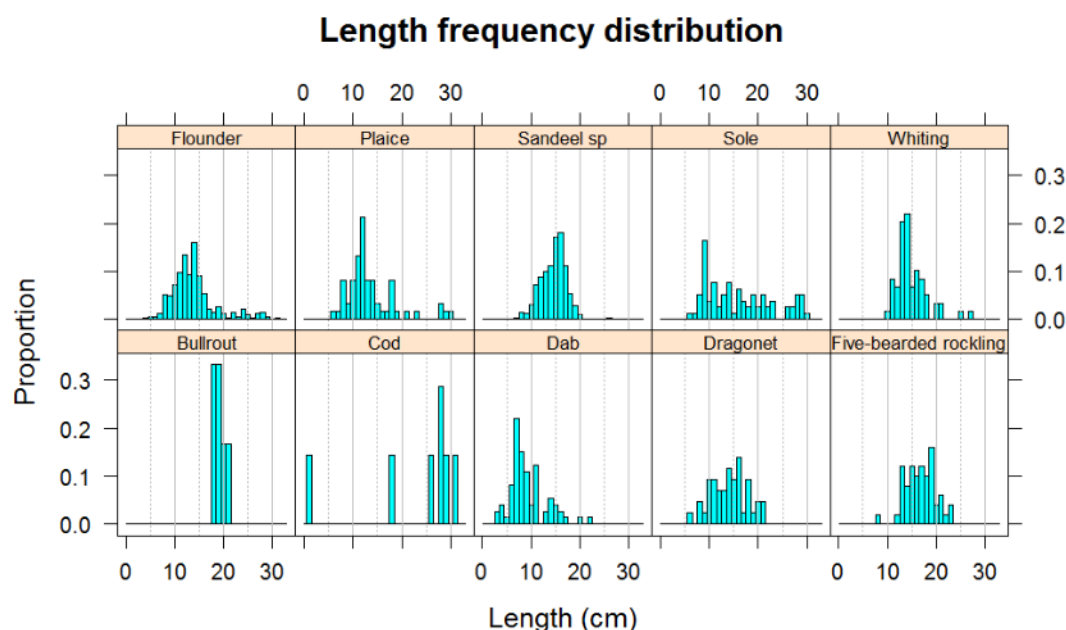
377   **Figure 4.** Length distribution of the 10 most common fish species found in scat samples

378   of harbour seals, collected 1999-2009.

379   The estimated average energetic content of the fish consumed (weighted by their relative

380   occurrence in the diet, see Figure 3) was 1.007 kcal/kg (Appendix S2, Table S2).

381   Assuming a daily energetic requirement of 4680 kcal per seal per day (Härkönen and

382   Heide- Jørgensen 1991), this amounts to approximately 4.6 kg per day per individual.

383

384   *Fish abundance*

385   The biomass of the 10 most important species consumed by harbour seals in the Dutch

386   Wadden Sea (i.e. plaice, sole, dab, flounder, sandeel, whiting, cod, five-bearded rockling,

387   common dragonet and bull-rout) are shown in Figure 5 (and Appendix S2: Figure S4).

388   Up to the mid 1980's the fish biomass increased in both the Wadden Sea and adjacent

22

389   coastal zone, but declined after that. In the most recent year (2016), the Wadden Sea

390   contained on average 535 kg/km^2 (corrected for catchability) and the adjacent coastal

391   zone (Figure 2) held 2104 kg/km^2. The total area of these areas are 2088 and 1707 km^2,

392   respectively. Hence, the average biomass observed in 2016 was 1117 tonnes for the

393   Wadden Sea and 3592 tonnes for the adjacent coastal zone. In the Wadden Sea in the

394   period between 2011 and 2015, the most abundant prey species were plaice (54%) and

395   flounder (16%). In the coastal zone the most abundant prey species in the same period

396   were dab (59%), whiting (28%) and dragonet (14%).
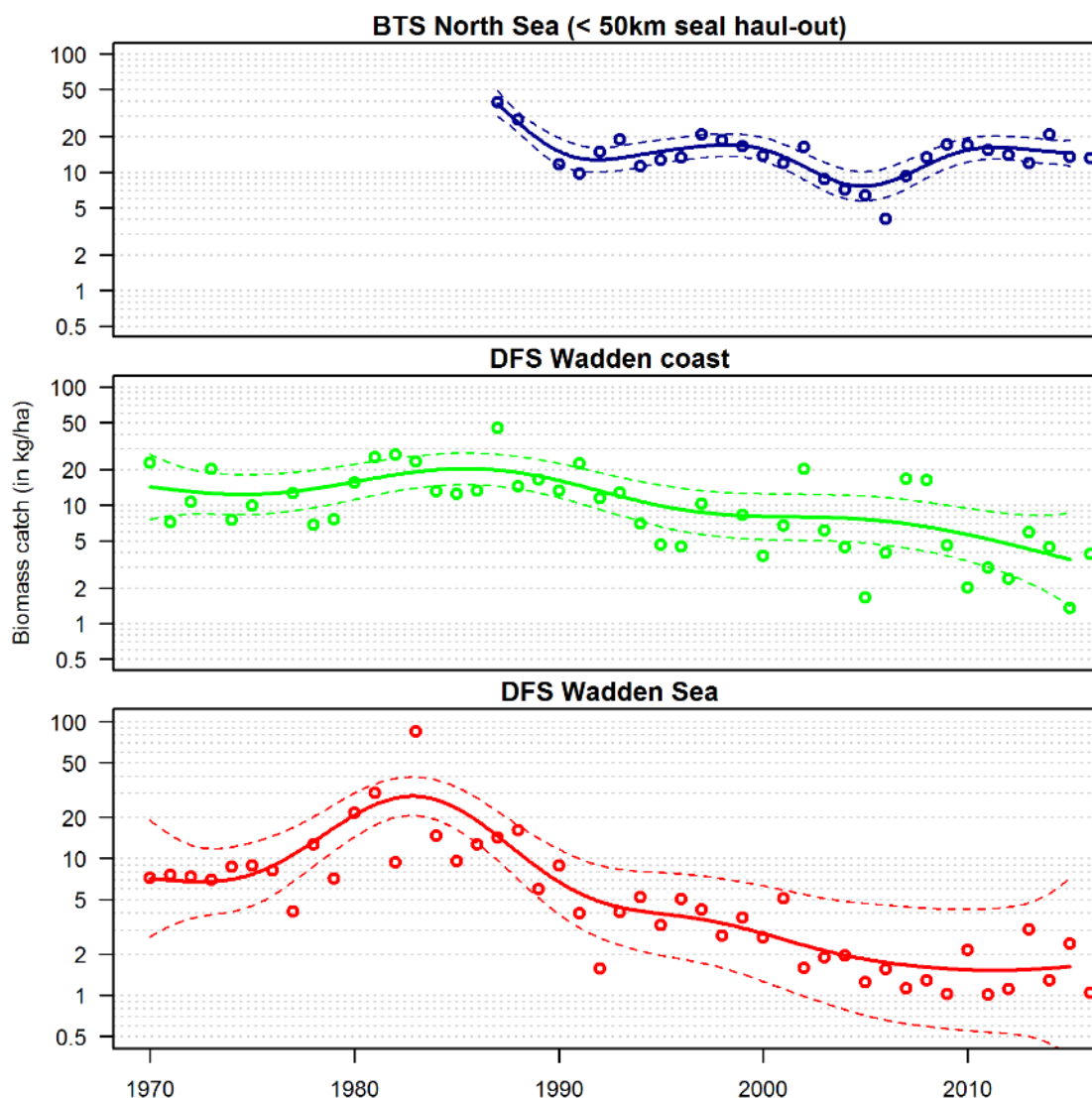
Figure 5 Trend in biomass (in kg/ha) of the 10 most important harbour seal prey species (based on scat samples), for the beam trawl survey (BTS) in the offshore zone, the demersal fish survey (DFS) in the coastal zone bordering the Wadden Sea (Wadden coast), and the DFS in the Wadden Sea (See also Figure 2). Note the log-scale on the y-axis.

404   *Fish growth*

405   The biomass of demersal fish in the Wadden Sea and nearby waters shows large seasonal

406   variability. Most 0-year old fish (e.g. plaice, sole, and flounder) 'settle' in early spring

407   (March/April). These 0-year olds can be highly abundant, but their total biomass is still

408   low. They grow during spring and summer, and once they exceed ~5 cm (around June-

409   July, Figure 6, Appendix S2: Figure S3a-e) they can be caught by DFS-type gear. From

410   September onwards, the apparent growth of 0-year old plaice and flounder is reduced

411   substantially, despite the high water temperature (Figure 6). The following spring

412   (March/April) they (now 1-year olds) start to grow, even though water temperature is still

413   low (Figure 6, Appendix S2: Figure S3a-e). They continue to grow up to the late summer

414   and fall. The predicted decline in length during the winter months is an 'artefact' of the

415   DEB model: Since length is defined as a function of volume $V^{1/3}$, a decrease in volume

416   will lead to an apparent decrease in length.

417
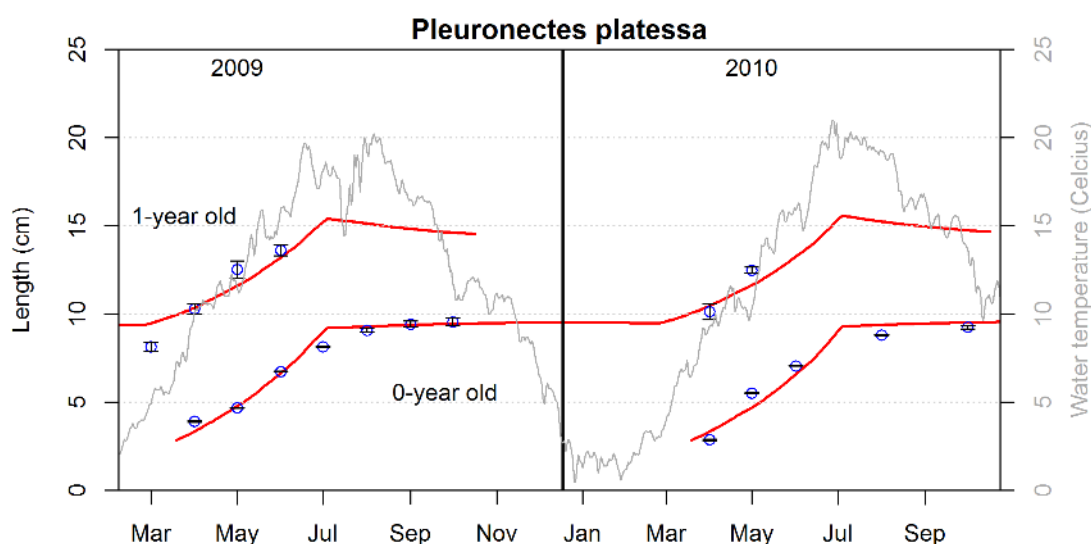
418   **Figure 6.** Observed length (circles and standard error bars) and predicted length (solid

419   red line) of 0- and 1-year old plaice. Grey line indicates water temperature. Predicted

420   growth (solid lines) is based on DEB model where food intake parameter f was allowed

421   to vary between the winter months (f=0.11) and other times of the years (f=0.66).

422

423   *Harbour seal spatial distribution and foraging activity*

424   Although harbour seals are often observed on the sandbanks located within the Wadden

425   Sea, on average they only spend 17% of their time on land (Appendix S2: Figure S1). Of

426   the remaining 83% of their time, harbour seals spend on average 26% within the Wadden

427   Sea, 28% in the adjacent coastal zone and the remaining time, 46%, in the offshore zone

428   (Figure 2, Appendix S2: Figure S1). There are however, large seasonal variations. During

429   summer months (April – September) seals spend most time on land (20-23%), and the

430   least amount of time in the regions outside the 50km buffer. During the winter months

431   seals spend most time further offshore beyond the 20m depth line (Appendix S2: Figure

432   S1).

433   The time spent in each region is not necessarily a good proxy for foraging, as seals also

434   perform other activities at-sea (like resting or transiting). When considering the total dive

435   time (<1.5 m depth) in each region, only 14% of their dive time is spent within the

436   Wadden Sea (substantially less than the total time spent there), 31% in the Wadden coast

437   and harbour seals spend most dive time (46%) in the areas further offshore, particularly

438   during the months January – March (63-74% of their dive time) (Appendix S2: Figure

439   S1).

440

441   *Consumption estimates*

442   The total number of seals counted in the Dutch Wadden Sea in 2016, was 8160 (Galatius

443   et al. 2017). Assuming a 0.68 haul-out probability during the Dutch aerial survey counts

444   (Ries et al. 1998), 12,000 were estimated to be present. Based on the estimated 4.6 kg of

445   fish consumed per seal per day, these 12,000 harbour seals in the Dutch Wadden Sea

446   consumed approximately 56,000 kg of fish per day, and 20,400 tonnes of fish that year.

447   In our study we excluded the Ems Estuary, and based our estimates on the remaining

448   area, which contained 10,300 harbour seals 2016, consuming 17,500 tonnes of fish that

449   year. The estimated consumption is substantially larger than the estimated fish biomass

450   present in the Wadden Sea (ca 1100 tonnes) and adjacent coastal zone at the time of the

451   survey (ca 3600 tonnes).

452   As fish growth is low during the winter months, harbour seals are expected to

453   substantially reduce the total fish number in this period. This will affect the fish

454   populations particularly when the estimated total numbers in September are low (e.g.

