2. ECHOES FROM THE PAST: REGIONAL VARIATIONS IN RECOVERY WITHIN A HARBOUR SEAL POPULATION

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SUMMARY

Terrestrial and marine wildlife populations have been severely reduced by hunting, fishing and habitat destruction, especially in the last centuries. Although management regulations have led to the recovery of some populations, the underlying processes are not always well understood. This study uses a 40-year time series of counts of harbour seals (*Phoca vitulina*) in the Wadden Sea to study these processes, and demonstrates the influence of historical regional differences in management regimes on the recovery of this population.

While the Wadden Sea is considered one ecologically coupled zone, with a distinct harbour seal population, the area is divided into four geo-political regions *i.e.* the Netherlands, Lower Saxony including Hamburg, Schleswig-Holstein and Denmark. Gradually, seal hunting was banned between 1962 and 1977 in the different regions. Counts of moulting harbour seals and pup counts, obtained during aerial surveys between 1974 and 2014, show a population growth from approximately 4500 to 39,000 individuals.

Population growth models were developed to assess if population growth differed between regions, taking into account two *Phocine Distemper* Virus (PDV) epizootics, in 1988 and 2002 which seriously affected the population. After a slow start prior to the first epizootic, the overall population grew exponentially at rates close to assumed maximum rates of increase in a harbour seal population. Recently, growth slowed down, potentially indicative of approaching carrying capacity. Regional differences in growth rates were demonstrated, with the highest recovery in Netherlands after the first PDV epizootic (*i.e.* 17.9%), suggesting that growth was fuelled by migration from the other regions, where growth remained at or below the intrinsic growth rate (13%). The seals' distribution changed, and although the proportion of seals counted in the German regions declined, they remained by far the most important pupping region, with approximately 70% of all pups being born there.

It is hypothesised that differences in hunting regime, preceding the protection in the 1960's and 1970's, created unbalance in the distribution of breeding females throughout the Wadden Sea, which prevailed for decades. Breeding site fidelity promoted the growth in pup numbers at less affected breeding sites, while recolonisation of new breeding areas would be suppressed by the philopatry displayed by the animals born there. This study shows that for long-lived species, variable management regimes in this case hunting regulations, across a species' range can drive population dynamics for several generations.

Keywords: conservation, density-dependence, Eastern Atlantic Harbour seals, *Phoca vitulina vitulina*, hunt, rate of increase, natal philopatry, site fidelity, management regime, population dynamics, abundance, distribution.

INTRODUCTION

Throughout history, humans have impacted wildlife populations. Initially, main impacts resulted from hunting and fishing for food and resources. Later, culling was also carried out to protect livestock, crops, game, or fish stocks. As the human population grew, so did the intensity of hunting, habitat destruction, pollution and effects on global climate, leading to fundamental changes in animal populations

(Burchard 1998, Pauly *et al.* 1998, Reijnders 1981, Woodroffe 2005). The combined and often synergistic effects of these threats render it complicated to identify the particular drivers for an observed change. Also, the compromising physiological stress exerted by these changes could make the populations susceptible to *e.g.* emerging infectious diseases both in terrestrial and marine ecosystems (Daszak *et al.* 2000). It is therefore not always clear why efforts to protect species and biodiversity (Wolff & Zijlstra 1980, Caughley & Sinclair 1994, Reijnders 1981, Halpern *et al.* 2008, Reijnders *et al.* 1993), succeed or fail (Burkey 1989, Clapham *et al.* 2008).
Hunting, both for subsistence and commerce or as a result of local bounties, was the main threat to seal populations until the second half of the 20th century, resulting in a gradual ban throughout most of Europe (Andersen & Olsen 2010, Kokko *et al.* 1999, Härkönen *et al.* 2005, Harding & Härkönen 1999, Brasseur *et al.* 2015b, Patterson *et al.* 2016, Joensen *et al.* 1976, Reijnders 1992, Vooys *et al.* 2012). For harbour seals, pollution and disturbance as a result of industrialisation and urbanisation, as well as virus epizootic events, further affected population development (Drescher *et al.* 1977, Reijnders 1981, Brouwer *et al.* 1989, Reijnders 1985, Reijnders 1986). Recently, British harbour seal populations have suffered new decreases for which the causes are uncertain (Lonergan *et al.* 2007, SCOS 2010, SCOS 2015), while in Southern Scandinavia and the Wadden Sea, harbour seal populations have shown recovery (Reijnders *et al.* 2010a, Olsen *et al.* 2010).
Harbour seals in the international Wadden Sea, between Den Helder in the Netherlands and Skallingen north of Esbjerg in Denmark, are considered a distinct

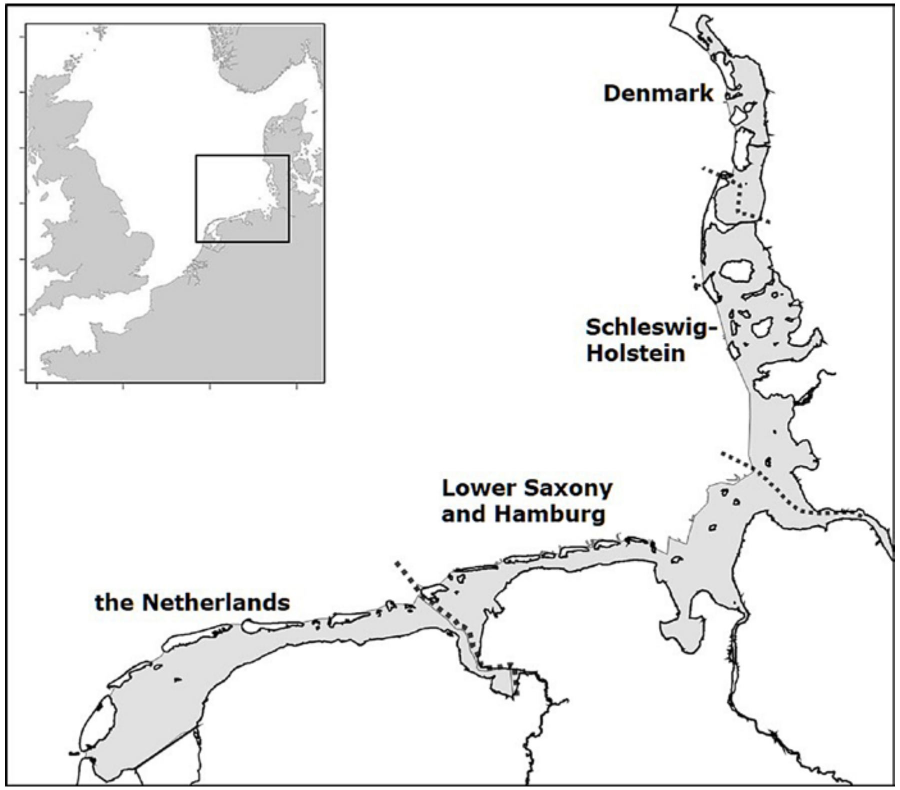

FIGURE 1. MAP OF THE INTERNATIONAL WADDEN SEA (GREY AREA) DOTTED BLACK LINES INDICATE THE BORDERS BETWEEN REGIONS. INLAY: THE NORTH SEA SITUATING THE STUDY AREA

population based on their genetic difference from seals in neighbouring regions in the North Sea area (Goodman 1998, Stanley *et al.* 1996). There are four management regions for the Wadden Sea: the Netherlands (NL), Lower Saxony and Hamburg (Germany; LS), Schleswig-Holstein (Germany; SH), and Denmark (DK) (Fig. 1). Despite challenges caused by virus epizootics and growing anthropogenic use of their habitat in the past 50 years, the Wadden Sea harbour seal population has shown exceptional recovery after being severely depleted by hunting. The close cooperation between these regions to monitor the development of this population since 1974 provides a unique dataset to study the population as a whole, but also to study regional differences in the population development and the factors controlling them.

