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How effective has the management of Cockle and Mussel fisheries on The Wash estuary been in ensuring that there is sufficient food for birds?

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Report to Natural England

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Executive summary

The Wash is England's largest Special Protection Area (SPA) with Oystercatchers *Haematopus ostralegus* being a designated feature. During the winter, Oystercatchers rely heavily on Cockles *Cerastoderma edule* and Blue Mussels *Mytilus edulis* for their food requirements, creating the potential for conflict with the human fisheries for these species.

During the 1980s, high fishing mortality of the Blue Mussel (hereafter Mussel) stocks led to an almost complete disappearance of Mussel beds in The Wash, with the Mussel fishery closing in 1994. Cockle stocks also collapsed due to a long run of poor recruitment that followed high fishing rates in the 1980s. During that same period, the number of wintering Oystercatchers on The Wash declined by 75%, which was linked to increases in adult mortality. We use a long-running volunteer-collected dataset to quantify the relationship between survival and winter climatic conditions and Mussel stock data to determine how much of the variation in survival is due to these factors. We also characterise a period of high mortality in the latter part of the 2022/23 winter.

Between the summer of 1968 and the winter of 2022/23, 38,385 Oystercatchers were ringed on The Wash, of which 1,558 were subsequently recovered dead. On average, annual Oystercatcher survival was high but was much lower in two winters: 1992/93 and 1995/96, and also somewhat reduced in the winter of 2022/23. The estimated overall annual mortality of adult and immature Oystercatchers on The Wash is, at ~9%, similar to figures obtained from other regions e.g., ~12% in the Wadden Sea and ~11% in the Exe estuary. Following the low survival in winters 1992/93 and 1995/96, juvenile survival appears to have remained at a low level.

Among adults, survival during the summer months was, on average, slightly lower than in winter. The only covariates to have an influential effect on adult survival in winter were Mussel and Cockle biomass. Survival tended to be high when either Cockle or Mussel stocks were high and lower when both were low, although the effect of Cockle stocks on survival was slightly greater than that of Mussels. Our measure of winter severity was not related to survival.

In the winter of 2022/23 a large number of dead birds were found on the east shore of The Wash in late January and early February 2023, although no reports were received from the west shore, perhaps due to poorer coverage there. Although the precise cause of death could not be established directly, birds showed signs of emaciation (e.g. lack of breast muscle) that suggested starvation as a likely contributing factor. Dead birds were on average older than the estimated age of the population as a whole.

Four cannon-net catches of roosting birds at high tide were made on east shore beaches during the 2022/23 winter season: 26 November, 21 January, 25 February, and 11 March, with an additional sample of birds mist-netted on 11 March. The individuals caught in these catches weighed substantially less than might be expected for the time of year, especially in January. Weights of the mist-netted birds (on saltmarsh on the south shore) were more similar to historical average, suggesting they may have escaped the worst effects of any reductions in food supply.

The 1992 Wash Fishery Order led to strengthened management of the shellfisheries in The Wash, allowing a harvest without adversely impacting Oystercatcher survival, which has remained high and relatively stable since these measures were put in place. However, the recent bout of high mortality suggests careful management of stocks is required going forwards.

Introduction

Shorebird populations globally are in general decline (Santos et al. 2023). The soft coasts of north-west Europe support internationally important numbers of wintering shorebirds (Rehfisch et al. 2003). Estuaries are extremely productive environments that are not only important for birds but are also economically important, due to the presence of substantial stocks of, for example, commercially fished shellfish, fish and crustaceans (Goss-Custard et al. 2004). Many of these sites are designated as Special Protection Areas (SPAs) and Special Areas of Conservation (SACs) for their shorebird populations and habitats and there is potential for conflict where the exploitation of these resources by shorebirds and humans overlaps (Atkinson et al. 2010). This issue is exemplified by the conflict between fisheries and Oystercatchers *Haematopus ostralegus*. During the winter, Oystercatchers rely heavily on Cockles *Cerastoderma edule* and Blue Mussels *Mytilus edulis* (hereafter Mussels) for their food requirements. The sizes of shellfish taken by Oystercatchers overlap with those harvested in the fishery and overexploitation of shellfish stocks has led to population level impacts on Oystercatcher (Andrews 1974, Smit et al. 1998, Ens 2002). In Britain, this conflict reached a climax in the early 1970s and led to the culling of ca. 10,000 Oystercatchers in the Burry Inlet, South Wales during the winters of 1972/73 and 1973/74 because of their perceived damage to the cockle fishery (Andrews 1974, Prater 1974). This caused major public outcry at the time, especially in Norway, where most of these birds bred.