455   2011 in the Wadden sea; Figure 7). During the more productive spring and summer

456   months, seals will continue to have an impact on the number of fish, however prey

457   biomass continues to increase due to growth. The estimated consumption in the Wadden

458   Sea and nearby coastal zone is presumed to be tightly linked to the number of fish present

459   in the more offshore areas: when offshore fish density is high, the intake per unit of time

460   (assuming a Type I functional response), will be higher (Figure 7). Figure 7 also shows

461   the decline in numbers of fish (all ages) observed in a specific year, and the number of

27

462   larger individuals (attempting to exclude 0-year olds) the following year. These

463   calculations show that seal predation is likely a major contributor to the apparent annual

464   fish mortality. However, for most years the fish mortality (or emigration) exceeds the

465   estimated mortality caused by seals (the difference between solid coloured lines (with

466   seal predation) and the dotted lines in Figure 7). This is particularly so for the offshore

467   regions, but also for the Wadden Sea. For the Wadden coast the estimated impact is

468   highest, and for several years the estimated mortality caused by seals exceeds the

469   observed decline in prey numbers from one year to the next. Based on all years combined

470   (2003-2016), the average estimated mortalities for the different regions are 43%

471   (SD=13%) for the Wadden Sea, 60% (SD=19%) for the Wadden coast and 20%

472   (SD=7%) for the North Sea region further offshore. Similar reductions were estimated for

473   the biomass of the seals' prey (Appendix S2: Figure S5). Since growth is limited during

474   the winter months, seal predation was estimated to reduce the overall biomass during the

475   winter months. However, during the productive summer months the increase in biomass

476   strongly outpaced the seal predation.
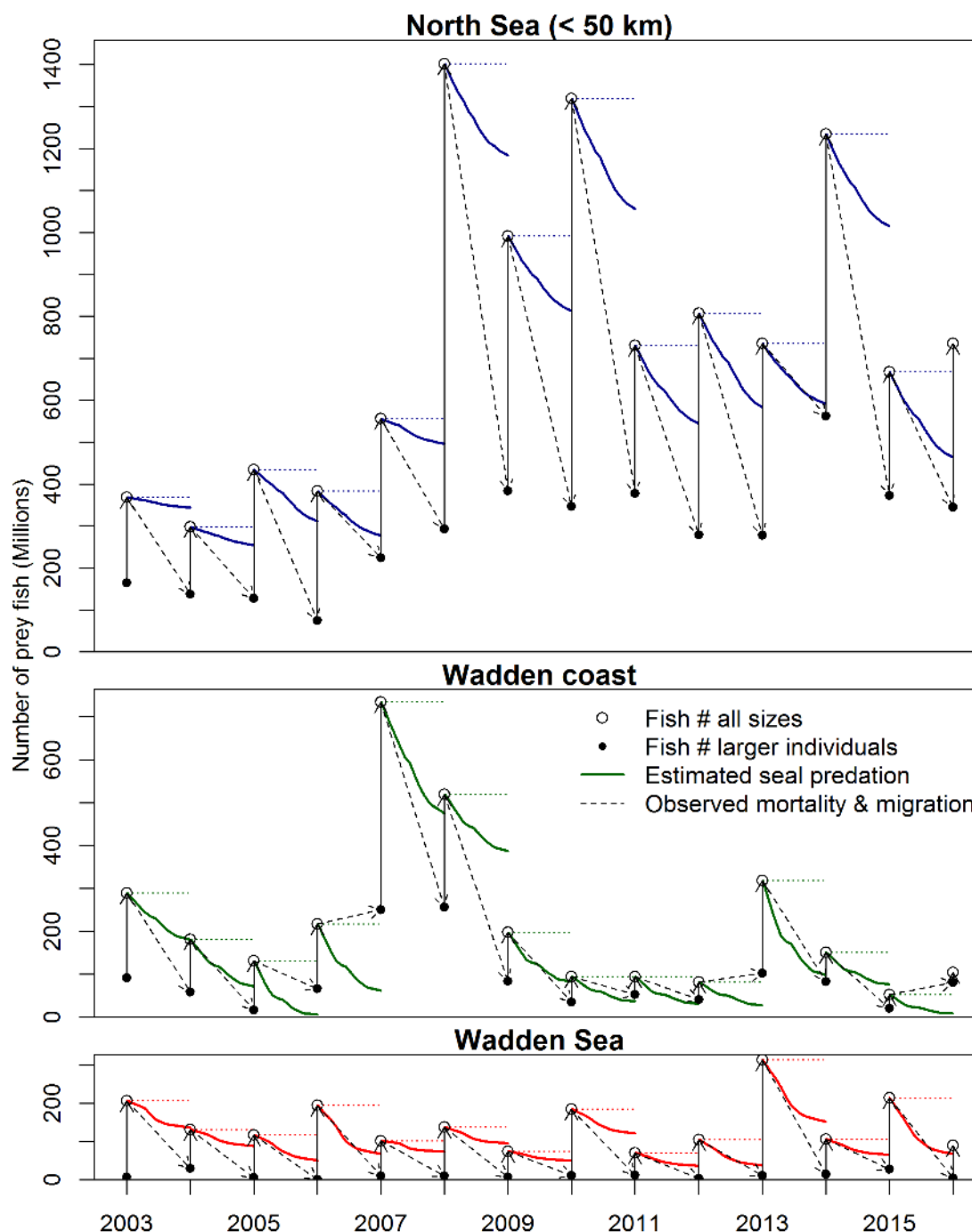
Figure 7. The estimated effect of seal predation on the number of prey fish for the

Wadden Sea (red lines), Wadden coast (green lines) and remaining areas up to 50km

from the haul-outs (blue lines, and see regions in Figure 2). The fish survey in September

29

481   (i.e. BTS for the North Sea areas within 50 km of the nearest haul-out, and DFS for the

482   Wadden coast and Wadden Sea) is the starting point (open circle, representing all size-

483   classes), after which numbers decline due to seal predation. In the subsequent survey in

484   September the following year, the number of remaining individuals (black dot,

485   representing larger individuals, >13.5cm, presumed 1+ year olds) have declined, but is

486   again supplemented with new recruits. In the Wadden Sea nearly all larger individuals

487   (black dots) have died or disappeared (due to movement).

488

489   In the estimated impact of seal predation there were a large number of uncertainties. One

490   of the largest source of uncertainty was the uncertainty in the catchability estimate, which

491   is shown for one year (2016) in Figure 8. For the Wadden Sea, for 2016, the number of

492   prey species still remaining in September (compared to the previous year) after seal

493   predation was estimated to be 35% of what was present the preceding year (i.e. 65%

494   reduction). However, the 95% CI was between 5% and 75%, implying that the estimated

495   impact of seal predation could be both substantially larger or smaller than our mean
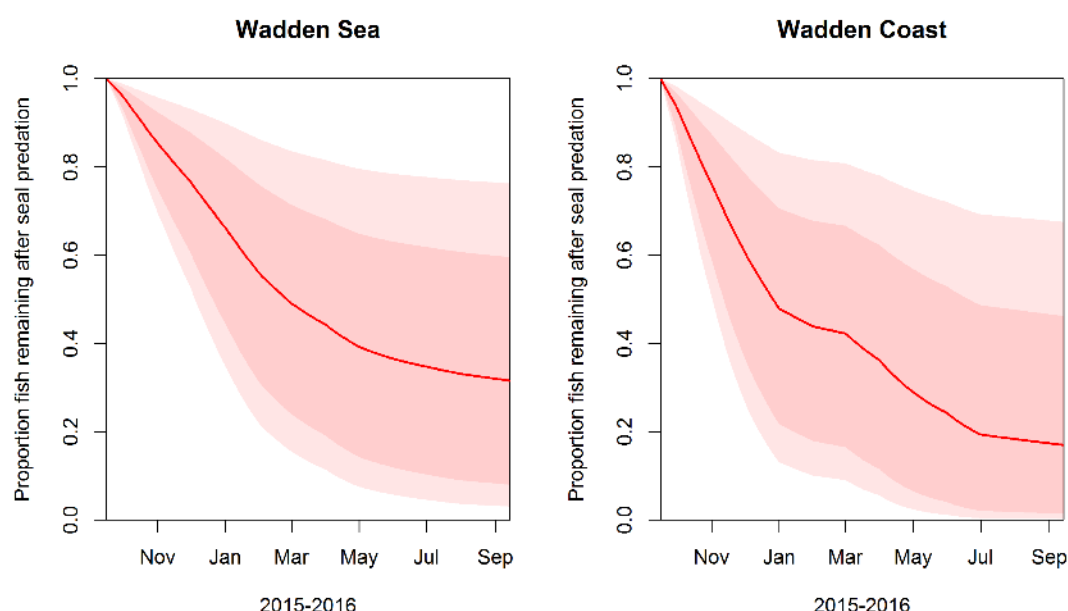
496   estimate.

Figure 8. Uncertainty in the effect of the estimated impact of seals on fish numbers in the Wadden Sea (left) and Wadden coast (right). 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

We estimate that current harbour seal population imposes a considerable predation pressure on fish populations in the Wadden Sea and adjacent coastal zone. In our study area, the Dutch sector of the Wadden Sea (excluding the Ems estuary) and adjacent waters, the estimated annual fish consumption by harbour seals in 2015-2016 (i.e. 17 500 tonnes) was about three times higher than the combined prey fish biomass estimated for

31

509   September in the Dutch Wadden Sea (1100 tonnes) and adjacent Wadden coastal zone

510   (3600 tonnes). Since fish growth (i.e. biomass production) is small during the 5-6 winter

511   months following the fish surveys, thus this region alone cannot sustain the entire harbour

512   seal population.

513   This probably explains why harbour seals only spend ~13% of their diving time in the

514   Wadden Sea. We estimated that seals consume approximately half of the fish present in

515   the Wadden Sea from September onwards. In the coastal zone bordering the Wadden Sea,

516   we estimated that the seals exert a similar predation pressure. There, the total fish

517   biomass is higher than in the Wadden Sea (particularly in recent years), but seals also

518   spend more time foraging in this region.

519   Although the total demersal fish biomass in the Wadden Sea and nearby waters has

520   decreased in the last two decades and the size of the harbour seal population has strongly

521   increased, it is unlikely that seals are the single cause of the decline in the fish

522   populations in the Wadden Sea. The decline in fish stocks in the Wadden Sea and coastal

523   waters started in the mid-80's, when seal numbers were still around their historic low.

524   Most probably the decrease in fish biomass in the mid-1980s is related to the decrease in

525   eutrophication and climate change (Teal et al. 2012, Støttrup et al. 2017). Furthermore,

526   the decline in demersal fish biomass (and fish numbers) in the coastal shallow waters

527   occurred in all age-classes including the 0-year olds (Støttrup et al. 2017). The majority

528   of fish in the seals' diet in our study area was larger than 10cm (Figure 4). Most 0-year

529   olds only reach that size at the end of the growth season (Appendix S2: Figure S3). Since

530   we expect the predation pressure by seals on these 0-year olds prior to the survey in

32

531   September to be rather low, we assume that bottom-up processes (e.g. low nutrient

532   loadings) in combination with mortality by birds or by-catch in the shrimp fishery is a

533   more likely explanation for the observed decline in 0-year old fish biomass. However,

534   during the winter months following the survey, seals can impose a considerable predation

535   pressure on the remaining prey. Hence, given the low fish density and high seal numbers

536   it is likely that at their current numbers seals are applying top-down pressure on local fish

537   populations, especially with regard to preferred prey species.

538   These results are in line with some studies that suggest that the predation pressure by

539   marine mammals can alter the abundances of prey species. For examples, grey seals

540   (*Halichoerus grypus*) may have impaired the recovery of over-exploited north-west

541   Atlantic cod stocks (Trzcinski et al. 2006, Cook and Trijoulet 2016). Benoît et al. (2011)

542   estimated that in that region, grey seal predation could explain 20-50% of natural

543   mortality of some demersal fish species, even if these species comprised a small

544   percentage (<25%) of the grey seal diet. In contrast, other studies elsewhere have

545   demonstrated low impacts by seals on fish communities (Houle et al. 2016). Such

546   differences between observed impacts undoubtedly relate to the sizes of seal and fish

547   stocks, the relative importance of other ecosystem components (e.g. predatory fish like

548   cod and whiting, Temming & Hufnagl 2015), and stock replenishment rates. The Wadden

549   Sea could be considered the seals' back-garden. In the vicinity of the haul-out sites from

550   which they forage seal predation is most likely to cause food depletion, a principle known

551   as Ashmole's halo (Gaston et al. 2007).

552

553 **Sources of uncertainty**

554 One main source of uncertainty was the lack of experimentally derived catchability

555 estimates for the DFS gear. Instead, we attempted to estimate catchability based on

556 experiments for plaice, which used different fishing gear (Kuipers (1975)). The

557 catchability of some species might be very different from plaice. For example sandeel is

558 the second most important prey item observed in the seal diet, but they are not caught

559 optimally by the used gears because of their pelagic and burial phase, and their thin

560 elongated shape. Surveys specifically designed for sandeel use gear that dislodges them

561 from the substrate notably catch higher numbers (Tien et al. 2017). Also other pelagic

562 species (e.g. herring, sprat, etc.) are poorly sampled by a demersal beam trawl gear

563 (Couperus et al. 2016). Although only two of the sampled scats contained herring (max 5

564 %), only five samples were collected between December - February. Harbour seals may

565 feed more on pelagic fish species (e.g. herring, sprat, etc.) during these winter months (de

566 la Vega et al. 2016). This could imply that the consumption of demersal prey, and impact

567 of seals on the demersal fish community, might be overestimated.

568 Another unknown factor, is where seals capture their prey. In this study, the prey removal

569 in each region was defined as the product between prey density and dive time in the

570 different regions. Clearly, some dive time is not related to foraging, and the amount of

571 non-foraging dives may differ between the regions, and even between seasons. Also the

572 distribution of their prey is not static. While, we accounted for changes in prey density

573 due to seal predation, relative changes in fish distribution were not taken into account.

574 For example, several studies have suggested an offshore movement of fish toward deeper

34

575   (warmer) waters during the winter months (de Veen 1978, Teal et al. 2012, van der Veer

576   et al. 2016). This also seems to be reflected in the movement of seals, who tend to forage

577   further offshore during the winter (Aarts et al. 2016). In addition, also other sources of

578   mortality (e.g. predation by cormorants or bycatch in the shrimp fishery (Leopold et al.

579   1998, Glorius et al. 2015)) could locally lower fish density. This would lead to lower

580   intake rates by seals, possibly over-estimating the effect of seal predation in the Wadden

581   Sea.

582   However, regardless of where exactly seals capture their prey, all living seals ultimately

583   need to acquire sufficient prey to meet the energy demands (Härkönen and Heide-

584   Jørgensen 1991). Since foraging sites within and close to the Wadden Sea require less

585   travelling, they are more beneficial. Therefore optimal foraging theory would suggest the

586   highest reduction in food density to occur near the colony.

587

588   **Other piscivorous 'predators' in the Wadden Sea**

589   In order to evaluate the relative importance of top-down regulation by harbour seals, we

590   need to consider other sources of mortality, such as predation by other marine mammals,

591   piscivorous birds, predatory fish, but also commercial fishery (Zijlstra and Van Eerden

592   1995, Leopold et al. 1998, Arnett and Whelan 2001, Glorius et al. 2015, van Kooten et al.

593   2015, Hansson et al. 2017).

594   Grey seal numbers in the Wadden Sea grew exponentially after 1990 (Brasseur et al.

595   2015), with a maximum of 4045 counted in the Dutch section of the Wadden Sea during

596   the moult in 2017 (Brasseur et al. 2017). Although grey seals in the North Sea primarily

597   feed on sandeel, they also feed on other benthic prey species (Brown et al. 2012). While

598   grey seals may visit areas >100km offshore, presumably to feed on sandeel banks, they

599   also spend a large amount of time in coastal waters near the Wadden Sea, overlapping

600   with harbour seal distribution.