Around 1900, the harbour seal population size in the Wadden Sea might have been at least 40,000 animals (Reijnders 1992), despite enduring centuries of hunting (Reijnders 1992, Joensen *et al.* 1976, de Vooys *et al.* 2012). Hunting pressure increased in the early 20th century due to the more intensive use of fire arms, and seal numbers dropped dramatically to approximately 8,000 harbour seals in 1960 (Reijnders 1992). As a response to the low numbers, seal hunting was gradually prohibited: first in the Dutch Wadden Sea in 1962, followed by Lower Saxony in 1971, Schleswig-Holstein in 1973, and finally the Danish Wadden Sea in 1976 (Reijnders 1981, Reijnders 1983). Despite the ban, numbers continued to drop and by 1974, counts in the international Wadden Sea were down to less than 4,000 animals (Reijnders 1981). Up to the 1980's, recovery was hindered by the low reproduction especially in the Netherlands, as a result of pollution by polychlorinated biphenyls (PCBs) (Reijnders 1986). Still, a slow recovery could be observed throughout the Wadden Sea. Then in 1988, an outbreak of *Phocine Distemper* Virus (PDV) killed over 50% of the Wadden Sea population (Reijnders *et al.* 1997a) and, as the population had recovered, a second outbreak of PDV struck in 2002, killing approximately the same proportion of the population (Harding *et al.* 2002, Härkönen *et al.* 2006a). Even with these set-backs, the population continued to grow, and in 2015 the population size in the international Wadden Sea was estimated at 39,000 animals (Galatius *et al.* 2015), approximately the same amount that were thought to be present in 1900 (Reijnders 1992).
The very low numbers after the first PDV epizootic in 1988, gave rise to the protection of harbour seals in Europe under the Habitat and Bird Directive of the EU (II), and since 1991 the Wadden Sea harbour seals have been protected by a Seal Agreement under the Convention on the Conservation of Migratory Species of Wild Animals (Anonymous 1983, Reijnders *et al.* 1997b) concluded between the Wadden Sea countries (Denmark, Germany and the Netherlands). This agreement is enforced by means of a Trilateral Seal Management Plan. A basis for management is the close cooperation between the countries in the Trilateral Seal Expert Group (TSEG), which strives, for example, to maintain the annual synchronised monitoring of the whole population by aerial surveys used to fine-tune trilateral or local management decisions.
This study represents one of the few long-term (40-year) animal population studies where management differed regionally, providing insight in factors affecting population trends and pup production in the processes of recovery from severe overexploitation. Results potentially have implications for successful conservation of long-lived, broad-ranging, species and the ecosystems in which they live.

MATERIAL AND METHODS

DATA COLLECTION

Harbour seals in the Wadden Sea were counted by aerial survey techniques annually over a 40-year period (1974-2014; Table S1 and S2). Aerial surveys were carried out from fixed-wing aircraft, flying at elevations of 500-1000 ft. (150-300 m) and speeds of 160 to 220 km/h. Surveys were conducted within a 4-h window between 2 h before and 2 h after low tide, on days when low tides occurred between 12:00 and 16:00 local time (Reijnders *et al.* 2003a). Surveys were performed on days with no or little rainfall (<10 mm precipitation, measured between 08:00 UTC the preceding day and 08:00 UTC of the flight day), and winds generally were below 25 knots. Prior to the mid 1990s, seals were counted directly by the observers during the flight in all regions, but from then onwards in Denmark, Schleswig-Holstein and the Netherlands seals were photographed using a camera with slide film (until 2000) or digital camera (from 2000 onwards). The animals were counted by the regional monitoring groups, from the pictures. In Lower Saxony, observers continued to count directly during the flight. The objective was to survey each geo political region (Denmark, Schleswig-Holstein, Lower Saxony including Hamburg and the Netherlands: Fig. 1) completely at least five times per year: at least three times during the pupping period (June/July) and at least twice during the moult period (August). The international teams aimed to survey on the same dates, but local circumstances sometimes led to changes or cancellation of flight dates. While data of the individual surveys were available for most years, only the maximum pup and maximum moult counts were available for Germany and Denmark in the first period (1974-1987).

During the pupping season, harbour seal pups can be discerned from older animals based on their coloration, size and often proximity to a larger seal (a mother). During the annual moult, shortly after the breeding period, however, pups cannot be discerned from yearlings and, hence, only total seal numbers were recorded. Because of the lack of dimorphism in the species, it was not possible to distinguish males from females during surveys. Grey seals recolonised the Wadden Sea in the late 1980s (Reijnders *et al.* 1995, Brasseur *et al.* 2015a, Abt & Engler 2009) and were distinguished from harbour seals based on their habit to lie in clusters, generally larger size, shape (elongated head, often broader thorax), and colouration (*e.g.* larger spots), and depending on the season, their moult status, as the two species moult at different times of the year. Single young grey seals lying amongst large groups of harbour seals might not have been recognised, but it is unlikely that these individuals compromised the accuracy of estimates of number of either species.

DATA PROCESSING

Count data were used to obtain population growth rates for the four Wadden Sea regions and to estimate proportion of pups. All data, including flight conditions and additional notes, were combined into a database for further analysis. Records were allocated to a period, based on the occurrence of the two PDV epizootics: 1974-1987 (I); 1989-2001 (II); and 2003-2014 (III). Data collected in the years of the virus outbreaks (*i.e.* 1988 and 2002) were excluded from our analysis as the outbreaks occurred during the monitoring period and biased the counts. For Lower Saxony in 1996 and 2008, no counts were available, so instead, numbers were estimated based on the trend in the counts (Brasseur *et al.* 2008).

Assuming that in most years the peak in the number of pups was captured at least

once during the three to five surveys, the response variable for the pups was defined as the annual maximum number of pups counted in each region (Table S2). The numbers recorded during the peak in pup numbers represent approximately 70% of the total annual pup production (Reijnders 1978b, Reijnders *et al.* 1997a, Fransz & Reijnders 1978, Thompson & Wheeler 2008).

The moult counts (including animals of all age classes) are often used as an index of the total population size (Thompson & Harwood 1990). During the moult, numbers of animals hauled out on the sandbanks show a less clear peak than the pupping peak. This is because they represent the sum of different age classes that haul-out in different proportions in relation to timing of their moult (Härkönen *et al.* 1999). For the German and Danish regions during period I (1974-1987), only maximum moult counts were available. Therefore maximum count during moult was used as response variable (Table S2).

POPULATION GROWTH RATE MODELS

Exponential and density-dependent growth models were fitted to both the pup and moult data. To estimate the exponential growth, generalized linear models (GLM) were fitted, assuming a negative binomial error distribution for the annual pup and moult estimates. The exponential growth model was defined as:

$$N_t = \exp(\beta_0 + rt) \qquad \text{eq. 1}$$

where N is either the estimated annual pup or moult count, t is the year (t_0=1974), $\exp(\beta_0)$ is the initial estimated count at t=0, and r is the instantaneous rate of increase. The initial analysis was performed on the total Wadden Sea population (the sum of all regions). The simplest model included an intercept and year t as an explanatory variable, *i.e.* assuming a continuous exponential growth between 1974 and 2014. This model was subsequently expanded by allowing the height (defined by the GLM intercept β_0) and growth rate (defined by the GLM slope parameter r) to vary between the periods (I, II, and III). Subsequently, new models were fitted to the regional count data, allowing the height and growth rate to also vary between the four regions (NL, LS, SH & DK) and periods, and with interactions between these. The density-dependent model was defined as:

$$N_t = \frac{K}{1 + \exp(a - rt)} \qquad \text{eq. 2}$$

where K is the carrying capacity parameter, a is the height and r the growth rate. As for the exponential models, the density-dependent models were first fitted to the total Wadden Sea counts. The simplest model included single estimates for K, a and r. Next, similar to the exponential model fitting, the models were extended by allowing a and/or r to vary by period. Finally, density-dependent models were fitted to the survey data by region, and a separate K for each region was estimated. These density-dependent models were fitted using generalized non-linear models (R-package "gnm"), producing estimates for the parameters K, a and r . The response variable (*i.e.* counts) was assumed to follow a negative binomial distribution, hence allowing for over-dispersion.

The Akaike Information Criteria, AIC (Burnham & Anderson 2002) was used to select the best model. All analysis were carried out in the software R (R Development Core Team 2009).

Finally, we estimated the proportion of pups (Härkönen *et al.* 2002) for each region.

We defined the proportion of pups as the maximum number of pups observed each year divided by the number of seals observed during the moult surveys (Reijnders *et al.* 1997a).

RESULTS

POPULATION DEVELOPMENTS

Despite the occurrence of the two PDV-epizootics in 1988 and 2002, the number of seals during the moult counts for the whole Wadden Sea grew considerably during the study period (Fig. 1 and Table 1). In the pre-epizootics period (period I), they increased from 3,571 in 1974 to 8,670 in 1987, *equi*valent to an annual rate of 7.2% (95% CI: 6.4%-8.1%; Table 2). The density-dependent model estimated that the number of moulting animals in the counts in 1988 declined from 8,200 to 3,600, a drop of 56%, while the exponential model estimated a drop of 54%. After this first PDV, the seals recovered during period II and counts reached pre-epizootic levels by 1995, and then grew to 16,738 animals in 2001. The annual rate of increase in period II was 12.7% (95% CI 11.7%-13.8%). Again in 2002 the PDV epizootic decimated the population and counts were down to 10,285 in 2003, *equi*valent to 50% and 47% for the density-dependent and exponential models, respectively. The population recovered and reached pre-epizootic levels by 2007, then grew to a count of 23,722 in 2014. The annual rate of increase of the total population in period III was 8.7%. Using a correction factor of 68% (Ries *et al.* 1998), based on the average proportion of the seals hauled out in august, the estimated total harbour seal population size grew during the whole study period (1974-2014) from approximately 4,500 animals to 39,000 animals.
The maximum pup numbers counted in the Wadden Sea grew from 687 in 1974 to 8,561 in 2014 and trended in a similar pattern to the moult counts (Fig. 2, Table 2).