Because shellfish stocks vary naturally depending on spatfall each year, annual adaptive management of shellfish populations is crucial not only to maintain enough food stocks for birds, but also to provide a harvestable proportion for commercial interests. In the 1990s, high fishing mortality and poor spatfall led to the almost complete disappearance of intertidal Mussel beds in the Dutch Wadden Sea. Cockle spatfall is driven by largely stochastic processes, and poor spatfall at this time led to low Cockle stocks which resulted in high mortality amongst the Oystercatcher and Eider *Somateria mollissima* populations due to a lack of food (Smit et al. 1998). This led to the revision of the Dutch fisheries policy to ensure adequate supplies were available to wintering shorebirds and sea ducks (Camphuysen et al. 1996, Smit et al. 1998).

Estuaries in north-west Europe have many stakeholders who use the area. There has been a historic Mussel, Cockle and Brown Shrimp *Crangon crangon* fishery in The Wash and a number of methods to collect shellfish have been used, ranging from the low-impact hand-raking to prop-blowing and suction-dredging which can be extremely damaging to the substrate and the invertebrates living within it (e.g. Ferns et al. 2001). It is also an area of very high conservation importance and has a number of designations, including under the international Ramsar Convention on Wetlands, European Special Protection Area (SPA), Special Area of Conservation (SAC), and as a national Site of Special Scientific Interest (SSSI). The SPA designation under the 'Birds' Directive (EC/1979/409), in particular, requires any activities not to harm the listed features, which includes many species of waterbird including Oystercatcher.

During the 1980s, high fishing mortality of the Mussel stocks led to an almost complete disappearance of Mussel beds in The Wash by the early 1990s, and the Mussel fishery closed in 1994. Cockle stocks also collapsed due to a long run of poor recruitment that followed high fishing rates in the 1980s (Bannister 1998, 1999). During that same period (1980s to mid 1990s), the number of wintering Oystercatchers on The Wash declined from ca. 40,000 to 11,000 birds, a loss of almost three-quarters of the peak population (Frost et al. 2021). During three of these winters (1992/1993, 1995/1996 and 1996/1997) thousands of dead Oystercatchers were reported on the shoreline of The Wash during the latter half of the winter, and many birds started to feed in fields and amenity grassland well inland of sea-walls (Atkinson et al. 2000, 2003). This was atypical behaviour for Wash Oystercatchers (Clark 1993, 1996), but typical of the behaviour exhibited in the Netherlands when shellfish stocks were inadequate to support the wintering population (Smit et al. 1998). Across the rest of the UK, Oystercatcher numbers were stable or increasing slightly (Frost et al. 2021) and the large decline in shellfish numbers during this period was confined to The Wash only.

The high mortality in adult Oystercatchers was reflected in large reductions in adult survival (Atkinson et al. 2003). Annual mortality in Wash-wintering Oystercatchers was estimated to be on average 11% per annum which is similar to that found in the Wadden Sea (Camphuysen et al. 1996). However, in contrast to the Wadden Sea populations, in normal years summer mortality was higher in Wash birds (8% compared with 3.6% in the Wadden Sea), and winter mortality was lower (2% compared with 8.4%) (Camphuysen et al. 1996). The reasons for this are unclear but are probably related to more severe winters in the Wadden Sea and the fact that Oystercatchers wintering in the Wadden Sea tend to be residents (Hulscher et al. 1996) whereas, for the majority of Oystercatchers that winter on The Wash, the summer survival period includes migrations to and from Norway. In the three winters where large numbers of dead birds were found, mortality ranged from five to 12 times normal winter mortality.