601   In addition to grey and harbour seals, 30-80 thousand harbour porpoises are estimated to

602   reside in the Dutch section of the North Sea (Geelhoed et al. 2013). Only a small part of

603   this population uses the Wadden Sea and nearby coastal zone. In Denmark and Germany

604   harbour porpoises are present near the Wadden Sea throughout the summer season, and

605   are known to feed on 0-year old flatfish species (Gilles 2008). However, stomachs of

606   harbour porpoises found stranded along the Dutch coast, mainly contain whiting, sandeel

607   and gobies and only a small proportion of flatfish (Leopold 2015).

608   Several bird groups e.g. cormorants and divers also feed on demersal fish species.

609   Cormorants are abundant and specialize mainly on 0-group flatfish, e.g. plaice, dab and

610   flounder (Leopold et al. 1998). Currently approximately 25,000 cormorants breed in the

611   Netherlands, of which half live in the vicinity of the Wadden Sea (www.sovon.nl).

612   Cormorants require approximately 460 – 500 g of fish per day (Zijlstra and Van Eerden

613   1995, Leopold et al. 1998). Assuming these cormorants feed continuously within and

614   near the Wadden Sea, this equates to a prey requirement of approximately 2300 tonnes

615   per year.

616   In addition to the natural sources of mortality, mortality due to commercial fisheries

617   should also be considered. In the North Sea, the total catch by the commercial fishery

36

618   exceeds by far the consumption by marine top-predators (Engelhard et al. 2013). A

619   pattern which is also evident in other regions, like the Baltic (Hansson et al. 2017).

620   However, locally near the coast with high densities of central-place foraging predators,

621   the impact of these predators may exceed that of fishing (see e.g. also (Hansson et al.

622   2017)). In the Dutch coastal zone, the fisheries targeting demersal fish species is rather

623   small (i.e. landing 723 tonnes, including 99 tonnes in the Wadden Sea (van Kooten et al.

624   2015)). The shrimp fishery is by far the most important fishery in and around the Wadden

625   Sea, with plaice being the most important by-caught species. In de Dutch Wadden Sea

626   alone, shrimp fisheries catch an estimated 99 million 0 and 1-year old plaice, mostly

627   during the summer months (adapted from (Glorius et al. 2015)). The total number of

628   plaice (corrected for catchability) present during the DFS in September was estimated at

629   89 million. This suggests that prior to the DFS, approximately 50% of plaice was already

630   caught away by the shrimp fishery.

631   Although the population size, food requirement and target species differ between marine

632   predators and fishery, they can collectively impose a considerable predation pressure on

633   the demersal fish communities of the Wadden Sea and nearby coastal waters. Recent

634   simulations for a North Sea ecosystem not only suggest that top-down fishing pressure

635   can be of tremendous importance for the dynamics of fish populations, the top-down

636   effects may also cascade down to lower tropic levels, including plankton abundance

637   (Lynam et al. 2017). This might also be the case for the effect of predators, such as seals,

638   in coastal areas.

639

37

640 **Are harbour seals food-limited?**

641 The estimated food requirement by harbour seals is well above the amount of prey

642 estimated to be available in the Wadden Sea and Wadden coast combined. Since harbour

643 seals are central-place foragers, some depletion near the colony is likely to occur.

644 However, seals also forage well beyond the coastal zone (Figure 2), where prey density is

645 higher (Figure 5) and the estimated depletion is substantially lower (Figure 7). In recent

646 years, harbour seals appear to be using the west coast of the Netherlands more frequently

647 (Aarts et al. 2013), which suggests that more distant areas have become more attractive

648 foraging locations than previously. Although the harbour seal population in the Dutch

649 part of the Wadden Sea is still increasing (but at a slower rate than before), in other

650 regions, like Denmark, the population seems to have reached a plateau (Brasseur et al.

651 2018). Given the estimated impact of harbour seals on the fish community, it is likely that

652 the slowing down in the population growth is at least partly the result of food limitation.

653

654 **Density dependent processes and possible interactions between seals and fishery**

655 While seals can impose a considerable mortality on individual fish, it is still debatable

656 whether seals have an overall impact on fish biomass. This ultimately depends on

657 whether seal predation keeps the fish numbers well below the level where intra- or inter-

658 specific competition for food will occur. Lorenzen and Enberg (2002) reported density

659 dependent growth (DD-growth) reduction in 9 out of 16 marine fish populations studied.

660 DD-growth is assumed to mainly occur in the early life of a cohort (Anderson et al. 2017)

661 and has been reported frequently in species that concentrate during their juvenile phase in

662   shallow coastal waters (Beverton 1995). For instance, DD-growth has been observed in

663   juvenile plaice and sole in years of exceptionally large year classes (Rijnsdorp and Van

664   Leeuwen 1996). The observed reduction in growth of 0-group fish species (e.g. plaice

665   and flounder) corroborates that in summer food becomes a limiting factor in the Wadden

666   Sea.

667   The density-dependent reduction in juvenile growth may have been a regular

668   phenomenon prior to the period of eutrophication of the coastal waters (Bolle et al.,

669   2004). Productivity in the coastal waters has decreased recently supposedly in response to

670   the decrease in nutrient inputs (Philippart et al. 2007, Støttrup et al. 2017), lowering the

671   biomass at which density-dependent competition for food will occur. Whether the

672   increased predation pressure from seals is sufficient to suppress the fish biomass below a

673   critical level and limit where resource competition starts to slow down growth requires

674   further study.

675   Another aspect that would require further study, is whether seals compete with other

676   predators, like the commercial fishery. When both marine mammals and fishery target the

677   same (over-exploited) fish species, the additional mortality imposed by seal predation

678   may hamper the recovery of some commercially important target species, as was

679   suggested for cod in the west Atlantic (e.g. Trzcinski et al. 2006, Cook et al. 2015, Cook

680   and Trijoulet 2016). However, if marine mammals and fishery target different species or

681   size classes, this could give rise to both positive and negative feedback loops, and the

682   competition between marine mammals and fishery might be less obvious (Morissette et

683   al. 2012, Houle et al. 2016).

39

684   A number of harbour seal prey species, e.g. sole and plaice, are also targeted by the

685   commercial fishery in the Southern North Sea. The Wadden Sea and adjacent coastal

686   areas are important nursery grounds for these species (van der Veer et al. 2011). Seals

687   feeding in these areas target fish before they move further offshore, and become available

688   to the fishery. This leads to the question whether or not the seal predation could

689   diminished catch opportunities for fisheries on these species later on. This depends on

690   how these populations are regulated (De Roos et al. 2007). When density-dependent

691   growth occurs in the juvenile stage, increased mortality can actually lead to higher

692   biomass of adults, because it removes the bottleneck which limits recruitment into larger

693   age-classes (van Kooten et al. 2007, De Roos et al. 2007). Seal predation would only

694   translate into a proportional reduction in stock size for fisheries when seal mortality

695   linearly translates into reduced numbers of adult fish, with no effects on growth. This

696   would be the case if seals would feed on the same sized fish that the fishery targets.

697   Interestingly, we find that the biomass of the species caught in the BTS (aimed at

698   sampling the larger commercially important flatfish species), in the region within 50 km

699   of seal haul-out sites has increased slightly in recent years (Figure 5), a pattern also

700   observed elsewhere (Støttrup et al. 2017). However, this is not necessarily a positive

701   effect of seal predation (for example, beam trawl fishing intensity has also strongly

702   diminished in the area), at least the increased seal presence does not coincide with a

703   decrease in fish abundance further offshore.

704

705   **ACKNOWLEDGEMENTS**

726

727   **Literature cited**

728   Aarts, G., J. Cremer, R. Kirkwood, J. T. van der Wal, J. Matthiopoulos, and S. Brasseur.

729   2016. Spatial distribution and habitat preference of harbour seals (Phoca vitulina) in

730   the Dutch North Sea. Page Wageningen University & Research Report C118/16.

731   Aarts, G. M., S. M. J. M. Brasseur, S. C. V Geelhoed, R. S. A. van Bemmelen, and M. F.

732   Leopold. 2013. Grey and harbour seal spatiotemporal distribution along the Dutch

733   West coast. IMARES, Den Burg.

734   Anderson, S. C., A. B. Cooper, O. P. Jensen, C. Minto, J. T. Thorson, J. C. Walsh, J.

735   Afflerbach, M. Dickey-Collas, K. M. Kleisner, C. Longo, G. C. Osio, D. Ovando, I.

736   Mosqueira, A. A. Rosenberg, and E. R. Selig. 2017. Improving estimates of

737   population status and trend with superensemble models. Fish and Fisheries 18:732–

738   741.

739   Arnett, R. T. P., and J. Whelan. 2001. Comparing the diet of cod (Gadus morhua) and

740   grey seals (Halichoerus grypus): an investigation of secondary ingestion. Journal of

741   the Marine Biological Association of the UK 81:365–366.

742   Baker, C. S., and P. J. Clapham. 2004. Modelling the past and future of whales and

743   whaling. Trends in Ecology and Evolution 19:365–371.

744   Baylis, A. M. M., R. A. Orben, J. P. Y. Arnould, F. Christiansen, G. C. Hays, and I. J.

745   Staniland. 2015. Disentangling the cause of a catastrophic population decline in a

746   large marine mammal. Ecology 96:2834–2847.

747   van Beek, F. A., A. D. Rijnsdorp, and R. De Clerck. 1989. Monitoring juvenile stocks of

748   flatfish in the Wadden Sea and the coastal areas of the southeastern North Sea.

749   Helgolandes Meeresuntersuchungen 43:461–477.

750 Benoît, H., D. Swain, W. Bowen, G. Breed, M. Hammill, and V. Harvey. 2011.

751   Evaluating the potential for grey seal predation to explain elevated natural mortality

752   in three fish species in the southern Gulf of St. Lawrence. Marine Ecology Progress

753   Series 442:149–167.

754 Bergman, M. J. N., H. W. van der Veer, A. Stam, and D. Zuidema. 1989. Transport

755   mechanisms of larval plaice (Pleuronectes platessa L.) from the coastal zone into the

756   Wadden Sea nursery area. Rapp . P.-v. Reun. Cons. int. Explor. Mer 191:43–49.

757 Beverton, R. J. H. 1995. Spatial limitation of population size; the concentration

758   hypothesis. Netherlands Journal of Sea Research 34:1–6.

759 Brasseur, S., R. Czeck, A. Galatius, L. F. Jensen, J. Armin, P. Körber, R. Pund, U.

760   Siebert, J. Teilmann, and S. Klöpper. 2017. TSEG Grey Seal surveys in the Wadden

761   Sea and Helgoland in 2016-2017. General growth but local drop in numbers.

762   Wilhemshaven, Germany.

763 Brasseur, S. M. J. M., T. D. van Polanen Petel, T. Gerrodette, E. H. W. G. Meesters, P. J.

764   H. Reijnders, and G. Aarts. 2015. Rapid recovery of Dutch grey seal colonies fueled

765   by immigration. Marine Mammal Science 31:405–426.

766 Brasseur, S. M. J. M., P. J. H. Reijnders, J. S. M. Cremer, E. H. W. G. Meesters, R. J.

767   Kirkwood, L. F. Jensen, A. Jeβ, A. Galatius, J. Teilmann, and G. Aarts. 2018.

768   Echo's from the past: Regional variations in recovery within a harbour seal

769   population. PloS one 13:e0189674.

770   Brown, S. L., S. Bearhop, C. Harrod, and R. A. McDonald. 2012. A review of spatial and

771   temporal variation in grey and common seal diet in the United Kingdom and Ireland.

772   Journal of the Marine Biological Association of the United Kingdom 92:1711–1722.

773   Clapham, P. J., S. B. Young, and R. L. Brownell. 1999. Baleen whales: conservation

774   issues and the status of the most endangered populations. Mammal Review 29:37–

775   62.

776   Cook, R. M., S. J. Holmes, and R. J. Fryer. 2015. Grey seal predation impairs recovery of

777   an over-exploited fish stock. Journal of Applied Ecology 52:969–979.

778   Cook, R. M., and V. Trijoulet. 2016. The effects of grey seal predation and commercial

779   fishing on the recovery of a depleted cod stock. Canadian Journal of Fisheries and

780   Aquatic Sciences 73:1319–1329.

781   Couperus, B., S. Gastauer, S. M. M. Fässler, I. Tulp, H. W. van der Veer, and J. J. Poos.

782   2016. Abundance and tidal behaviour of pelagic fish in the gateway to the Wadden

783   Sea. Journal of Sea Research 109:42–51.

784   Dawson, A. S., and A. S. Grimm. 1980. Quantitative seasonal changes in the protein,

785   lipid and energy content of the carcass, ovaries and liver of adult female plaice,

786   Pleuronectes platessa L. Journal of Fish Biology 16:493–504.

787   Dickson, W. 1993. Estimation of the capture efficiency of trawl gear. I: Development of a

788   theoretical model. Fisheries Research 16:239–253.

789   Engelhard, G. H., M. A. Peck, A. Rindorf, S. C. Smout, M. van Deurs, K. Raab, K. H.

790   Andersen, S. Garthe, R. A. M. Lauerburg, F. Scott, T. Brunel, G. Aarts, T. van

44

791   Kooten, and M. Dickey-Collas. 2013. Forage fish, their fisheries, and their

792   predators: who drives whom? ICES Journal of Marine Science 71:90–104.

793 Estes, J. A., M. Heithaus, D. J. McCauley, D. B. Rasher, and B. Worm. 2016.

794   Megafaunal Impacts on Structure and Function of Ocean Ecosystems. Annual

795   Review of Environment and Resources 41:83–116.

796 Freitas, V., J. F. M. F. Cardoso, K. Lika, M. A. Peck, J. Campos, S. A. L. M. Kooijman,

797   and H. W. Van Der Veer. 2010. Temperature tolerance and energetics : a dynamic

798   energy budget-based comparison of North Atlantic marine species. Philosophical

799   Transactions of the Royal Society B: Biological Sciences 365:3553–3565.

800 Galatius, A., S. M. J. M. Brasseur, R. Czeck, J. Armin, P. Körber, P. Ralf, U. Siebert, J.

801   Teilman, and S. Klöpper. 2017. Trilateral Seal Expert Group (TSEG). Aerial surveys

802   of Harbour Seals in the Wadden Sea in 2017. Population counts still in stagnation,

803   but more pups than ever.

804 Gaston, A., R. Ydenberg, and G. Smith. 2007. Ashmole's halo and population regulation

805   in seabirds. Marine Ornithology 35:119–126.

806 Geelhoed, S. C. V., M. Scheidat, R. S. A. van Bemmelen, and G. Aarts. 2013. Abundance

807   of harbour porpoises (Phocoena phocoena) on the Dutch Continental Shelf, aerial

808   surveys in July 2010-March 2011. Lutra 56:45–57.

809 Gilles, A. 2008. Characterisation of harbour porpoise (Phocoena phocoena) habitat in

810   German waters. Christian-Albrechts University, Kiel.

811 Glorius, S., J. Craeymeersch, T. van der Hammen, A. Rippen, J. Cuperus, B. van der

812   Weide, J. Steenbergen, and I. Tulp. 2015. Effecten van garnalenvisserij in Natura

813   2000 gebieden. IJmuiden.