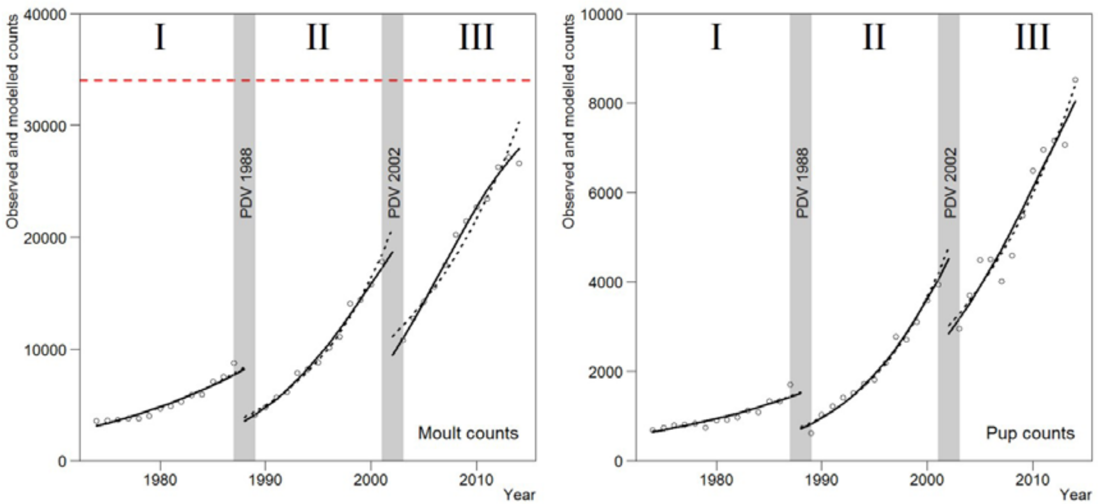

FIGURE 2. OBSERVED (POINTS) AND MODELLED (LINES) COUNTS FOR THE TOTAL WADDEN SEA POPULATION DURING THE YEARS 1974-2014. DASHED LINES REPRESENT THE BEST FITTING EXPONENTIAL MODELS (I.E. INTERACTION BETWEEN YEAR AND PERIOD), AND SOLID LINES REPRESENT DENSITY-DEPENDENT MODELS (ALSO INTERACTION BETWEEN YEAR AND PERIOD). THE HORIZONTAL DASHED RED LINE INDICATES THE ESTIMATED CARRYING CAPACITY FOR THE MOULT COUNTS.

		Exponential model			Density-dependent model		
	model	df	logLik	AIC	Df	logLik	AIC
Moult count	year	2	-345.00	690.00	3	-345.00	696.01
	year + period	4	-322.37	654.73	5	-322.37	654.73
	year : period	4	-322.51	655.01	5	-348.62	707.23
	year * period	6	-302.39	618.83	7	-297.39	608.79
Pup count	year	2	-289.47	584.95	3	-289.47	584.95
	year + period	4	-277.62	565.24	5	-277.62	565.24
	year : period	4	-277.72	565.43	5	-289.62	589.24
	year * period	6	-258.48	530.96	7	-257.61	529.22

TABLE 1. SUMMARY OF THE EXPONENTIAL AND DENSITY-DEPENDENT MODELS FITTED TO THE MOULT COUNT (TOP) FOR ALL REGIONS COMBINED AND PUP COUNTS (BOTTOM). VARIABLES SHOWN ARE THE DEGREES OF FREEDOM (DF), LOG-LIKELIHOOD (LOGLIK) AND AIC.

		Period		
moult		I	II	III
Region	NL	5.4% (4.1,6.8)	17.9% (16.3,19.5)	10.6% (9,12.3)
	LS	6.7% (5.4,8)	12.4% (10.9,13.9)	8.5% (6.9,10.2)
	SH	6.7% (5.5,8.0)	12.8% (11.3,14.4)	7.1% (5.6,8.7)
	DK	12.3% (10.9,13.8)	8.6% (7.1,10.0)	9.9% (8.3,11.6)
	Wadden Sea	7.2% (6.4,8.1)	12.7% (11.7,13.8)	8.7% (7.6,9.8)
pups		I	II	III
Region	NL	5.7% (3.4,8)	17.7% (15.3,20.1)	10.7% (8.4,13.0)
	LS	5.4% (3.5,7.3)	11.3% (9.2,13.4)	7.9% (5.7,10.1)
	SH	5.6% (3.8,7.4)	16.6% (14.4,18.8)	8.8% (6.6,11.0)
	DK	12.7% (10.4,15.0)	9.7% (7.5,11.9)	8.5% (6.2,10.9)
	Wadden Sea	6.3% (5,7.5)	14.1% (12.7,15.6)	8.9% (7.4,10.5)

TABLE 2. ESTIMATED AVERAGE GROWTH RATES ((λ-1)x 100) IN THE MOULT COUNTS (TOP) AND PUP COUNTS (BOTTOM) FOR THE DIFFERENT REGIONS OF THE WADDEN SEA AND PERIODS OF THE STUDY, BASED ON THE BEST FITTING EXPONENTIAL MODEL (YEAR * PERIOD * REGION). REGIONS: THE NETHERLANDS (NL), LOWER SAXONY (LS), SCHLESWIG-HOLSTEIN (SH) AND DENMARK (DK). PERIODS: 1974-1987 (I), 1989-2001 (II), 2003-2014 (III).

The estimated drop in pup numbers as a result of the PDV epidemics seemed lower than the moult counts. In 1988, modelled pup numbers dropped 53% or 51%, respectively for the density-dependent model and the exponential model, and in 2002, modelled pup numbers dropped 39% and 37%, for the respective models.
For the moult data of the total population, the exponential population model (*i.e.* GLMs) that fitted best (*i.e.* lowest AIC) was one where both the height and growth rate differed between periods (*i.e.* model year * period, Table 1). Adding this interaction led to a substantial improvement in the model fit (*i.e.* higher log-likelihood). For the same data the density-dependent model led to a drop in the AIC from 619 (*i.e.* exponential model) to 609, suggesting that the growth rate in the total popu-

lation could have levelled off. For the pup data, the density-dependent model only led to a minor improvement (AIC declines from 531 to 529), and hence there was limited support for a slowing down of the growth rate in pup production.

REGIONAL DIFFERENCES

In many ways, the developments in the pup counts were similar to the moult counts (Fig. 3). For both counts, a model where both the number of seals and growth rate differed between periods and regions (*i.e.* model year * period* region; Table 3) was the best model.
All regions showed a general recovery, interrupted in 1988 and 2002 by the PDV-epizootic events. However, the speed of recovery varied between the regions (Fig. 3). Throughout the years, the highest moult and pup counts occurred in