The poor state of the Mussel and Cockle stocks led to the development of The Wash Fishery Order 1992, a statutory instrument that laid down the regulation of the different fisheries (EIFCA 2017). Under it, Eastern Inshore Fisheries and Conservation Authority (Eastern IFCA) were granted 30 years to manage the fisheries. It allows for areas in The Wash to be leased for aquaculture, especially Mussels, and also undertakes annual Cockle stock assessments. Working with Natural England and other organisations, Eastern IFCA ensures that Cockle harvest quotas leave enough stock for birds as a designated feature. This process of setting annual shellfish quotas specifically takes into account the requirements of the birds. An individual behaviour-based model (Stillman et al. 2003) linked shellfish stocks to Oystercatcher mortality in The Wash and correctly identified the years in which mass mortality was observed. The model's outputs were used to formulate fishery policy and this report evaluates whether the fishery has been sustainably managed from the perspective of preventing mass mortality of Oystercatchers over the 20 years it has been in place.

A previous analysis of long-term mark-recovery data (to 1998) of Oystercatchers using The Wash highlighted the link between shellfish stocks and individual survival (Atkinson et al. 2003). Here we update the analysis using an extra two decades of capture and recovery effort, during which time numbers of Oystercatchers using The Wash have increased, although they have remained below the pre-crash peak numbers seen in the late 1980s (Fig. 1b). Specifically, we quantify the relationship between survival and winter climatic conditions and shellfish stock data to determine how much of the variation in survival is due to these factors.

METHODS

We quantified changes in the survival of individual Oystercatchers on The Wash over the last ~60 years using standard multinomial models of mark-recovery data. Records of Oystercatchers caught and ringed mostly at high tide roosts around The Wash, and subsequently recovered dead anywhere, from 1968 to 2023, were supplied by the Wash Wader Research Group (WWRG). Birds were divided into three age classes based on colouration of the eye and bare parts (Prater et al. 1977): **juveniles** if they were in their first year of life, **immatures** if they were greater than one year old but had not yet achieved full adult colouration, and **adults** if they were in full adult colouration (usually attained after two years).

All models were fitted in JAGS (Plummer 2003), using the jagsUI package (Kellner & Meredith 2023), in R 3.6.1 (R Core Team 2018). We ran three chains for each model for 15,000 iterations, discarding the first 5,000 as 'burn in' and thinning the remainder by a factor of 10, leaving 3,000 samples from the posterior distribution. We checked for convergence of chains by visually inspecting trace plots and confirming that R-hat values were < 1.1.

Annual survival models

We constructed a matrix of the number of individuals ringed and subsequently recovered in each following year, with rows representing the ringing occasion and columns representing the recovery occasion (see Supplementary Materials Table S1). Because Oystercatchers are primarily present on The Wash during the non-breeding period, recovery years ran from July of one year to June in the following year. The final column represents those ringed and never recovered (because they either had not died during the study period, or they did die but were not found and/or reported). The number of individuals of each age class (a) ringed in a given year (i.e., forming a release cohort) being recovered in year t is a product multinomial of the annual survival probabilities (ϕ_a) between ringing and the year prior to recovery (t – 1), the probability of mortality in the year t (i.e. $1 - \phi_{a,t}$), and the probability that a bird, having died, is found and reported in that year ($p_{a,t}$). The probability that a bird ringed in a given year is never recovered is then 1 minus the sum of the annual probabilities for that release cohort. We estimated survival and recovery probabilities using a Bayesian framework (Kéry & Schaub, 2012).