814   Hansson, S., U. Bergström, E. Bonsdorff, T. Härkönen, N. Jepsen, L. Kautsky, K.

815   Lundström, S.-G. Lunneryd, M. Ovegård, J. Salmi, D. Sendek, and M. Vetemaa.

816   2017. Competition for the fish – fish extraction from the Baltic Sea by humans,

817   aquatic mammals, and birds. ICES Journal of Marine Science

818   fsx207:https://doi.org/10.1093/icesjms/fsx207.

819   Härkönen, T. 1986. Guide to the otoliths of the bony fishes of the northeast Atlantic.

820   Danbiu ApS. Biological Consultants. Hellrup, Denmark.

821   Härkönen, T. 1987. Seasonal and Regional Variations in the Feeding-Habits of the

822   Harbor Seal, Phoca-Vitulina, in the Skagerrak and the Kattegat. Journal of Zoology

823   213:535–543.

824   Härkönen, T., and M. P. Heide- Jørgensen. 1991. The Harbor Seal Phoca-Vitulina as a

825   Predator in the Skagerrak. Ophelia 34:191–207.

826   Heessen, H. J. L., and N. Daan. 1996. Long-term trends in ten non-target North Sea fish

827   species. ICES Journal of Marine Science – ICES Journal of Marine Science

828   53:1063–1078.

829   Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological

830   consequences of marine top predator declines. Trends in Ecology and Evolution

831   23:202–210.

832   Houle, J. E., F. de Castro, M. A. Cronin, K. D. Farnsworth, M. Gosch, and D. G. Reid.

46

833 2016. Effects of seal predation on a modelled marine fish community and

834 consequences for a commercial fishery. Journal of Applied Ecology 53:54–63.

835 Innes, S., D. M. Lavigne, W. M. Earle, and K. M. Kovacs. 1987. Feeding Rates of Seals

836 and Whales. The Journal of Animal Ecology 56:115.

837 Kastelein, R. A., C. Staal, and P. R. Wiepkema. 2005. Food Consumption and Body Mass

838 of Captive Harbor Seals (Phoca vitulina). Aquatic Mammals 31:34–42.

839 Kavanagh, A. S., M. a. Cronin, M. Walton, and E. Rogan. 2010. Diet of the harbour seal

840 (Phoca vitulina vitulina) in the west and south-west of Ireland. Journal of the Marine

841 Biological Association of the United Kingdom 90:1517–1527.

842 van Keeken, O. A., M. van Hoppe, R. E. Grift, and A. D. Rijnsdorp. 2007. Changes in the

843 spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for

844 fisheries management. Journal of Sea Research 57:187–197.

845 van Kooten, T., C. M. Deerenberg, R. Jak, R. van Hal, and M. A. M. Machiels. 2015. An

846 exploration of potential effects on fisheries and exploited stocks of a network of

847 marine protected areas in the North Sea. IJmuiden.

848 van Kooten, T., L. Persson, and A. M. de Roos. 2007. Size-dependent mortality induces

849 life-history changes mediated through population dynamical feedbacks. The

850 American naturalist 170:258–70.

851 Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice

852 (Pleuronectes platessa). Netherlands Journal of Sea Research 9:69–85.

853 de la Vega, C., B. Lebreton, U. Siebert, G. Guillou, K. Das, R. Asmus, and H. Asmus.

854   2016. Seasonal Variation of Harbor Seal's Diet from the Wadden Sea in Relation to

855   Prey Availability. PLOS ONE 11:e0155727.

856 Leopold, M. F. 2015. Eat and be eaten: Porpoise diet studies. Wageningen University and

857   Research.

858 Leopold, M. F., C. J. G. Damme, C. J. M. Philippart, and C. J. N. Winter. 2001. Otoliths

859   of North Sea fish-Fish identification key by means of otoliths and other hard parts.

860   ETI (Expert Centre for Taxonomic Identification), University of Amsterdam,

861   Amsterdam, The Netherlands.

862 Leopold, M. F., C. J. G. van Damme, and H. W. van der Veer. 1998. Diet of cormorants

863   and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea.

864   Journal of Sea Research 40:93–107.

865 Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the

866   regulation of fish populations: evidence from among-population comparisons.

867   Proceedings. Biological sciences 269:49–54.

868 Lynam, C. P., M. Llope, C. Möllmann, P. Helaouët, G. A. Bayliss-Brown, and N. C.

869   Stenseth. 2017. Interaction between top-down and bottom-up control in marine food

870   webs. Proceedings of the National Academy of Sciences of the United States of

871   America 114:1952–1957.

872 Markussen, N. H., M. Ryg, and N. A. Øritsland. 1990. Energy requirements for

873   maintenance and growth of captive harbour seals, Phoca vitulina. Canadian Journal

874   of Zoology 68:423–426.

48

875   Morissette, L., V. Christensen, D. Pauly, M. Hammill, and H. Bourdages. 2012. Marine

876   Mammal Impacts in Exploited Ecosystems: Would Large Scale Culling Benefit

877   Fisheries? PLoS ONE 7:e43966.

878   Pedersen, J., and J. R. G. Hislop. 2001. Seasonal variations in the energy density of fishes

879   in the North Sea. Journal of Fish Biology 59:380–389.

880   Philippart, C. J. M., J. J. Beukema, G. C. Cadee, R. Dekker, P. W. Goedhard, J. M. van

881   Iperen, M. F. Leopold, and P. M. J. Herman. 2007. Impacts of nutrient reduction on

882   coastal communities. Ecosystems.

883   Reijnders, P. J. H. 1992. Retrospective Population Analysis and Related Future

884   Management Perspectives for the Harbour Seal Phoca vitulina in the Wadden Sea.

885   Netherlands Institute for Sea Research 20:193–197.

886   Reiss, H., I. Kröncke, and S. Ehrich. 2006. Estimating the catching efficiency of a 2-m

887   beam trawl for sampling epifauna by removal experiments. ICES Journal of Marine

888   Science 63:1453–1464.

889   Ries, E. H., L. R. Hiby, and P. J. H. Reijnders. 1998. Maximum likelihood population

890   size estimation of harbour seals in the Dutch Wadden Sea based on a mark-recapture

891   experiment. Journal of Applied Ecology 35:332–339.

892   Rijnsdorp, A. D., and P. I. Van Leeuwen. 1996. Changes in growth of North Sea plaice

893   since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature.

894   ICES Journal of Marine Science – ICES Journal of Marine Science 53:1199–1213.

895   Robinson, L. A., S. P. R. Greenstreet, H. Reiss, R. Callaway, J. Craeymeersch, I. de

49

896   Boois, S. Degraer, S. Ehrich, H. M. Fraser, A. Goffin, I. Kröncke, L. L. Jorgenson,

897   M. R. Robertson, and J. Lancaster. 2010. Length–weight relationships of 216 North

898   Sea benthic invertebrates and fish. Journal of the Marine Biological Association of

899   the United Kingdom 90:95.

900 Rogers, S. I., A. D. Rijnsdorp, U. Damm, and W. Vanhee. 1998. Demersal fish

901   populations in the coastal waters of the UK and continental NW Europe from beam

902   trawl survey data collected from 1990 to 1995. Journal of Sea Research 39:79–102.

903 Roman, J., M. M. Dunphy-Daly, D. W. Johnston, and A. J. Read. 2015. Lifting baselines

904   to address the consequences of conservation success. Trends in Ecology &

905   Evolution 30:299–302.

906 De Roos, A. M., T. Schellekens, T. van Kooten, K. van de Wolfshaar, D. Claessen, and

907   L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-

908   specific biomass when mortality increases: the influence of maturation versus

909   reproduction regulation. The American naturalist 170:E59-76.

910 Rosen, D. A., and D. Renouf. 1998. Correlates of seasonal changes in metabolism in

911   Atlantic harbour seals (Phoca vitulina concolor). Canadian Journal of Zoology

912   76:1520–1528.

913 Sousa, T., T. Domingos, J.-C. Poggiale, and S. A. L. M. Kooijman. 2010. Dynamic

914   energy budget theory restores coherence in biology. Philosophical Transactions of

915   the Royal Society of London B: Biological Sciences 365.

916 Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner,

917   K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North

918   Pacific Ocean: an ongoing legacy of industrial whaling? Proceedings of the National

919   Academy of Sciences of the United States of America 100:12223–12228.

920   Støttrup, J. G., P. Munk, M. Kodama, and C. Stedmon. 2017. Changes in distributional

921   patterns of plaice Pleuronectes platessa in the central and eastern North Sea; do

922   declining nutrient loadings play a role? Journal of Sea Research 127:164–172.

923   Teal, L. R., R. van Hal, T. van Kooten, P. Ruardij, and A. D. Rijnsdorp. 2012. Bio-

924   energetics underpins the spatial response of North Sea plaice (Pleuronectes platessa

925   L.) and sole (Solea solea L.) to climate change. Global Change Biology 18:3291–

926   3305.

927   Temming, A., and M. Hufnagl. 2015. Decreasing predation levels and increasing

928   landings challenge the paradigm of non-management of North Sea brown shrimp

929   (Crangon crangon). ICES Journal of Marine Science 72:804–823.

930   Tien, N. S. H., J. A. M. Craeijmeersch, C. J. G. van Damme, A. S. Couperus, J. Adema,

931   and I. Y. M. Tulp. 2017. Burrow distribution of three sandeel species relates to beam

932   trawl fishing, sediment composition and water velocity, in Dutch coastal waters.

933   Journal of Sea Research 127:194–202.

934   Tollit, D. J., S. P. R. Greenstreet, and P. M. Thompson. 1997. Prey selection by harbour

935   seals, Phoca vitulina, in relation to variations in prey abundance. Canadian Journal

936   of Zoology-Revue Canadienne De Zoologie 75:1508–1518.

937   Trzcinski, M. K., R. Mohn, and W. D. Bowen. 2006. Continued decline of an Atlantic

938   cod population: How important is gray seal predation? Ecological Applications

939   16:2276–2292.

940   Tulp, I., L. J. Bolle, and A. D. Rijnsdorp. 2008. Signals from the shallows: In search of

941   common patterns in long-term trends in Dutch estuarine and coastal fish. Journal of

942   Sea Research 60:54–73.

943   Tulp, I., C. Chen, H. Haslob, K. Schulte, V. Siegel, J. Steenbergen, A. Temming, and M.

944   Hufnagl. 2016. Annual brown shrimp (Crangon crangon) biomass production in

945   Northwestern Europe contrasted to annual landings. ICES Journal of Marine Science

946   73:2539–2551.

947   Tulp, I., H. W. van der Veer, P. Walker, L. van Walraven, and L. J. Bolle. 2017. Can

948   guild- or site-specific contrasts in trends or phenology explain the changed role of

949   the Dutch Wadden Sea for fish? Journal of Sea Research 127:150–163.

950   Tyrrell, M. C., J. S. Link, and H. Moustahfid. 2011. The importance of including

951   predation in fish population models: Implications for biological reference points.

952   Fisheries Research 108:1–8.

953   de Veen, J. 1978. On selective tidal transport in the migration of North Sea Plaice

954   (pleuronectes platessa) and other flatfish species. Netherlands Journal of Sea

955   Research 12:115–147.

956   van der Veer, H., J. Koot, G. Aarts, R. Dekker, W. Diderich, V. Freitas, and J. Witte.

957   2011. Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery

958   function of the Balgzand intertidal, Dutch Wadden Sea. Marine Ecology Progress

959   Series 434:143–154.

960   van der Veer, H. W., J. F. M. F. Cardoso, M. A. Peck, and S. A. L. M. Kooijman. 2009.

961   Physiological performance of plaice Pleuronectes platessa (L.): A comparison of

962   static and dynamic energy budgets. Journal of Sea Research 62:83–92.

963   van der Veer, H. W., A. S. Jung, V. Freitas, C. J. M. Philippart, and J. I. Witte. 2016.

964   Possible causes for growth variability and summer growth reduction in juvenile

965   plaice Pleuronectes platessa L. in the western Dutch Wadden Sea. Journal of Sea

966   Research 111:97–106.

967   Watt, J., G. J. Pierce, and P. R. Boyle. 1997. Guide to the identification of North Sea fish

968   using premaxillae and vertebrae. Page ICES Cooperative Research Report. ICES.

969   Zijlstra, M., and M. R. Van Eerden. 1995. Pellet production and the use of otoliths in

970   determining the diet of Cormorants Phalacrocorax carbo sinensis: Trials with captive

971   birds. Ardea 83:123–131.

972

973

974   **APPENDIX S1. Estimating catchability of the fish surveys**

975   Estimating the catchability of the survey gears is essential for estimating absolute fish

976   abundance, and hence for estimating the impact of seals on fish stocks. Two approaches

977   exist for estimating catchability. The first approach is to estimate the total stock size

978   using stock assessments, and subsequently comparing the catch per unit of area with the

979   expected numbers per unit of area based on these assessments (e.g. (Fraser et al. 2007,

980   Walker et al. 2017)). Because the survival rates for the younger age classes (e.g. 0 and 1-

981   year olds) are not well known the stocks size estimates of these age-classes are likely

982   inaccurate. As a result the derived catchability estimates for these age-classes will be

983   poor.

984   The second approach to estimate catchability involves experimentally estimating the

985   proportion of fish escaping the net. (Kuipers 1975) defines four main processes that cause

986   fish to escape the net: 1) Lateral escape, 2) Disturbance caused by the ship, 3) Escape

987   through the net and 4) Escape underneath and above the net. (Kuipers 1975) attempted to

988   experimentally estimate the effect of these 4 processes using a 1.9m wide small meshed

989   beam trawl. This resulted in a catchability equation which was specified as function of

990   the beam width. Here we re-estimated that function, and use it to estimate the catchability

991   of the 3m and 6m DFS gear.

992

993   **The efficiency of a 1.9 m beam trawl**

994   The experimental study area was located on the tidal flats of the Balgzand, in the

54

995   Dutch Wadden Sea. Fishing was carried out by a rubber dingy, fishing at a speed of 0.5-

996   0.58 m/s, and a stretched mesh size of 1cm, using 1.9 m (or 3m) beam and 0-3 tickler

997   chains. Given the relative small (stretched) mesh size of 1cm, only fish <2.5 cm were

998   considered to partly disappear through the net (item 3 above). Catch rates depended on

999   whether tickler chains were used, but fishing with more than one tickler chain did not

1000   lead to higher observed catch rates. Hence, the proportion of fish escaping underneath the

1001   net was assumed to be negligible when fishing with more than 1 tickler chain (item 4

1002   above).

1003   To estimate the effect of **boat disturbance**, catch rates were compared when fishing

1004   with a 8m and 400m long fishing line. The observed discrepancy between catch rates

1005   increased with length. The efficiency E_d as function of length was provided, but this did

1006   not match the function provided in the corresponding figure of (Kuipers 1975). Hence,

1007   the data were reconstructed (Figure S1) and a new efficiency function was estimated.