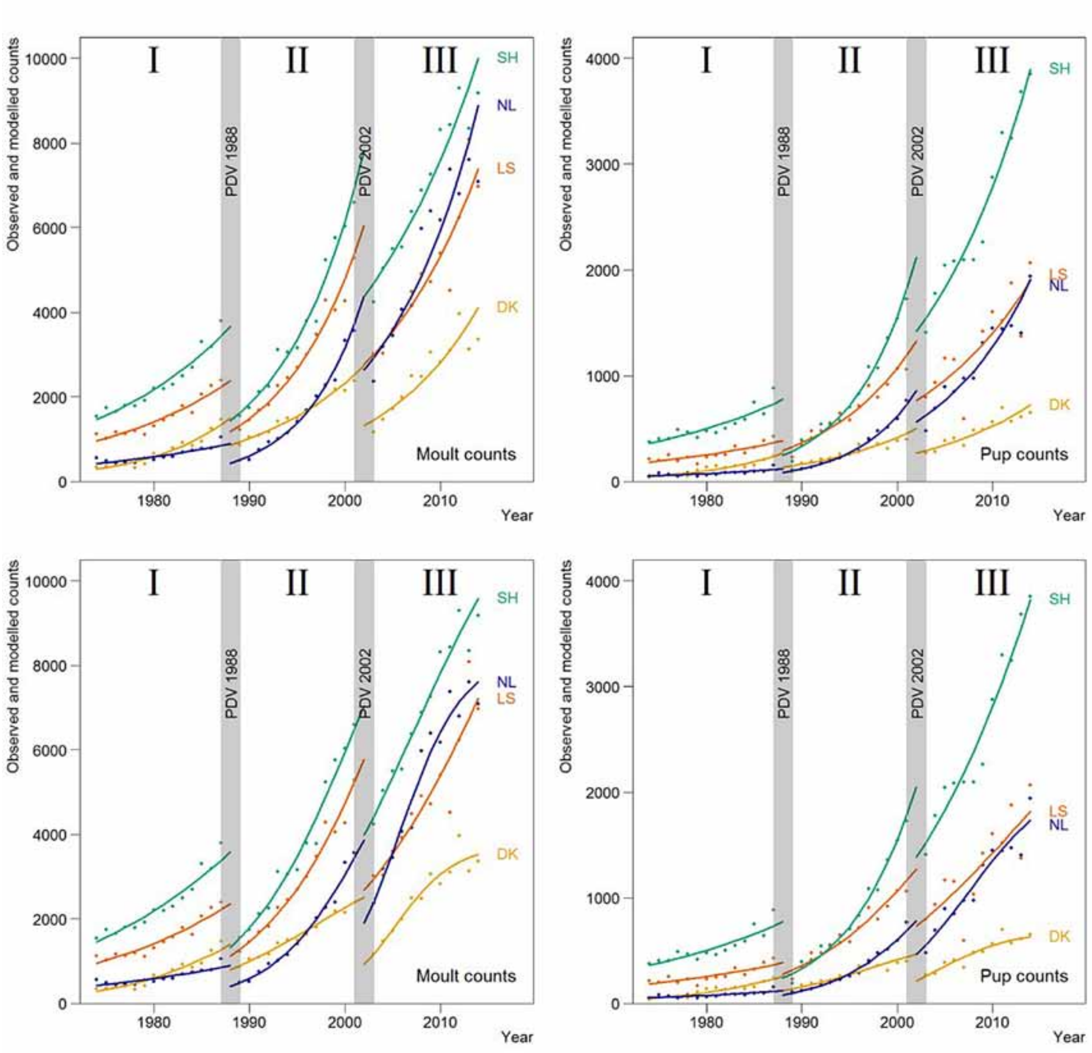

FIGURE 3. RESULTS FOR THE BEST FITTING EXPONENTIAL (TOP) AND DENSITY DEPENDENT MODELS (BOTTOM) FOR THE HARBOUR SEALS IN THE FOUR REGIONS (THE NETHERLANDS (NL), LOWER SAXONY (LS), SCHLESWIG-HOLSTEIN (SH) AND DENMARK (DK)) OF THE WADDEN SEA. THE LINES REPRESENT THE ESTIMATES FOR THE MOULT COUNTS (LEFT) AND PUP COUNTS (RIGHT), AND DOTS THE OBSERVED MAXIMUM COUNTS.

		Exponential model			Density-dependent		
	Model	df	logLik	AIC	df	logLik	AIC
Moult count	Year*period+region	9	-1181.58	2383.16	13	-1207.01	2440.03
	year*period+region *period	15	-1093.56	2219.13	19	-1072.88	2183.77
	year*period*region	24	-1043.95	2137.89	28	-1026.71	2109.43
Pup count	Year*period+region	9	-966.03	1952.07	13	-972.32	1970.64
	year*period+region *period	15	-884.30	1800.61	19	-872.27	1782.54
	year*period*region	24	-855.75	1761.50	28	-850.3	1756.61

TABLE 3. SUMMARY OF BOTH THE EXPONENTIAL AND DENSITY-DEPENDENT MODEL FITTED TO THE MOULT COUNT (TOP) AND PUP COUNTS (BOTTOM). VARIABLES SHOWN ARE THE DEGREES OF FREEDOM (DF), LOG-LIKELIHOOD (LOGLIK) AND AIC.

Schleswig-Holstein. The only exception was in the years just after the 1988-epizootic, where the PDV caused a drop of 69% in pup numbers of Schleswig-Holstein, while in Lower Saxony and the Netherlands, the pup production was only reduced by 27% and 31%, respectively (Table 4). Interestingly, during period II, the pup numbers in Schleswig-Holstein recovered, and the area was re-affirmed as the stronghold for pup production by the population. In the 1970's, just after hunting ceased, Denmark and the Netherlands were the regions with the lowest numbers, but after the first epizootic, the number of animals observed in the Netherlands grew most, while the growth in Denmark seemed to level off, especially following the second, 2002-epizootic event.

As pup numbers in the Netherlands grew faster than the Wadden Sea average, numbers in this area outgrew Denmark and, in the course of the study period, approached the numbers in Lower Saxony. Compared to other regions, the numbers in Denmark grew less and were more affected by the second PDV epizootic. At the end of period II, fewer pups were born in the Danish Wadden Sea, compared to the Netherlands and, by 2014, pup numbers in Denmark represented less than 10% of the total pup production.
Estimated average growth rates are summarised in Table 2 and shown in Fig. 3 and 4. The better fit of the density-dependent models indicated a possible slowing down in growth during the study period. This was most obvious in Denmark where, in the period after the first epidemic in 1989-2002, the growth remained lower than in the other regions, while the total Wadden Sea population was growing close to its assumed intrinsic rate of increase (13%) (Härkönen *et al.* 2002). In the last period, growth rates in all regions had dropped.

In the first period (I) from 1974 up to the PDV epidemic of 1988, the growth rate in both the moult and pup counts in Denmark was by far the largest (Table 2 and Fig. 4). After the first epidemic in 1988 (period II), the highest growth rate was observed in the Netherlands, while growth in the German regions approximated the intrinsic growth rate estimated for this species, and growth in Denmark slowed down. For all regions, the density-dependent model showed an initial high rate after the epizootic, which slowed down gradually.

		PDV 1988		PDV 2002	
Density-dependent		moult	pup	moult	pup
Region	NL	55%	31%	51%	40%
	LS	52%	27%	53%	42%
	SH	63%	69%	43%	32%
	DK	43%	53%	63%	54%
	Wadden Sea	56%	53%	50%	39%
Exponential					
Region	NL	51%	27%	40%	34%
	LS	51%	24%	54%	42%
	SH	61%	68%	44%	33%
	DK	42%	49%	52%	46%
	Wadden Sea	54%	51%	47%	37%

TABLE 4. ESTIMATED MORTALITY (IN THE MOULT COUNTS), OR REDUCTION OF THE PUP PRODUCTION DURING PDV IN 1988 AND 2002 BASED ON DENSITY DEPENDENT MODEL (TOP) AND EXPONENTIAL MODEL (BOTTOM).

Overall the growth in pup numbers was similar to the growth rate in moult counts. However, there were some differences (Fig. 3 and 4). For example, between 1989 and 2002 in Schleswig-Holstein and initially also in Denmark and The Netherlands, there was a substantially higher growth rate in pup number compared to the growth in moult counts.

The proportion of pups (pup/moult count) for the different regions changed over time (Fig. 5). Overall the largest proportion of pups was observed in the third period. Schleswig-Holstein consistently had the highest proportion of pups. Generally, the proportions of pups were lower in the Dutch and Danish regions, than in the German regions.

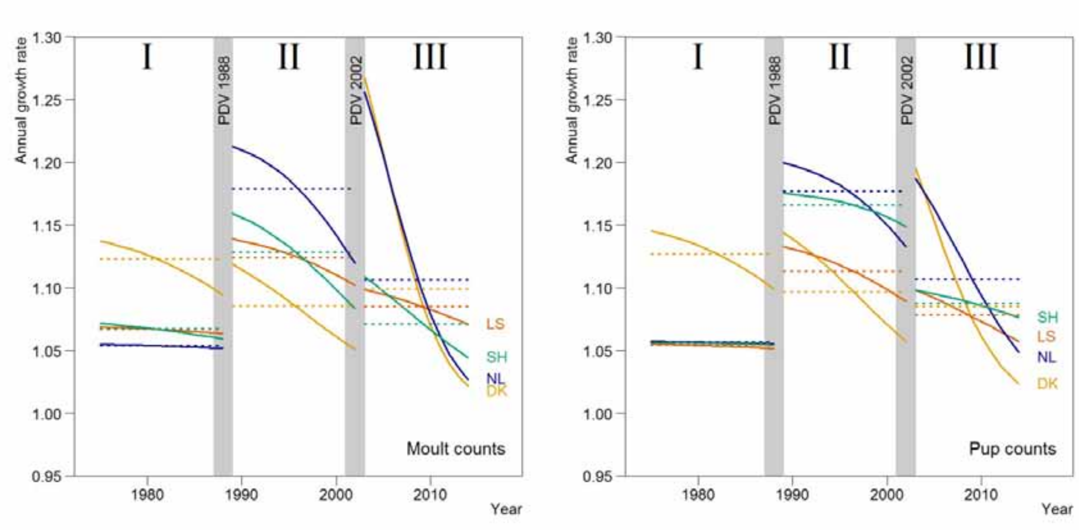

FIGURE 4. DENSITY-DEPENDENT ANNUAL GROWTH RATES ESTIMATES FOR THE DIFFERENT REGIONS OF THE WADDEN SEA, 1974-2014 BASED ON THE HARBOUR SEAL MOULT COUNTS (LEFT), AND THE PUP COUNTS (RIGHT). DOTTED LINES SHOW THE GROWTH RATES OF THE BEST FITTING EXPONENTIAL MODEL, AS A COMPARISON.