We assumed survival probabilities are normally distributed (on the logit-scale), annual deviations (with a variance of σ_2) from an overall mean for each age class, and that recovery probabilities follow a linear trend over time, based on the observation that, across a wide range of species, including Oystercatchers, recovery rates have decreased over time (Robinson et al. 2009). We tested the need for separate recovery probabilities for different age classes, but too few data were available to produce reliable estimates for immature and juvenile birds. We tested models with fully time-dependent recovery parameters, where recovery was estimated separately for each year, treating year as either a fixed or random effect, but these models did not converge. We therefore included a single linear trend in recovery across the three age classes. We specified non-informative priors for survival, Beta(1,1), but, to improve convergence, weakly informative priors for recovery probabilities, Beta(1.1,2), reflecting the relatively low expected recovery probabilities.

Six-monthly survival model

Sufficient data were available from the WWRG to apply an equivalent model to adult Oystercatcher survival for six-monthly periods, which ran from October to March (hereafter termed the winter period) and from April to September (the summer period). These periods were chosen to make best estimates of winter mortality, when factors on The Wash may impact survival, and summer mortality, where factors on the breeding grounds (for birds wintering on The Wash, mostly in Norway) or on migration are more likely to affect survival. There are too few recoveries to estimate six-monthly survival rates for immature or juvenile birds.

Factors influencing survival

We explored whether changes in survival related to shellfish stock abundance, winter weather, and Oystercatcher population size (a measure of relative competition over resources) by setting six-monthly survival as a logistic function of these variables. The time series for this model began from the winter of 1982, corresponding to the earliest available quantitative Mussel stock data, until 2020, corresponding to the latest data available from the Wetland Bird Survey.

Estimates of total annual Mussel and Cockle biomass (Fig. 1a) were obtained from the Centre for Environment, Fisheries and Aquaculture Science (Dare et al. 2004) and the Eastern Inshore Fisheries & Conservation Authority (Jessop 2019). Although survey information is intermittently available going back to ~1920, quantitative estimates of Mussel stocks are only available from 1982 onwards, and for Cockle stocks from 1994 onwards. Prior to 1994, Cockle stock data are available on an ordinal scale from 1 (low stock) to 4 (abundant stock) (Dare et al. 2004). Prior to 2003, estimates may be incomplete, and may underestimate stocks.

We calculated winter severity on The Wash as the number of ‘cold’ days between 1 January and 31 March each year (after Camphuysen et al. 1996) using data from the Meteorological Office stations at Terrington St. Clement (52°75´N, 0°29´E) and Holbeach (52°87´N, 0°14´E) obtained from the MIDAS Daily Weather Observation Data (Meteorological Office 2006). Records from the former were only available until 2007, and from the latter from 1991. Temperature estimates from both stations during the period of overlap were quantitatively similar (Fig. 1b). We used mean daily temperatures from both stations for this period. The ‘cold’ days score was calculated as follows: each day with an average air temperature ((maxT + minT)/2) of 0° to -5°C scored 1, each day with a mean between -5° and -10°C scored 2 and a mean less than -10°C scored 3 (after Atkinson et al. 2003). A total number of ‘cold’ days was then calculated for each winter and termed the winter severity index (Fig. 1c).

Wader counts have been carried out at monthly intervals on The Wash since 1970, led by the UK’s national waterbird monitoring scheme, the Wetland Bird Survey (WeBS 2017). These counts have been carried out at monthly intervals on 24 different sectors on The Wash running in an unbroken line from Gibraltar Point (53°05’N 0°20’E) to Holme (52°51’N 0°34’E). Indices of Oystercatcher population sizes were calculated for the winter and summer of each year by applying the Underhill method to counts from 1 October to 31 March and 1 April to 30 September respectively (matching the periods chosen for the six-monthly survival analysis). The Underhill method calculates indices by modelling counts as a function of site, year and month; missing counts are imputed where necessary. The total number of observed and imputed bird months are summed and used as the index for that year, and scaled so that the last period (in this case the winter of 2019 and summer of 2020) equals 100 (Underhill & Prys-Jones 1994, Fig. 1d). Eleven (29%) of the summer indices used in the survival model have been subject to a high degree of imputation, so are less reliable.