55

1008
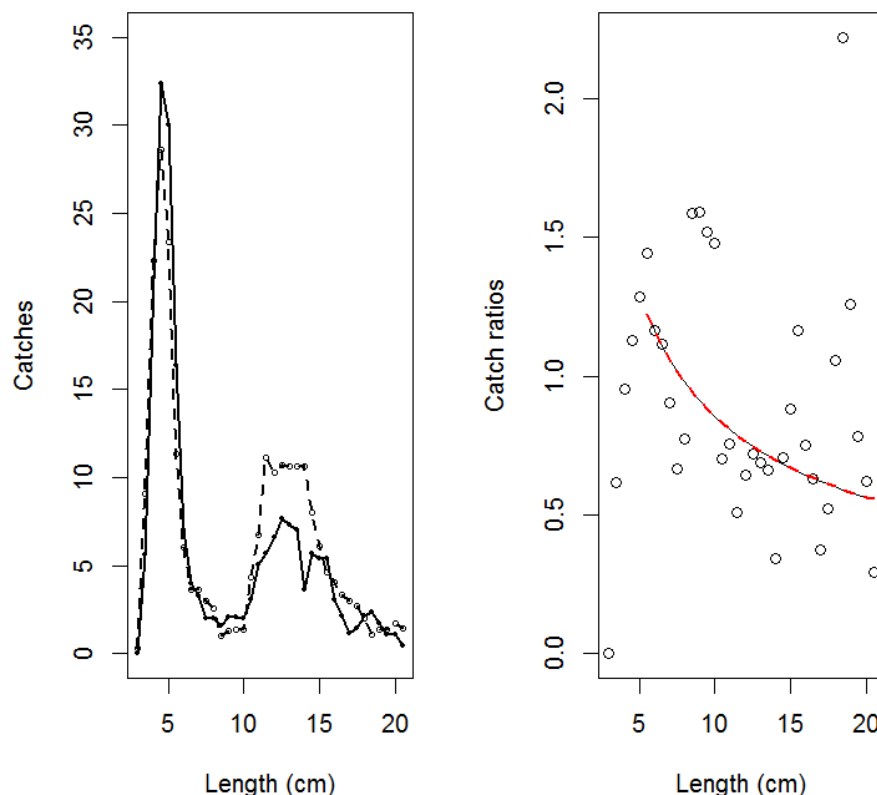
Figure S1. (Figure 5 in (Kuipers 1975)). Catches of plaice by length class of the 2m beam trawl with 8m (solid line) and with 400m (dashed line) fishing line (moving averages of 3). Right, efficiency in respect of disturbance (E_d) against plaice length. Curve represents the log of catch-ratio as function of log of length.

A Generalized Linear Model (GLM) assuming a quasi-Poisson distribution was fitted to the data. The response variable was defined as the catch rate of the 8m fishing line, and modelled as a function of the log of fish length (L), with the log of the catch rate of the 400m fishing line included as an offset. Similar to (Kuipers 1975), only data from fish > 5cm were included in the model fitting. This results in the following efficiency (as

56

1018   fraction) caused by boat disturbance

$$E_d = \exp\left(1.2263863 - 0.6000988\, Ln(L)\right) \qquad \text{eq. S1}$$

1020

1021   The effect of **the lateral escape** was estimated by comparing the catch rates of a 1.9m

1022   beam and two 1.9m beam fitted together side-by-side. Similar to the analysis based on the

1023   8 and 400m fishing line, a GLM was fitted to the data, with the catch rate of the single

1024   beam as the response variable, and the log of the catch rate of the double beam (i.e. 2 x

1025   1.9m) as model offset (Figure S2)

1026
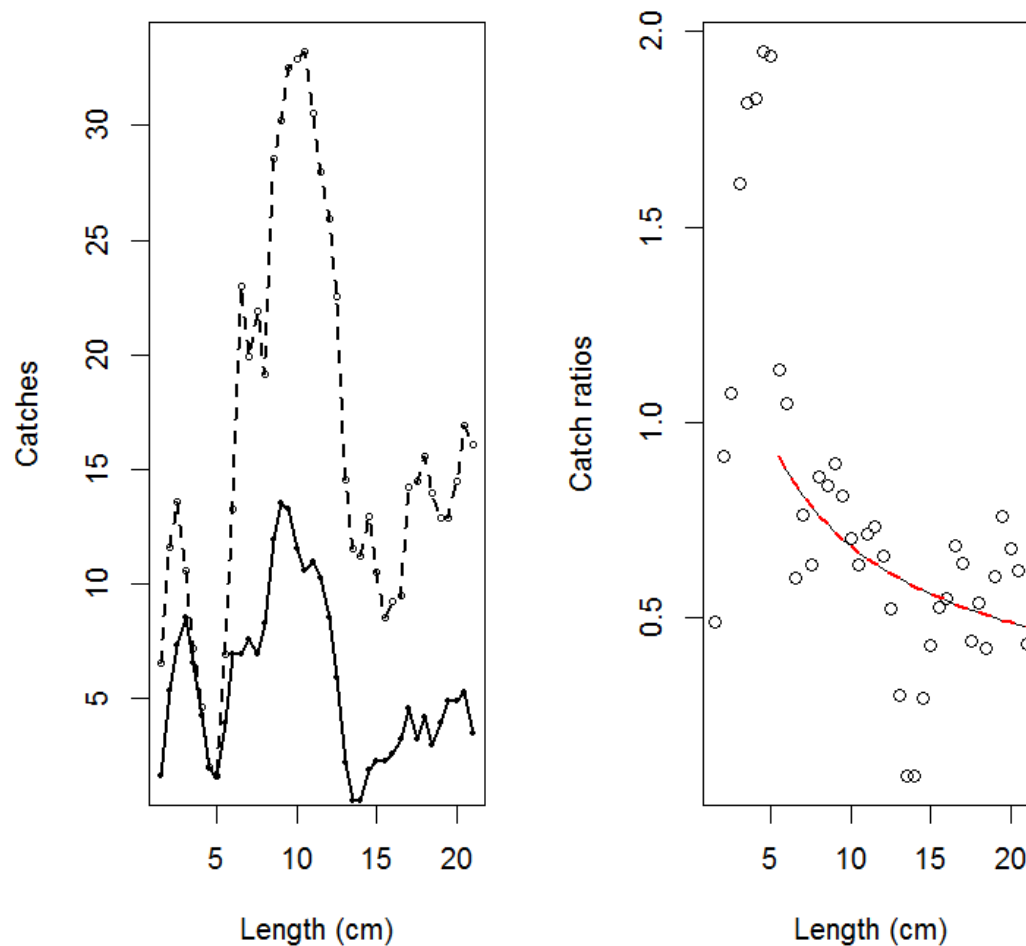
1027   Figure S2. (Figure 6 in (Kuipers 1975)). Catches of plaice by length class of the 1.9m

1028   beam trawl (solid line) and 2x1.9m beam trawl (dashed line) (moving averages of 3).

1029   Right, catch-ratio in respect of lateral escape (E_l) against length of the plaice. Note that

1030   the catch rates (right figure) were corrected for beam-width. Curve represents the log of

1031   catch-ratio as function of log of length.

1032

1033   This resulted in the following catch-rate ratio of the 1.9 m beam (c) relative to the

1034   catch rate of the 2 x 1.9m beam (C).

1035
$$R_c(L) = \frac{c}{C} = \exp(0.7334693 - 0.4834846\, Ln(L)) \qquad \text{eq. S2}$$

1036   The philosophy underlying the lateral escape, is that within a fixed section (width = b cm)

1037   on either side of the net, fish escape. Hence, the ratio between the catch rate can be defined

1038   as

1039
$$R_c = \frac{c}{C} = \frac{a-2b}{2a-2b} \qquad \text{eq. S3}$$

1040   Where a is the size of the single net (i.e. 1.9m) and 2a the size of the double net. The size

1041   of b is length dependent, with b being larger for larger fish, due to their higher swim speed.

1042   Hence, b can be estimated as

1043
$$b(L) = \frac{a\left(1-\frac{1}{2}R_c(L)\right)}{\left(1-R_c(L)\right)} \qquad \text{eq. S4}$$

1044   The total efficiency regarding the lateral escape of the 1.9 m relative to no lateral escape

1045   can now be defined as

1046
$$E_l = \frac{a-2b(L)}{a} \qquad \text{eq. S5}$$

1047

1048   , where here a=1.9m.

1049   The total efficiency E, taking both lateral escape and boat disturbance into account, can be

1050   defined as

59

1051 $$E = E_d \cdot E_l \qquad \text{eq. S6}$$

1052

1053 **The efficiency of the DFS beam trawl**

1054 Similar to the gear used by (Kuipers 1975), the DFS uses a net with a similar mesh size

1055 (i.e. 2cm) and 1 tickler chain. However, the DFS differs in a number of other aspects. 1.

1056 The survey takes place at a higher speed (i.e. 1.03-1.54 m/s, instead of 0.5 m/s). 2. It uses

1057 a larger beam width (3 m in the Wadden Sea, and 6 m in the Wadden coastal zone), 3.

1058 Most fishing takes place in the Wadden Sea gullies, and not on the relative flat tidal mud

1059 flats as in, which may lead to a different proportion of escape underneath .

1060

1061 Using eq. 5 it is now possible to correct the efficiency to take the larger beam width into

1062 account (Figure S3). (Kuipers 1975) did not find evidence for fish escaping underneath

1063 the net when using at least one tickler chain, but fishing took place on the relative flat

1064 mud flats. In contrast, (Reiss et al. 2006) towed three nets behind each other, and found

1065 that on average only 37% of the flatfish dab (*Limanda limanda*) remained in the first net,

1066 while the others escape underneath. This might be due to a difference in behaviour

1067 between dab and plaice, but could also be due to a difference in topography and bottom

1068 structure. Since the DFS surveys the gullies and coastal waters of the North Sea, we

1069 assume that the proportion of escape underneath is better represented by the study of

1070 (Reiss et al. 2006). When combining the reconstructed length-specific efficiency and

1071 accounting for possible escape underneath the net based on (Reiss et al. 2006), the

1072   efficiency becomes substantially lower (solid red and purple line, Figure S3). These

1073   efficiency estimates will be used in the subsequent calculations.

1074   We expect this to be an under-estimate of efficiency, particularly because the DFS fishes

1075   at twice the speed of the (Kuipers 1975) study. However, there appears to be a close

1076   correspondence with the efficiency estimates from (Bergman et al. 1989) (green line and

1077   solid purple line in Figure S3), who also used a 3m beam trawl. However, unfortunately

1078   no details or data are presented in (Bergman et al. 1989), and hence their estimated

1079   efficiency cannot be validated.
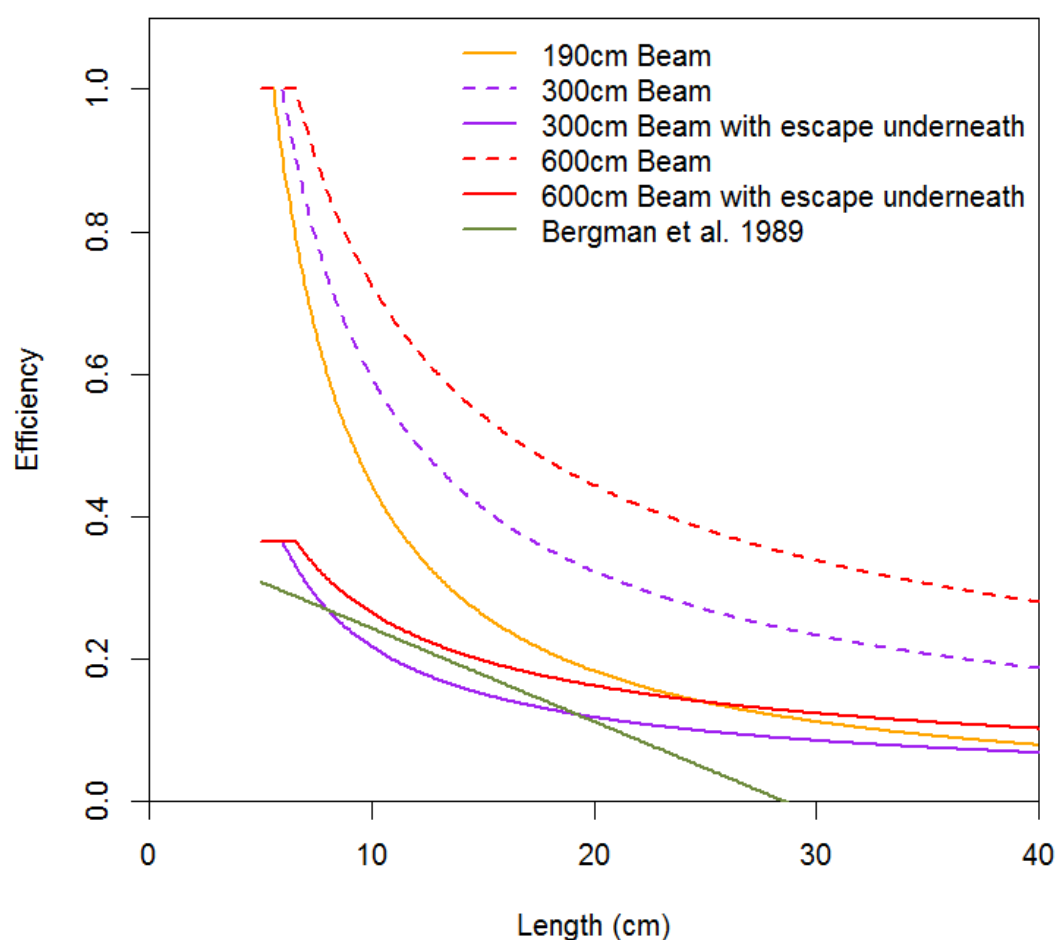
Figure S3. Efficiency estimates for flatfish for different gear types taking the size-selective catchability into account. The orange line is the total estimated efficiency for plaice based on (Kuipers 1975). The dashed purple and red line are based on (Kuipers 1975), but correcting for the larger beam-width (i.e. 3 and 6m, respectively). The solid purple and red line, also take escape underneath into account (Reiss et al. 2006). These lines will be used as the catchability estimates of the DFS in the Wadden Sea (3m beam) and Wadden coastal zone (6m beam). The green line represents the estimated efficiency

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1088   of a 3m beam based on simultaneously fishing with a 1.9 and 3m beam trawl (Bergman et

1089   al. 1989). Catchability estimates exceeding 1, where truncated to 1.

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1091   The efficiency of the IBTS, SNS and BTS

1092   For the regions bordering the Wadden Sea, data from the international bottom trawl

1093   survey (IBTS), sole net survey (SNS) and beam trawl survey (BTS) are available.