The relative importance of the different regions from a population perspective changed over time. Schleswig-Holstein remained the strong-hold of the population, with 35 to 45% of the moulting seals and 35 to 55% of the pups (Fig. 6). Interestingly, the sharp drop in the number of pups born in Schleswig-Holstein just after the first PDV in 1988, recovered during the following period. The opposite happened in Lower Saxony, where the relative number of pups counted increased from 27% to 40% during the 1988 PDV event, but then steadily declined during the following period II. Most growth over time was in the Netherlands, with approximately 10% of seals and 10% of pups present in the first period, rising to 25% of seals and 20% of pups in the third period.

DISCUSSION

The recovery of the Wadden Sea harbour seal population has been an ongoing process since the hunting ceased progressively in the different regions between

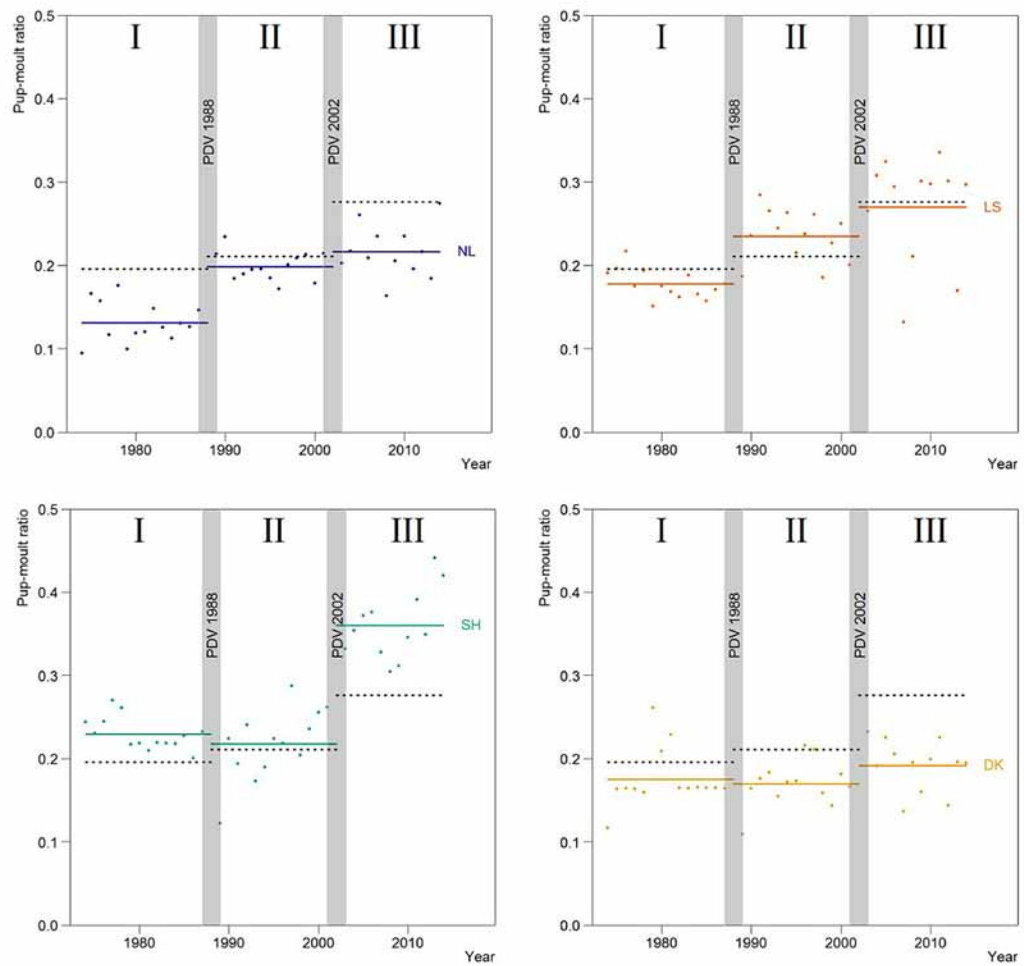

FIGURE 5. OBSERVED PUP NUMBERS AS A PROPORTION OF TOTAL SEAL OBSERVED DURING THE MOULT IN DIFFERENT REGIONS OF THE WADDEN SEA AND THE THREE TIME PERIODS (I, II AND III). WITHIN EACH PERIOD, SOLID COLOURED LINES INDICATE AVERAGE MODEL ESTIMATES FOR THE REGION, AND BLACK DOTTED LINES INDICATE THE AVERAGE FOR THE WADDEN SEA.

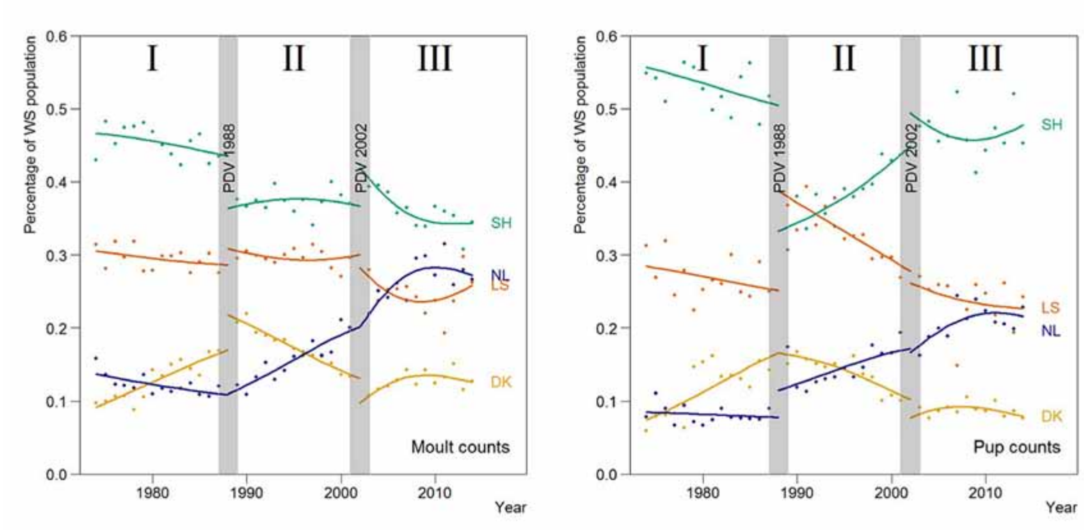

FIGURE 6. OBSERVED AND ESTIMATED PROPORTION OF HARBOUR SEALS IN THE DIFFERENT REGIONS OF THE WADDEN SEA (GREEN = SCHLESWIG-HOLSTEIN, RED = LOWER SAXONY, BLUE = NETHERLANDS AND YELLOW = DENMARK) EXPRESSED AS PERCENTAGE OF THE TOTAL POPULATION, BASED ON COUNTS DURING THE MOULT PERIOD (A) AND NUMBERS OF PUPS (B).

1962 and 1976 (Galatius *et al.* 2015, Reijnders 1976, Reijnders 1996, Reijnders *et al.* 1997a, Reijnders *et al.* 2003b, Reijnders *et al.* 2010a, Harding *et al.* 2002, Härkönen *et al.* 2002). Clearly, the increase was slowed down by the occurrence of two PDV epizootics in 1988 and 2002 killing on both occasions around over 50 % of the population (Reijnders *et al.* 1997a, Harding *et al.* 2002, Härkönen *et al.* 2002). Nevertheless, the population recuperated after the epizootics and continued to grow. The number of moulting seals grew almost tenfold throughout the forty-year study period (1974-2014). Growth rates measured in this study differ only slightly from earlier studies of the Wadden Sea harbour seal population (Reijnders *et al.* 1997a, Ries *et al.* 1998).

For the pups, with clear peak timing in birth, the maximum number is likely to be the best estimate and index for the pup production, despite the shifted forwards of the peak in the course of the years (Reijnders *et al.* 2010b, Cordes & Thompson 2013). During the moult however, numbers of animals hauled out on the sandbanks show a less clear peak. This is because they represent the sum of different age classes that haul-out in different proportions in relation to their specific moult timing (Härkönen *et al.* 1999). Possibly, if the moult counts were averaged, this would buffer the potential effects on the variance introduced by tide, weather and occasional disturbances, however, this was not possible in this study as only the maximum count was saved in the database for some of the early years.