Covariates were log-transformed and scaled to improve convergence and interpretability of effects. We converted logged Mussel abundance to an index, following Atkinson et al. (2010), ranging from 0 (low stocks) to 4 (abundant stocks). Similarly, we converted logged Cockle abundance data to match them to pre-1994 indices, which range from 1 to 4. The strength of their effects was determined by their posterior means and credible intervals, assuming posterior distributions for non-influential variables to be centred on or substantially overlapping with 0, and 95% of posterior distributions shifted substantially away from 0 in either a positive or negative direction to indicate support for a positive or negative effect, respectively.

Figure 1: Annual estimates for the covariates potentially explaining Oystercatcher survival on The Wash, England between 1982 and 2023, showing (a) total shellfish biomass (t); (b) Underhill index of winter (Δ) and summer (●) population sizes of Oystercatchers, with the final periods set to a value of 100. The years correspond with the start of winter i.e., 1982 = 1 October 1982 to 30 September 1983; (c) average daily temperature (°C) recorded by the Meteorological Office stations at Terrington St. Clement, Norfolk, and Holbeach, Lincolnshire between January and the end of March; and (d) winter severity, calculated as the number of 'cold' days between 1 January and 31 March each year.

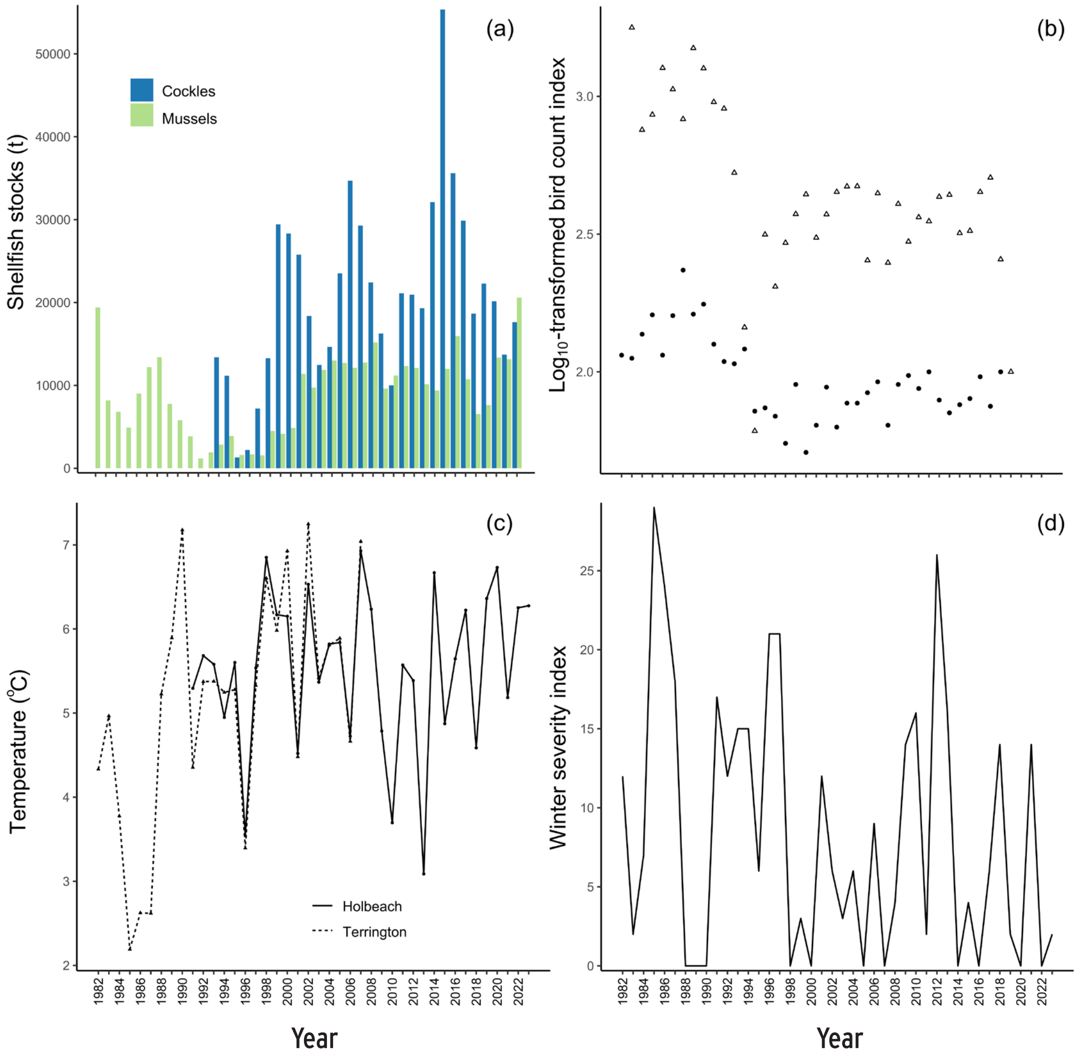


Table 1. Recovery matrices for Oystercatchers on The Wash from 1968, separated by age class and grouped into five-year periods. Each period runs from July to June i.e., 1968–1973 runs from June 1968 to July 1973. Rows represent the ringing occasion and columns represent the recovery occasion. The final column represents the number of birds ringed and never recovered.