1094   Although, surveys also take place in a larger area, further offshore, some fish hauls occur

1095   in the same region as the coastal DFS. For those sampling stations in the overlapping

1096   years (here data from 1987 onwards were used) it was possible to directly compare the

1097   length-specific catch per unit area estimates of the IBTS, SNS and BTS survey, with

1098   those from the DFS. This will provide a measure of relative efficiency. Since, we now

1099   have a (rough) estimate of the efficiency of the DFS, we can reconstruct the absolute

1100   catchability.

1101   95% of the DFS sampling locations occur at depths shallower than 20m, hence we only

1102   select the IBTS, SNS and BTS survey data from similar depths and within at least 50km

1103   of the nearest seal haul-out site in the Wadden Sea. The catch-ratios are shown in the top-

1104   figures of Figure S4a-c. Up to approximately 10 cm, the catch per unit of area are higher

1105   in the DFS, compared to the BTS and SNS, which is possible due to the larger mesh size

1106   of the latter two gears (i.e. 4 cm). However, catch-rates are substantially larger at larger

1107   length classes. For example, for a length-class of >20cm, the BTS and SNS catch at least

1108   3 times more individuals per unit of area. This is most likely due to the larger fishing

1109   speed (BTS/SNS = 4nm, DFS= 2-3 nm). Overall, the catch rate of the IBTS is much

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1110   lower, which is most likely due to the fact it does not use a heavy beam.
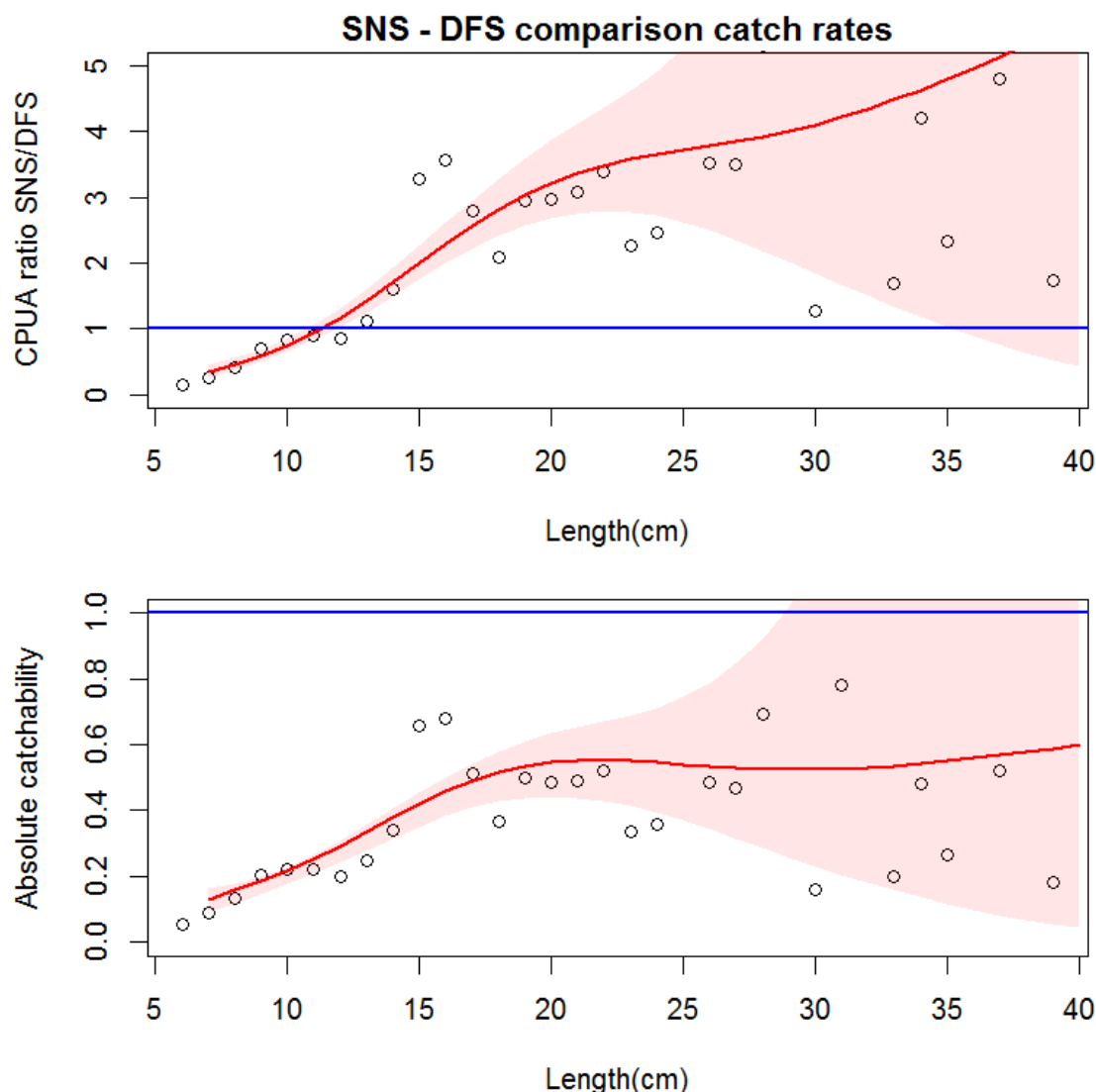
1111

1112   Figure S4a. Catch ratios for plaice of SNS and DFS (top figure). Values <1 imply that the

1113   absolute numbers per ha caught in the DFS are higher than in the SNS. Red line is a

1114   GAM fitted to the data (shaded area is 95% CI). Lower figure is absolute catchability of

1115   the SNS survey, taking the catch-ratio between SNS/DFS and the absolute catchability

1116   estimate of the DFS (Figure S3, red solid line) into account.

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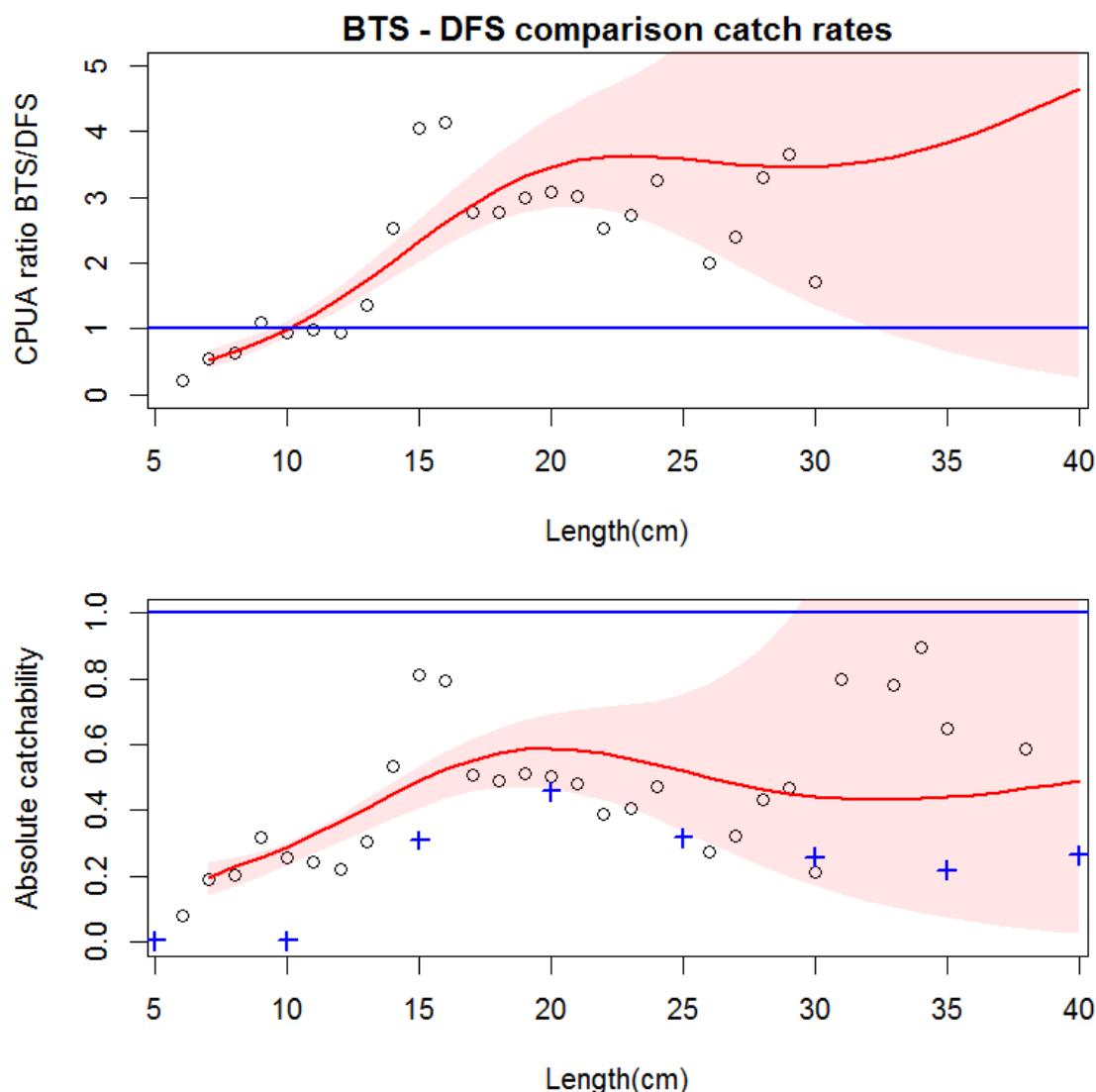
1119   Figure S4b. BTS catchability estimates. See Figure S4a. Blue plusses are the absolute

1120   catchability estimates for plaice based on (Walker et al. 2017). The higher catchability

1121   estimates for the larger length classes, might be explained by a higher turbidity in the

1122   coastal waters, possible causing lower lateral escape.

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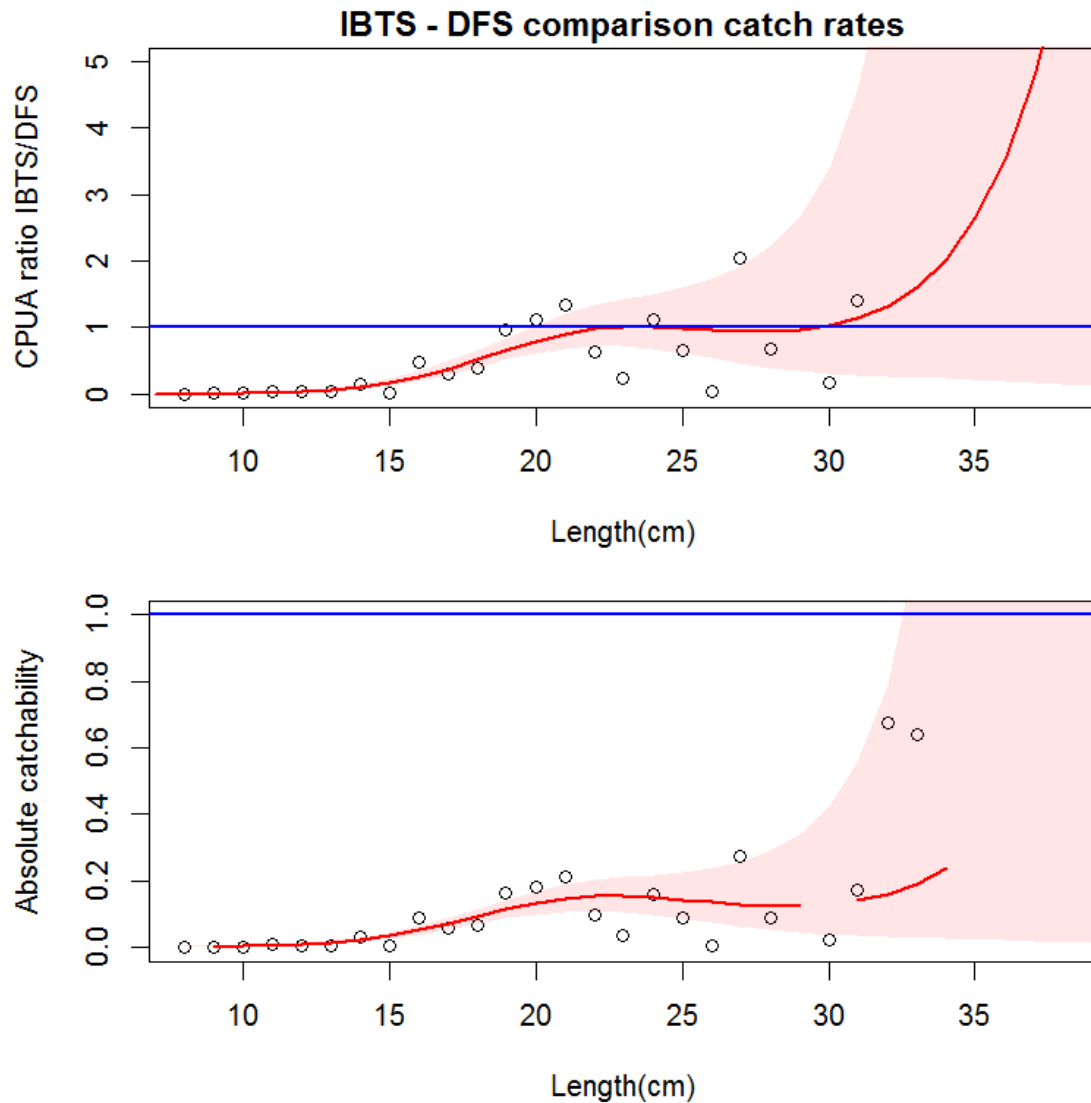
1125 Figure S4c. IBTS catchability estimates. See description Figure S4a.

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1127 **LITERATURE CITED**

1128 Bergman, M. J. N., H. W. van der Veer, A. Stam, and D. Zuidema. 1989. Transport

1129 mechanisms of larval plaice (Pleuronectes platessa L.) from the coastal zone into the

66

1130   Wadden Sea nursery area. Rapp . P.-v. Reun. Cons. int. Explor. Mer 191:43–49.

1131 Fraser, H. M., S. P. R. Greenstreet, and G. J. Piet. 2007. Taking account of catchability in

1132   groundfish survey trawls: Implications for estimating demersal fish biomass. ICES

1133   Journal of Marine Science 64:1800–1819.

1134 Kuipers, B. 1975. On the efficiency of a two-metre beam trawl for juvenile plaice

1135   (Pleuronectes platessa). Netherlands Journal of Sea Research 9:69–85.

1136 Reiss, H., I. Kröncke, and S. Ehrich. 2006. Estimating the catching efficiency of a 2-m

1137   beam trawl for sampling epifauna by removal experiments. ICES Journal of Marine

1138   Science 63:1453–1464.

1139 Walker, N. D., D. L. Maxwell, W. J. F. Le Quesne, and S. Jennings. 2017. Estimating

1140   efficiency of survey and commercial trawl gears from comparisons of catch-ratios.