As the hunting ban was implemented gradually throughout the Wadden Sea, it is to be expected that initially, the dynamics of the recovery were different for the different regions, depending on the timing of the ban. For example, in 1974, the Netherlands hunting had been banned for more than a decade; the German regions had just banned hunting while in Denmark hunting continued until 1976. One could expect the changes in the first period to mirror this. In contrary, exponential growth rates are highest in Denmark and lowest in the Netherlands, where high pollutant (PCB) burdens affected the reproduction (Reijnders 1986, Reijnders *et al.* 1997a, Reijnders 1981).

Throughout the study period, pup production was relatively low in the Netherlands (on average 18% of all Wadden Sea pups were born there), compared to the moult growth, which was 17.9 % and 10.6% respectively for period II and III). Especially in the latest period between 2002 and 2014 Schleswig-Holstein and Lower Saxony performed at or above the Wadden Sea average, with average pup ratios of almost 35% and 28% respectively, while Denmark and the Netherlands show a pup ratio below average, respectively 19% and 21%. Even though by far most pups were born in Schleswig-Holstein (46% of all pups), in absolute numbers, but also in relative numbers, moult growth rates there were not higher, but close to the average of the Wadden Sea, (12.7% in period II and 8.7% in period III). To a lesser extent this also held for Lower Saxony (26% of the pups). It is therefore likely that there was a net influx from other regions into the Netherlands during moult, especially between the epizootic events, when growth rate in the Netherlands (17.9%) was well above the maximum intrinsic rate of increase estimated at 13% (Härkönen *et al.* 2002).

The fact that growth rates in pup numbers in Schleswig-Holstein were significantly higher than the growth in moult counts indicates that in Schleswig-Holstein, the number of breeding females (producing a pup) grew at a higher rate than the numbers during the moult. This implicates that compared to other areas, a large proportion of the seals in Schleswig Holstein migrate out of the region after the breeding season (these could be females, but also males or juveniles).

Extreme high growth rates in the moult count found just after the epizootics (Fig. 4) and high growth in pup numbers indicate a change in demographic structure throughout the Wadden Sea, as was observed in the Kattegat-Skagerrak (Härkönen *et al.* 2002). In periods II and III, in the absence of hunting and as pollution diminished, circumstances in the regions should have been more similar, however regional differences in growth rates persisted, albeit becoming less obvious.

As throughout the study the growth rate of the total Wadden Sea population did not exceed the intrinsic rate of increase for the species, it seems unlikely that the growth was influenced, let alone fuelled by immigration from colonies outside the Wadden Sea. This is supported by earlier findings that indicate the Wadden Sea harbour seal population being a distinct genetic population (Goodman 1998, Stanley *et al.* 1996) though recent findings indicated there was a strong connection with harbour seals from France and southern UK (Olsen *et al.* 2017). In addition to this, the occurrence of virus epizootics did affect population growth temporarily, but did not prevent the population from continuing its recovery. Interestingly, as the model including both the different periods and the regions shows the best fit, there seems to be significant differences between the recoveries in the different regions, which on its turn are affected by the PDV outbreaks.

The density-dependent model performs slightly better than the exponential model (Table 3), indicating, though not conclusively, that the population growth might be affected by the limits of the carrying capacity of the area. However, biased estimates of the rates of increase in the population can be expected, as a result of age specific mortality, for example during the PDV epidemic, due to variation in haul-out between the different age and sex classes, especially in the five years following the epidemic (Härkönen *et al.* 1999, Härkönen *et al.* 2002, Härkönen *et al.* 2007b).

To test a possible effect the density-dependent model was also fitted to the count data excluding the first 5 years following the PDV epidemics. When excluding the first five years after the two epidemics, the difference in AIC between the density-dependent (AIC: 1600.46 for moult counts) and exponential models (AIC: 1602.14) are much less prominent, providing less support for a hypothesis that the population is approaching its carrying capacity. However for this latter exercise, much less points were available, and therefore the ability to detect a density dependent effect is reduced.

In the third period after the 2002 epizootics, average growth rate was positive in the total Wadden Sea (8.7% pa), but was below the intrinsic rate across the regions. Based on the AIC, the density dependent model performs slightly better than an exponential model, again indicating a possible start of density dependence. The density-dependent model indicates that the estimated carrying capacity *K* would currently be at a population size of 50,000 (95% CI 37,000-63,000) animals when correcting for animals not seen during the counts (correction factor 1.47 (Ries *et al.* 1998)). The population estimate for 2014, using the same factor is almost 35,000 animals. In future years it should become clear whether the population is reaching the carrying capacity for the current Wadden Sea ecosystem.

REGIONAL DIFFERENCES IN POPULATION DEVELOPMENT

The potential reasons for the observed differences in growth rates between regions include human related effects such as disturbance, pollution and management but also the effects of the PDV epizootics and environmental differences such as area size (Table 5).

The trilateral agreement has insured a similar management of the Wadden Sea area, with regards to seals. This includes for example disturbance of the seals, but excludes effects extending from the adjacent North Sea. The southern North Sea area bordering the Wadden Sea is one of the busiest marine areas in the world with intensive fishing activities and shipping to and from large harbours, such as Rotterdam, Hamburg and Antwerp. In addition there has been an extensive growth in exploitation of fossil fuels: comprising seismic surveys, platform construction, pipelaying and drilling, growing areas of sand mining and recent development of wind farms in the Economic Exclusive Zones of all the Wadden Sea countries. However, though these activities might affect the carrying capacity of the area, there is no indication that one region has been consistently more affected by these activities than the others, in such a way that might drive the differences found. More likely, other factors have played a role in the differences found between the regions.

PCB's were found to cause reproductive failure (Reijnders 1986) in the 1970's, especially in the Netherlands. Levels in seals from the Dutch Wadden Sea were ten times higher than in Denmark and Schleswig Holstein (Reijnders 1981). The latter regions showed the highest proportion of pups through the period, possibly supporting this hypothesis. However, as many pollutants were banned, the situation ameliorated and gradually the differences in levels of PCB in the Wadden Sea have become marginal (Laane *et al.* 2013, Reijnders & Simmonds 2003, Reijnders *et al.* 1997a).

Between the two epizootic events (1989-2001, period II), average growth rate of the whole population attained its highest level (12.7% pa), matching the intrinsic rate of increase for this seal species (Härkönen *et al.* 2002). This could indicate that the earlier problems in relation to pollution had become of minor importance. Possibly, the PDV epidemics could have selectively eliminated many animals carrying a high pollutant burden and hampered in their reproduction, as a result reproduction was somewhat normalised after the first outbreak and a high growth could be attained (Reijnders *et al.* 1997a).

Our study shows marked differences between the regions when looking at the mortality during the PDV outbreaks (Table 4). It still remains unclear, however, how the two occurrences of PDV in 1988 and 2002 might have been responsible for the observed patterns in the seal populations' recovery. Though both occurrences started on the island of Anholt, east of Denmark in the Kattegat, the timing and spread were different (Härkönen *et al.* 2006b). In 1988 the virus swept through the Wadden Sea from east to west, while practically the contrary was the case in 2002 as a second epicentre seemed to have started in the Netherlands just after the first outbreak at Anholt. Moreover, for most regions the virus was several weeks later in 2002. Especially for Schleswig-Holstein and Denmark, the virus outbreak came later to the Wadden Sea, possibly affecting other age or sex groups of the population than in 1988, as the haul-out patterns of the different groups are expected to change throughout the breeding and moulting season. However, these differences do not seem to explain the observed differences in mortality of the two occurrences. Despite the later arrival of PDV in Lower Saxony, total mortality was similar between the two epizootics and to a lesser extent this was also the case in the Netherlands. In both regions pup mortality was higher than in 1988. On the other hand, despite a two month difference, the mortality in Denmark was much higher in 2002, and with a similar timing for both epizootics, mortality in Schleswig-Holstein was much lower (Table 4).