1141   ICES Journal of Marine Science 74:1448–1457.

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APPENDIX S2. Supplementary figures and tables

Table S1. Characteristics of the different survey gear types -

	Kuipers 1975	Reiss et al. 2006	DFS-WZ	DFS-WC	GOV	SNS	BTS	Bergmann et al. 1989
Net mesh	?	20mm	35mm	35mm	100mm	80mm	120mm	?
Cod end	10mm	4mm	20mm	20mm	20mm	40mm	40mm	20mm
Fishing speed	0.51m/s	0.51 m/s	1.0-1.5m/s (2-3nm)	1.0-1.5m/s (2-3nm)	2.1 m/s (4nm)	1.8-2.1m/s (3.5 – 4 nm)	2.1 m/s (4nm)	1.5 m/s (2nm)
Beam width	1.9m	2m	3m	6m		6m	8m	3m

*Bergmann et al. 1989 specify a mesh size of 10 x 10mm, which equals a stretched mesh size of 20mm

Table S2. Caloric density of the 10 main prey items found in the harbour seal diet.

Species/Family	Latin name	Caloric density (kcal/g)	Range	Source
European flounder	*Platichthys flesus*	1.09	0.99-1.20	(Summers 1979)[f]
Sandeel	*Ammodytes sp.*	1.41	0.88-1.48	(Pedersen and Hislop 2001)[*]
Dover sole	*Solea solea*	0.91	0.61-1.20	(Soriguer et al. 1997)‡
Five-bearded rockling	*Ciliata mustela*	1.02	0.88-1.29	Average of round fish; cod and whiting
Whiting	*Merlangius merlangus*	1.10	0.91-1.29	(Pedersen and Hislop 2001)[*]
European Plaice	*Pleuronectes platessa*	0.87	0.61-0.87	(Costopoulos and Fonds 1989)§
Atlantic cod	*Gadus morhua*	0.94	0.88-1.05	(Härkönen and Heide- Jørgensen 1991)
Common dragonet	*Callionymus lyra*	1.02	0.88-1.29	Average of round fish; cod and whiting
Common dab	*Limanda limanda*	0.87	0.61-0.87	Assumed similar to Plaice
Bull-rout	*Myoxocephalus scorpius*	1.02	0.88-1.29	Average of round fish; cod and whiting

†based on the average caloric density for 0 and I group flounder measured in July-Sept of 4.6 kcal/g dry weight. For July, the relationship between wet weight (x, in g) and dry weight (y, in g) was defined as y = - 0.36 + 0.24x (Summers 1979). Therefore, the wet-dry weight conversion factor for a 100 g flounder was 0.236, resulting in an estimated energy density of 1.09 kcal/g wet weight.

*Converted from kJ/g to kcal/g using the conversion factor of 0.239. Caloric density estimates were based on fish >10cm caught in quarter 3. Range was based on minimum and maximum energy density observed in all size-classes and seasons.

§In the Wadden Sea, the condition factor varied between 0.75 in winter, and 0.95 in summer, which corresponds to caloric densities between 0.61-0.87 (Costopoulos & Fonds 1989).

‡ Range based on minimum and maximum value of the range for plaice and flounder.
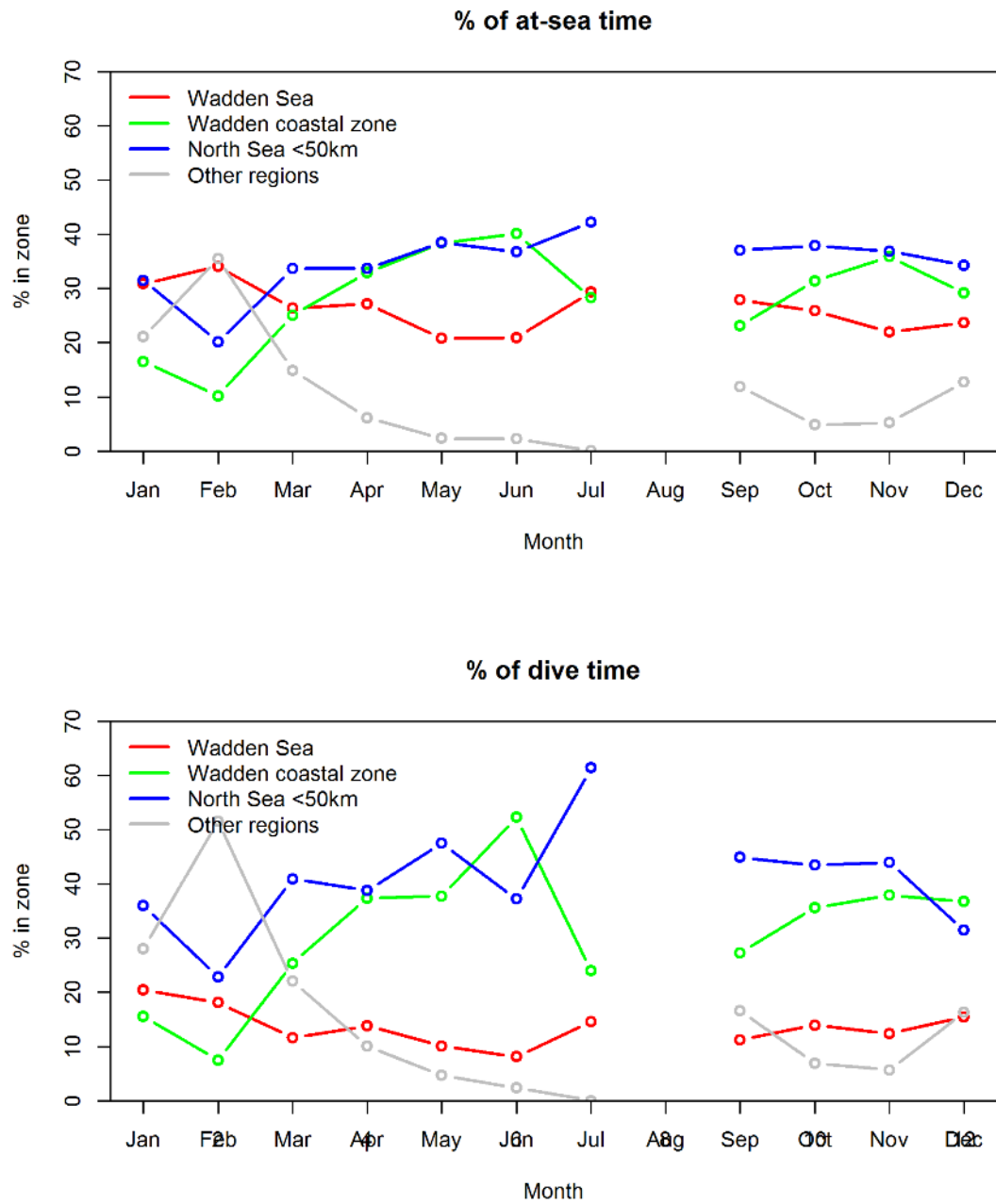
Figure S1. Proportion of time spent (top figure) and proportion of dive time (< -1.5m, bottom figure) in the different regions