The population is currently well below critical herd immunity for PDV, which caused a much higher mortality in the earlier epizootics (Härkönen & Harding 2010). Though the details of the start of a new outbreak are not understood, it is advisable consider a reoccurrence in the near future, and keep an adequate mo-

		Netherlands	Lower Saxony	Schleswig-Holstein	Denmark	Total Wadden Sea
PDV						
25% found dead	1988	8-Aug	8-Aug	27-Jul	5-Jul	
50% found dead	1988	4-Sep	4-Sep	17-Aug	3-Aug	
25% found dead	2002	21-Aug	3-Sept	10-Sept	9-Sept	
50% found dead	2002	2-Sep	18-Sep	21-Sep	20-Sep	
Area size/ density						
Length North Sea coastline (km)		158	161	101	80	500
Seal density moult/pups(km)	1974	3.48/ 0.34	7.00/ 1.34	15.29/ 3.73	4.38/ 0.51	7.14/ 1.37
	2014	*39.65/12.29*	*42.62/12.84*	*74.06/38.15*	*38.95/ 8.18*	*47.44/17.03*
Wadden Sea area (km2)		2685	2462	2534	706	8387
Seal density moult/pups(km2)	1974	0.20/ 0.02	0.46/ 0.09	0.61/ 0.15	0.50/ 0.06	0.43/ 0.08
	2014	*2.33/ 0.72*	*2.79/ 0.84*	*2.95/ 1.52*	*4.41/ 0.93*	*2.83/ 1.02*
Subtidal area		53%	39%	44%	46%	45%
Hunting						
Until 1900		Open hunt	Open hunt	Open hunt	Open hunt	
From 1934		Open hunt	Hunt regulated	Hunt regulated	Open hunt	
Hunting ban	since	1962	1971	1973	1977	
Rehabilitation centres	since	1952* 1971	1978	1985	1978-1995**	

TABLE 5. OVERVIEW OF DIFFERENCES BETWEEN REGIONS IN THE WADDEN SEA, INCLUDING AREA SIZES AND SEAL DENSITIES AT THE BEGINNING AND END OF THE STUDY PERIOD, TIMING OF STRANDING EXPRESSED AS PERCENTAGE OF THE TOTAL NUMBER OF ANIMALS FOUND DEAD DURING THE PDV EPIZOOTICS OF 1988 AND 2002. ADOPTED AFTER (HÄRKÖNEN ET AL. 2006A), HUNTING REGULATIONS AND REHABILITATION. * IN THE NETHERLANDS THERE WERE TWO REHABILITATION CENTRES, ** IN DENMARK REHABILITATION CEASED AFTER 1995.

nitoring operable. This is also the case for other diseases. In the autumn of 2014 an avian flu epidemic caused elevated mortality in the eastern Wadden Sea area (Denmark and Schleswig-Holstein) and practically no effect in the west (Lower Saxony and the Netherlands) (Bodewes *et al.* 2015). This event occurred after our study period.

The carrying capacity for the number of animals hauled out within regions may be influenced by size or quality of the habitats available. This could be either feeding habitats or habitats for resting and breeding. Telemetry data show that, even though they haul-out in the Wadden Sea, the majority of the seals forage in the adjacent North Sea (Brasseur *et al.* 2010a, Brasseur *et al.* 2011b, Kirkwood *et al.* 2015, Brasseur & Kirkwood 2016, Tougaard *et al.* 2006). Within the Wadden sea area the regions vary considerably in size (Table 5). Of the four Wadden Sea regions, Denmark is the smallest both in coastline (a proxy for accessibility to feeding grounds) and area (possible haul-out), and is therefore expected to have the lowest carrying capacity. Possibly, the higher seal density per km^2, as a result, might explain the slower growth observed in the later periods, although the area does not hold the highest density of pups, nor the most animals per km coastline. However the relation between seal density and surface area or coast length is not always clear when observing the densities in both the numbers of seals and pups born. For example, based on coastline, Schleswig-Holstein clearly is more densely used than are the other regions and especially for pup production, which in Schleswig-Holstein is 2-4 times the density of other regions. Interestingly, the Netherlands is the largest both in coastline and area, while numbers were initially lowest, the highest growth has been observed in this region.

Though there are differences in growth rates that are possibly related to the carrying capacity, it is unlikely that the available land habitat would be the sole driver of the differences in growth between the regions, especially in the earlier periods, when numbers were still relatively low. We conclude therefore that there must have been other factors that contributed to these differences.

Since 1952, seals have been captured, rehabilitated and released in the Wadden Sea. While in Denmark seals which are found orphaned or injured have not been taken in for rehabilitation since 1995, in the Netherlands and Germany, rehabilitation has been common practice throughout the study period. Two rescue centres have been active during the study period in the Netherlands. In Germany, there are also two rescue centres; one in Lower Saxony, and one in Schleswig-Holstein. Though total numbers of seals (adults and pups) released into the wild were relatively low, amounting to approximately two hundred seals in average and tree hundred in extreme years (Trilateral Seal Expert Group, unpublished data; 2000-2010) this might also have somewhat affected the observed changes in the population, especially when the total number of seals were low. In order to study the exact magnitude of the effect and differences between regions, more information is needed.

Historical findings show that seals throughout the Wadden Sea have been hunted by man for centuries, ever since man colonised the area around 3500 BC (Waterbolk 1976). In addition to hunting for subsistence or profit, seals became persecuted because of their perceived or actual impacts on fish catches and damage to fishing gear. In the Netherlands, for example, one of the first bounty hunts was proclaimed in the late 1500s (de Vooys *et al.* 2012, Hart 2007). Generally, pressure increased as better hunting techniques developed – especially through modernisations in firearms which made hunting much more effective (de Vooys *et al.* 2012). However, during the 19th and 20th centuries, regional differences developed as the different

countries applied different management strategies. The situation in the Netherlands was very similar to Denmark, where more or less any citizen could hunt for seals. Bounty systems effectively reduced the seal population significantly (Joensen *et al.* 1976). Especially after the 2nd World War in the Netherlands, annual hunting mortality was estimated to be 55% of the total counts (Bemmel 1956). In contrast, hunting mortality in Germany was estimated to be much lower, 7%. Moreover, hunting during the pupping season was forbidden from 1938 onwards (Hoffmeyer 1962). Following the hunting law, only specially appointed game keepers, "Jagdaufseher", were entitled to capture and kill seals. Seals were completely protected from hunting in the Netherlands in 1962, in Germany 1971-73 and in Denmark in 1976.

We hypothesise that the differences in hunting regulations and pressure in the first half of the 1900s, which led to local dissolution of seal breeding grounds in the Danish and Dutch regions, could be one of the most important causes for the observed differences in seal densities during the breeding period.

The mechanism for sustaining the different pup densities could be the high degree of site fidelity and natal philopatry shown by harbour seals (Härkönen & Harding 2001, Dietz *et al.* 2012, Womble & Gende 2013, Sharples *et al.* 2012). The assumption is that relatively many females and their pups survived in the more sustainably hunted German breeding area, as less seals were killed and mothers and pups were not hunted during breeding. During other periods seals could redistribute, only to come back to breed. As 70% of the pups are born in the German regions, there must be an unequal post-breeding dispersal of reproductive females throughout the area. As such, more pups could be born in the preferred breeding areas than can be expected from the seal distribution outside the breeding season. This breeding migration towards the German Wadden Sea has been confirmed from the Netherlands on several occasions (Brasseur *et al.* 2011b, Kirkwood *et al.* 2015, Brasseur & Kirkwood 2016). Some indication for this behaviour can also be found in the recovery of Schleswig-Holstein after the first PDV epidemic. Then pup counts dropped below those of Lower Saxony indicating that breeding animals had been killed disproportionally in that region. However within period II pup numbers grew and Schleswig-Holstein attained higher pup numbers compared to the other areas. Possibly this recovery was fuelled by animals returning to their natal sites as they reached reproductive age. Possibly this effect was magnified in the Netherlands by the suppression of the reproduction by PCB's, especially in period I and beginning of II (Reijnders 1986, Reijnders *et al.* 1997a).

For the Wadden Sea, the German regions could be considered to be sources and Denmark and the Netherlands sinks (Pulliam 1988). However pupping habitat quality, in terms of available sandbanks, access channels, protection from disturbance, seems to be relatively uniform throughout the region. Therefore, the regional developments are more likely driven by breeding and natal site-fidelity. A form of "hidden source sink dynamics" (Contasti *et al.* 2013, Gundersen *et al.* 2001), may more accurately describe the situation. Here, animals migrate from areas where more pups are born to areas where fewer pups are born, prompting growth throughout the range.