a.   b.
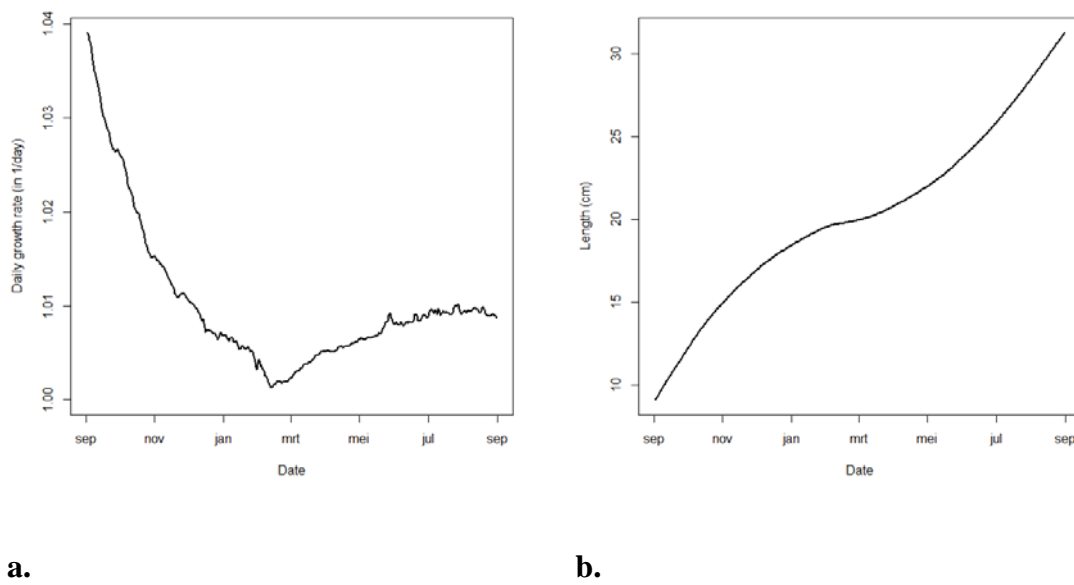
Figure S2. Growth of 0-group plaice per day based on *optimal* DEB model conditions (**a**), and how this leads to the change in length (in cm, **b**) and weight (in gram, **c**) throughout the year.
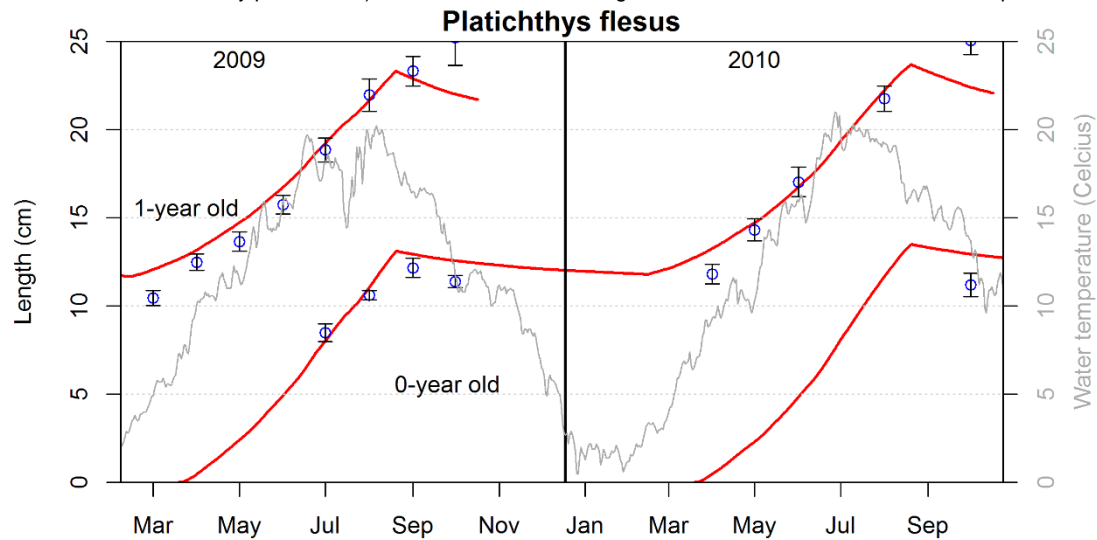
Platichthys flesus
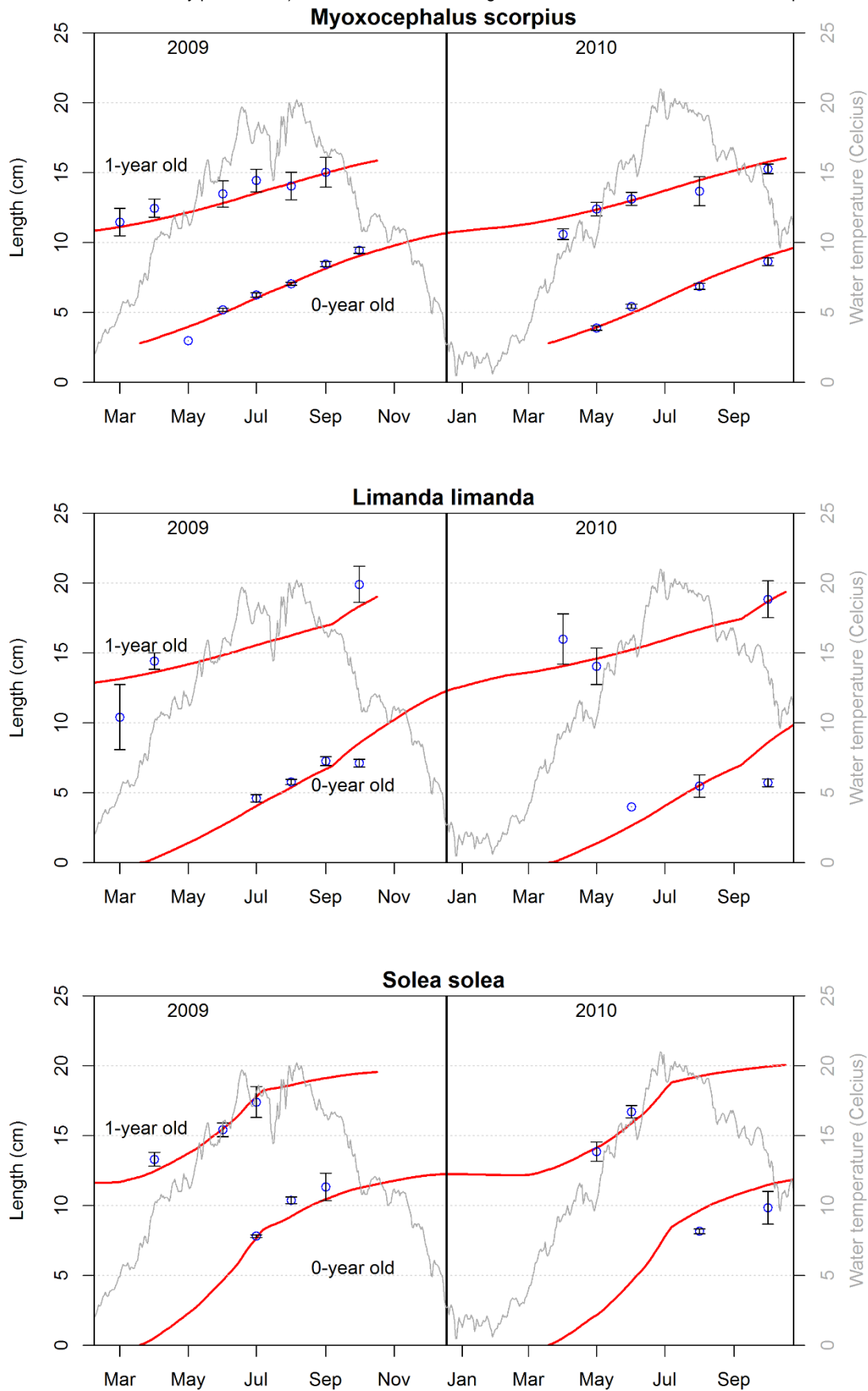
Figure S3a-e. Observed length (circles and standard error bars) and predicted length (solid red line) of 0- and 1-year old flounder (*Platichthys flesus*), bull-rout (*Myoxocephalus scorpius*), dab (*Limanda limanda*) and sole (*Solea solea*). Grey line indicates water temperature. Predicted growth (solid lines) is based on DEB model where food intake parameter is allowed to vary between the winter months and other times of the years.
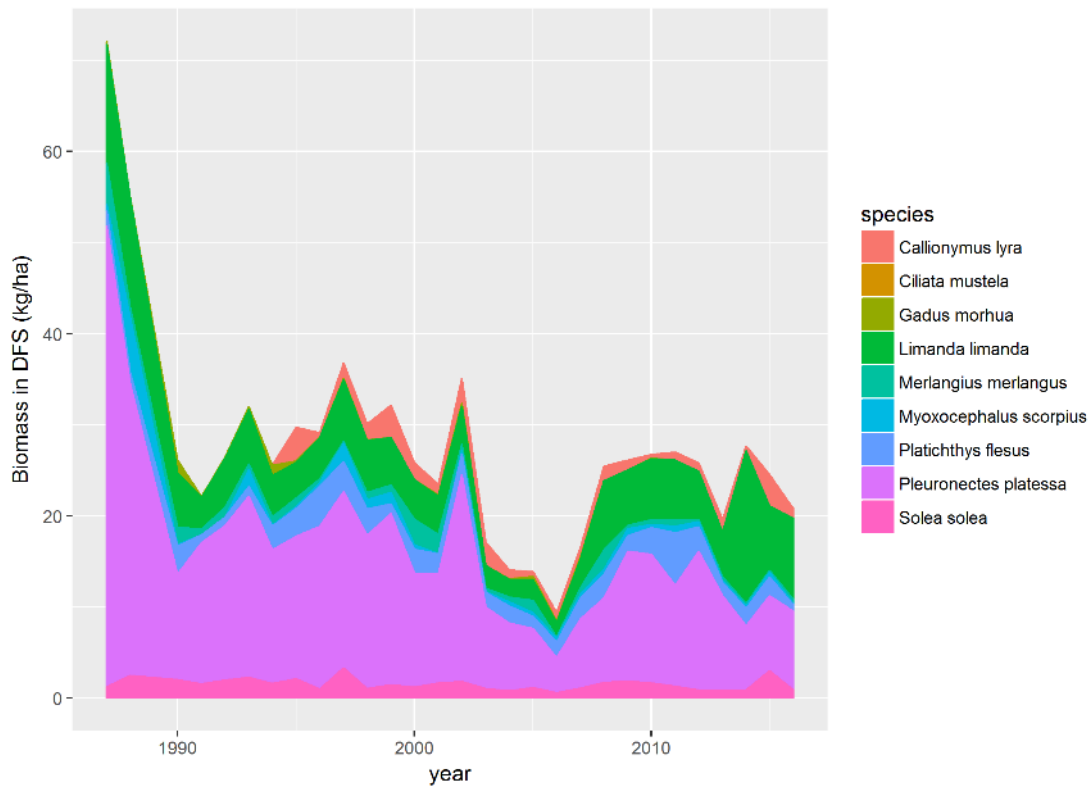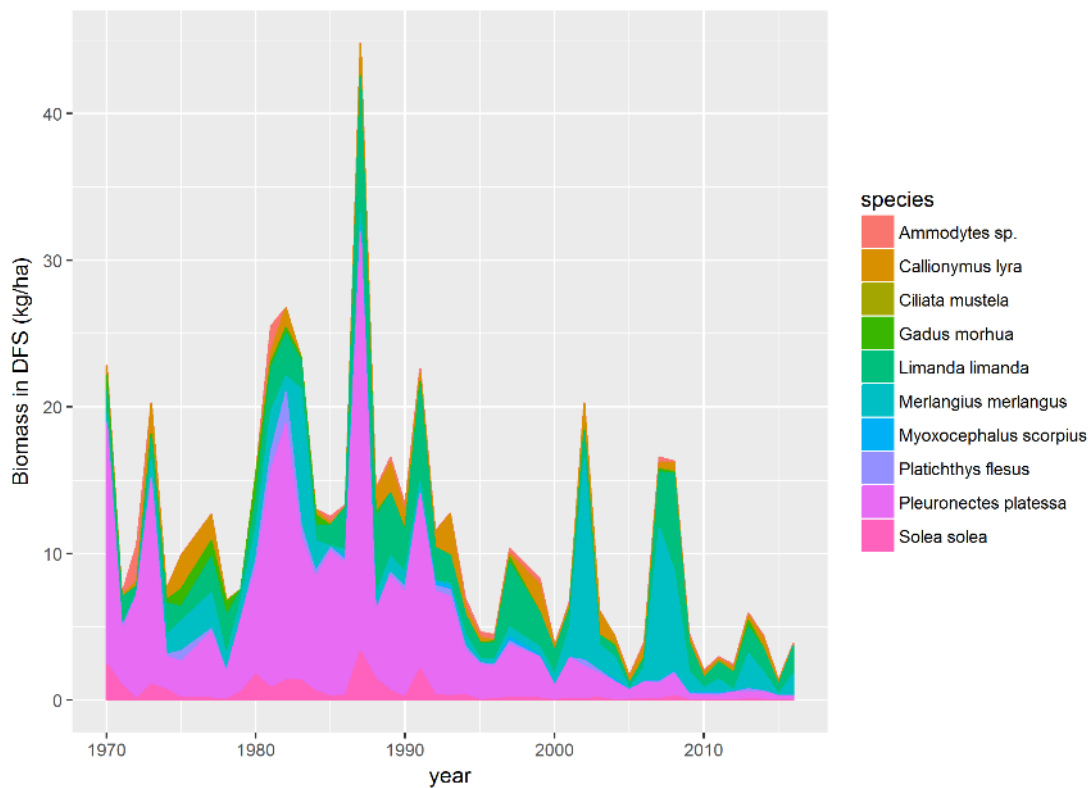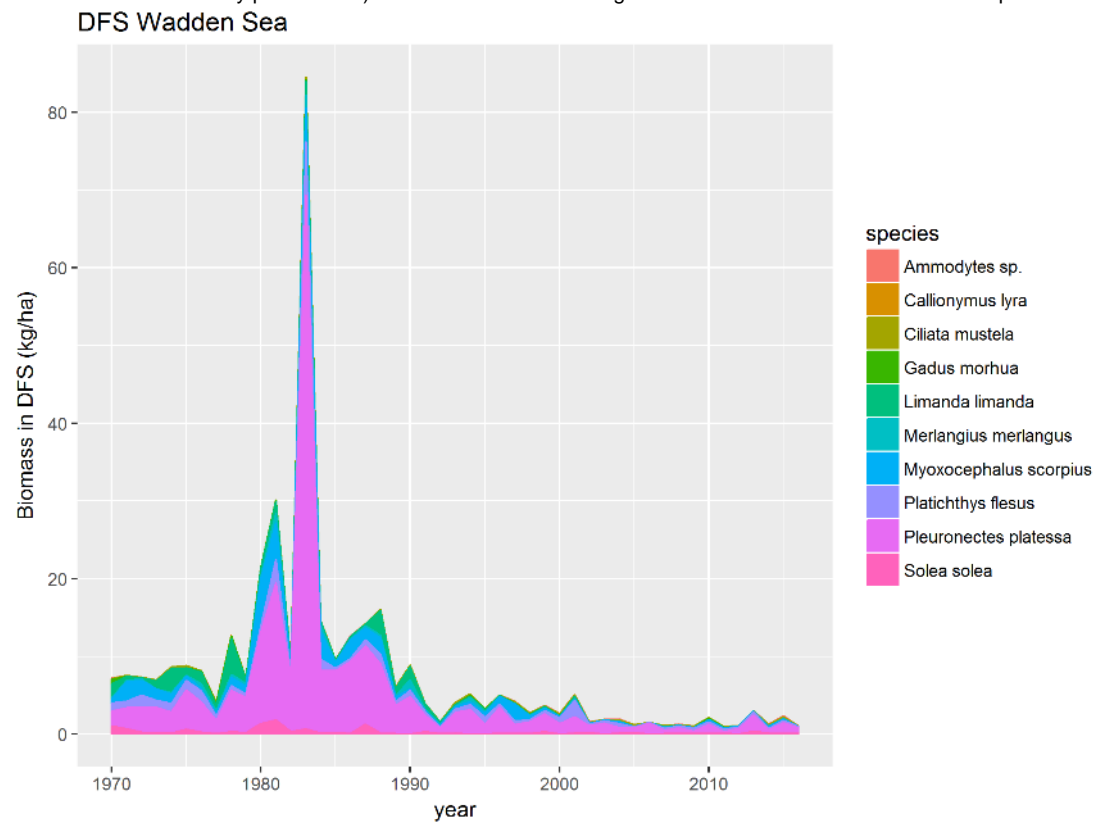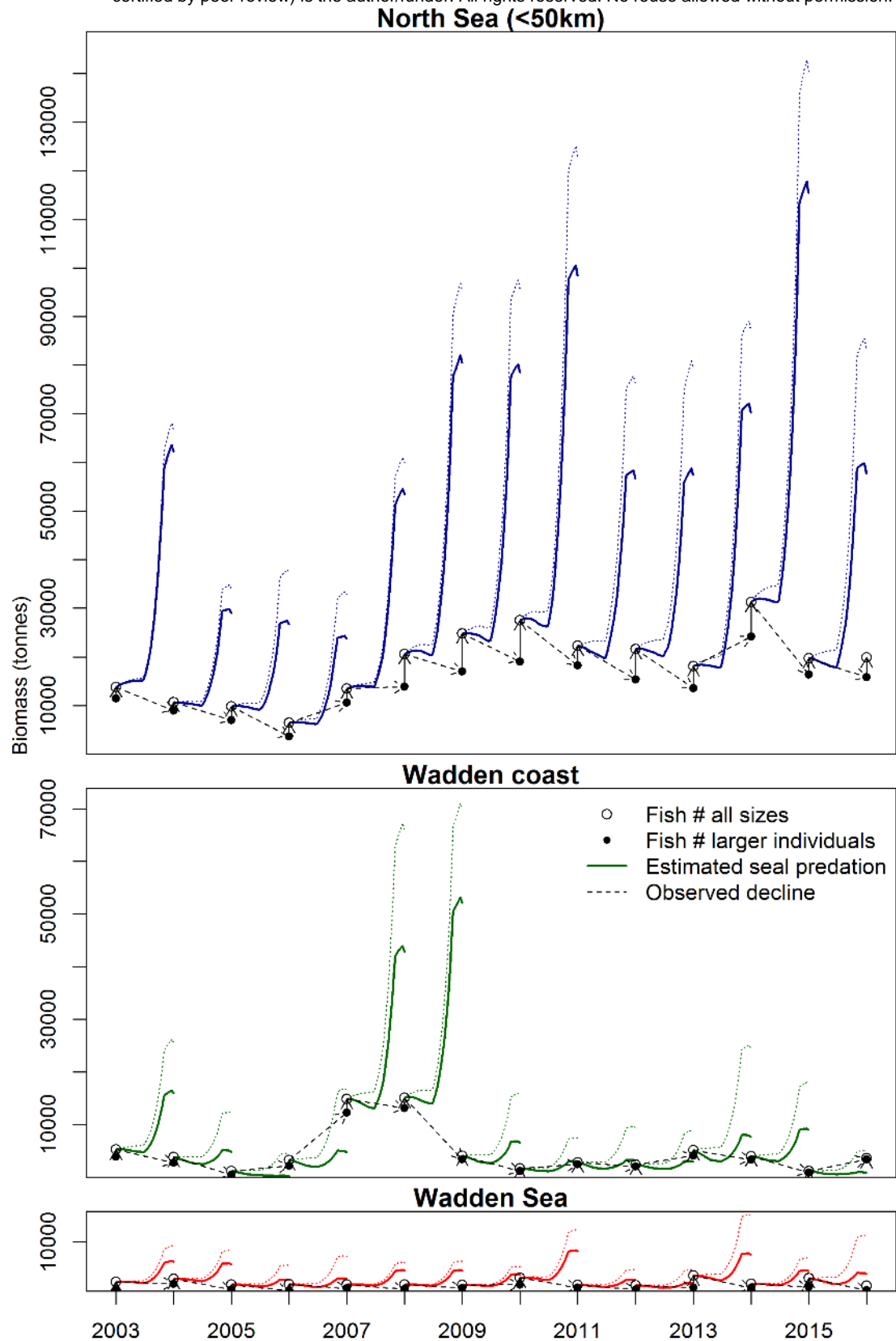
Figure

Figure S4. Species composition. Biomass (kg/ha) in BTS (top figure) and DFS Wadden coast and Wadden Sea (bottom figure)

Figure S5. The estimated effect of seal predation on the biomass of prey fish for the Wadden

Sea (red lines), Wadden coast (green lines) and remaining areas up to 50km from the haul-

outs (blue lines, and see regions in Figure 1). The fish survey in September (i.e. BTS for the North Sea offshore zone up to 50km from the nearest haul-out, and DFS for the Wadden coast and Wadden sea) is the starting point (open circle), after which biomass decline due to seal predation. During the summer season, a rapid increase in biomass occurs, except in years when the number of individuals has drastically reduced. In the subsequent survey, the biomass of remaining fish (i.e. larger individuals, >13.5cm) has declined, but is again supplemented with new recruits.

LITERATURE CITED

Costopoulos, C. G., and M. Fonds. 1989. Proximate body composition and energy content of plaice (Pleuronectes platessa) in relation to the condition factor. Netherlands Journal of Sea Research 24:45–55.

Härkönen, T., and M. P. Heide- Jørgensen. 1991. The Harbor Seal Phoca-Vitulina as a Predator in the Skagerrak. Ophelia 34:191–207.

Pedersen, J., and J. R. G. Hislop. 2001. Seasonal variations in the energy density of fishes in the North Sea. Journal of Fish Biology 59:380–389.

Soriguer, F., S. Serna, E. Valverde, J. Hernando, A. Mart??n-Reyes, M. Soriguer, A. Pareja, F. Tinahones, and I. Esteva. 1997. Lipid, protein, and calorie content of different atlantic and mediterranean fish, shellfish, and molluscs commonly eaten in the south of Spain. European Journal of Epidemiology 13:451–463.

Summers, R. W. 1979. Life cycle and population ecology of the flounder *Platichthys flesus* (L.) in the Ythan estuary, Scotland. Journal of Natural History 13:703–723.