Migration between sites could also help to explain the very high growth rates attained in the Netherlands (Reijnders 1981, Reijnders 1983). Previously, an unbalanced age structure has been proposed as an explanation for this growth, where a relatively higher proportion of adult females could produce a high pup rate for

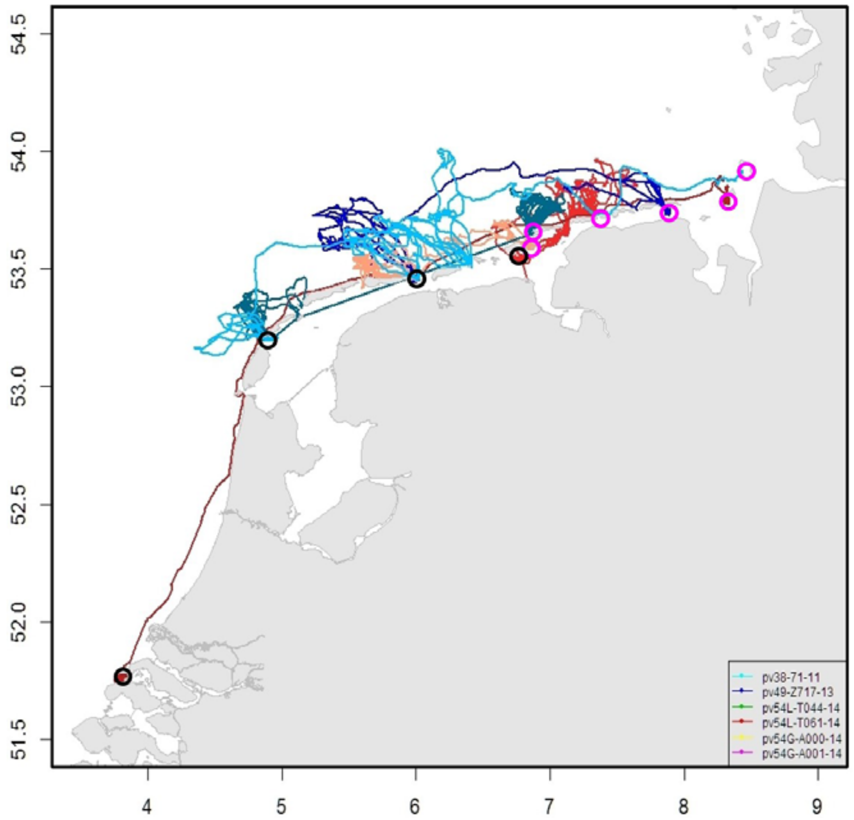

FIGURE 7. EXAMPLES OF TRACKS OF SIX ADULT FEMALES TAGGED IN THE NETHERLANDS (BLACK CIRCLES), MIGRATING TOWARDS GERMANY DURING THE PUPPING SEASON (PINK CIRCLES)(BRASSEUR ET AL. 2011B, KIRKWOOD ET AL. 2015, BRASSEUR & KIRKWOOD 2016) .

a number of years (Härkönen & Harding 2001, Härkönen *et al.* 2007b). However, such an imbalance is unlikely to prevail for decades. In the years between the epizootic events, numbers in the Dutch Wadden Sea grew at an average of 17.9% pa, while for the total Wadden Sea; growth remained below 13% pa. The latter is close to the intrinsic rate of increase for harbour seals (Härkönen *et al.* 2002). So more likely, high levels of migration explained the higher growth rate in the Netherlands at that time.

CONCLUSION

Although the international Wadden Sea could be regarded as a single connected ecological system, where seals are capable of migrating between the geo-political regions, large regional differences within the harbour seal population growth rate and pupping success are apparent. Though there seems to be some factors differing between the regions, differences in hunting pressure and in regulations enforced in the past seem to be a dominant factor in the observed patterns.
These findings reveal that different management regimes operating 40 years ago still influence the current population structure, distribution and demography. This long-term effect is a consequence of the longevity of the animals and their site faithful-

ness during breeding. It is important to realise that, management decisions regarding seals, could affect the distribution and development of populations even long after their implementation. The same could hold for many other species though few populations have been studied or monitored as long as the Wadden Sea harbour seals. These effects could also occur under much less drastic management regimes, such as closure or opening of areas for the public, or for (industrial) development, affecting the carrying capacity of the area, but might also affect certain groups in the population more than others. Though the disturbances might be less crucial for the survival of individual animals than hunting, they could cause displacement which in-turn might have long term effects.

year	Denmark		Schleswig-Holstein		Lower Saxony		The Netherlands	
	TOTAL	PUPS	TOTAL	PUPS	TOTAL	PUPS	TOTAL	PUPS
1974	350	41	1544	377	1127	215	569	54
1975	360	59	1749	403	1019	200	509	82
1976	389	64	1653	404	1165	253	481	71
1977	410	67	1806	488	1131	198	463	54
1978	332	53	1795	469	1199	232	458	78
1979	421	110	1919	417	1109	168	543	54
1980	671	140	2202	481	1310	230	514	61
1981	656	150	2200	461	1458	246	578	69
1982	789	130	2300	504	1569	254	654	88
1983	924	152	2500	547	1789	337	712	87
1984	853	141	2700	589	1630	270	738	83
1985	958	158	3300	750	2062	324	775	101
1986	1261	208	3195	641	2272	389	798	101
1987	1477	243	3793	882	2400	427	1051	154
1989	869	94	1558	191	1401	229	533	108
1990	1048	172	1786	391	1458	344	559	122
1991	1097	193	2132	411	1977	481	750	138
1992	1168	214	2608	541	2246	482	957	178
1993	1433	222	3118	540	2457	555	1074	198
1994	1507	259	3086	580	3078	647	1230	227
1995	1610	261	3527	707	3184	583	1410	261
1996	1634	353	4260	830	3489	713	1690	290
1997	1924	380	4664	1084	4272	909	2020	405
1998	2300	359	5278	1071	4529	795	2280	477
1999	2183	313	5853	1358	4725	920	2399	511
2000	2145	389	6300	1540	5167	1067	3330	594
2001	2380	396	7190	1727	6092	1060	3594	765
2003	1256	270	5038	1407	3393	799	2366	480
2004	1479	283	6044	1781	3968	933	3194	694
2005	1899	388	6762	2046	4766	1166	3531	897
2006	2216	411	7160	2085	4574	1157	4065	850
2007	2499	341	7416	2095	4550	594	4572	978
2008	2656	484	8352	2096	6030	1035	5972	976
2009	3063	490	8415	2263	6226	1421	6399	1313
2010	2909	564	9720	2873	6395	1605	6181	1451
2011	3386	699	10941	3294	7163	1517	7378	1445
2012	3966	570	11262	3247	8029	1876	7328	1473
2013	3133	613	11892	3682	8082	1373	7605	1403
2014	3368	654	13420	3853	9343	2067	7356	1942

SI TABLE 1. OVERVIEW OF NUMBER OF SURVEYS PER YEAR. M = MOULT, P = PUPPING SEASON.

	The Netherlands			Lower Saxony			Schleswig-Holstein			Denmark		
	M	P	Total	M	P	Total	M	P	Total	M	P	Total
1974	2	2	4	1*	1*		1*	1*		1*	1*	
1975	2	7	9	1*	1*		1*	1*		1*	1*	
1976	3	6	9	1*	1*		1*	1*		1*	1*	
1977	2	6	8	1*	1*		1*	1*		1*	1*	
1978	3	5	8	1*	1*		1*	1*		1*	1*	
1979	2	4	6	1*	1*		1*	1*		1*	1*	
1980	2	5	7	1*	1*		1*	1*		1*	1*	
1981	2	5	7	1*	1*		1*	1*		1*	1*	
1982	1	6	7	1*	1*		1*	1*		1*	1*	
1983	1	5	6	1*	1*		1*	1*		1*	1*	
1984	1	5	6	1*	1*		1*	1*		1*	1*	
1985	2	4	6	1*	1*		1*	1*		1*	1*	
1986	2	5	7	1*	1*		1*	1*		1*	1*	
1987	2	6	8	1*	1*		1*	1*		1*	1*	
1989	3	6	9	3	7	10	3	6	9	1	2	3
1990	3	6	9	1	5	6	2	5	7	2	5	7
1991	2	6	8	2	8	10	3	5	8	1	7	8
1992	2	7	9	2	8	10	2	5	7	2	6	8
1993	2	7	9	2	7	9	1	5	6	3	5	8
1994	2	6	8	1	6	7	1	7	8	1	4	5
1995	2	4	6	1	5	6	2	4	6	1	2	3
1996	1	3	4		5	5	2	2	4	2	1	3
1997	2	5	7	2	6	8	2	4	6	2	2	4
1998	2	3	5	2	3	5	1	2	3	1	2	3
1999	2	3	5	2	3	5	1	3	4	3	1	4
2000	2	4	6	2	5	7	2	3	5	2	3	5
2001	1	3	4	2	3	5	2	3	5	2	2	4
2003	2	3	5	2	3	5	2	3	5	2	2	4
2004	1	3	4	2	3	5	2	2	4	2	2	4
2005	2	2	4	2	3	5	2	3	5	1	3	4
2006	2	3	5	2	3	5	2	2	4	1	3	4
2007	2	3	5	2	2	4	2	3	5	2	2	4
2008	2	3	5		2	2	2	3	5	2	3	5
2009	2	3	5	1	3	4	2	3	5	2	3	5
2010	2	2	4	2	2	4	2	3	5	2	3	5
2011	2	2	4	1	3	4	1	3	4	2	3	5
2012	2	3	5	2	3	5	2	2	4	2	3	5
2013	1	3	4	2	2	4	2	1	3	2	3	5
2014	3	4	7	2	3	5	2	3	5	2	3	5

SI TABLE 2. ANNUAL MAXIMUM COUNTS FOR TOTAL NUMBERS (DURING MOULT) AND PUPS. LEFT COLUMN INDICATES THE PERIODS.