	1968–1973	1973–1978	1978–1983	1983–1988	1988–1993	1993–1998	1998–2003	2003–2008	2008–2013	2013–2018	2018–2023	Not recovered
ADULTS												
1968–1973	33	42	30	11	10	4	1	0	0	0	0	1,645
1973–1978	0	68	107	47	56	28	2	2	2	0	0	6,528
1978–1983	0	0	24	29	51	20	3	1	2	1	0	2,597
1983–1988	0	0	0	17	51	31	6	3	3	3	1	2,124
1988–1993	0	0	0	0	83	49	13	15	10	8	2	3,027
1993–1998	0	0	0	0	0	30	20	11	9	3	5	1,879
1998–2003	0	0	0	0	0	0	5	14	4	7	5	1,626
2003–2008	0	0	0	0	0	0	0	16	24	10	12	2,290
2008–2013	0	0	0	0	0	0	0	0	8	15	16	1,520
2013–2018	0	0	0	0	0	0	0	0	0	10	12	2,080
2018–2023	0	0	0	0	0	0	0	0	0	0	5	1,335
IMMATURES												
1968–1973	15	15	4	2	1	1	0	0	0	0	0	680
1973–1978	0	12	41	17	8	3	2	1	1	0	0	2,026
1978–1983	0	0	7	14	5	0	1	0	1	1	0	749
1983–1988	0	0	0	5	8	5	1	2	1	0	0	407
1988–1993	0	0	0	0	21	9	2	1	4	0	1	602
1993–1998	0	0	0	0	0	8	1	3	1	0	0	366
1998–2003	0	0	0	0	0	0	2	3	2	1	0	380
2008–2013	0	0	0	0	0	0	0	0	2	2	0	156
2013–2018	0	0	0	0	0	0	0	0	0	0	0	290
2018–2023	0	0	0	0	0	0	0	0	0	0	1	160
JUVENILES												
1968–1973	12	18	5	3	4	2	0	1	2	0	0	186
1973–1978	0	13	21	4	10	4	1	0	2	0	0	746
1978–1983	0	0	9	7	5	8	5	0	2	1	0	532
1983–1988	0	0	0	4	10	5	1	0	1	1	0	268
1988–1993	0	0	0	0	24	6	2	0	1	0	0	318
1993–1998	0	0	0	0	0	17	3	2	1	0	0	591
1998–2003	0	0	0	0	0	0	3	9	1	1	0	140
2003–2008	0	0	0	0	0	0	0	3	5	4	1	242
2008–2013	0	0	0	0	0	0	0	0	0	0	1	66
2013–2018	0	0	0	0	0	0	0	0	0	1	3	365
2018–2023	0	0	0	0	0	0	0	0	0	0	1	160

Figure 2. Estimates of Oystercatcher survival on The Wash, showing (a) the annual survival of adults, immature, and juvenile birds, and (b) the seasonal survival of adults. Points represent the mean of the posterior sample of survival probabilities. Shaded areas represent 95% credible intervals around these.

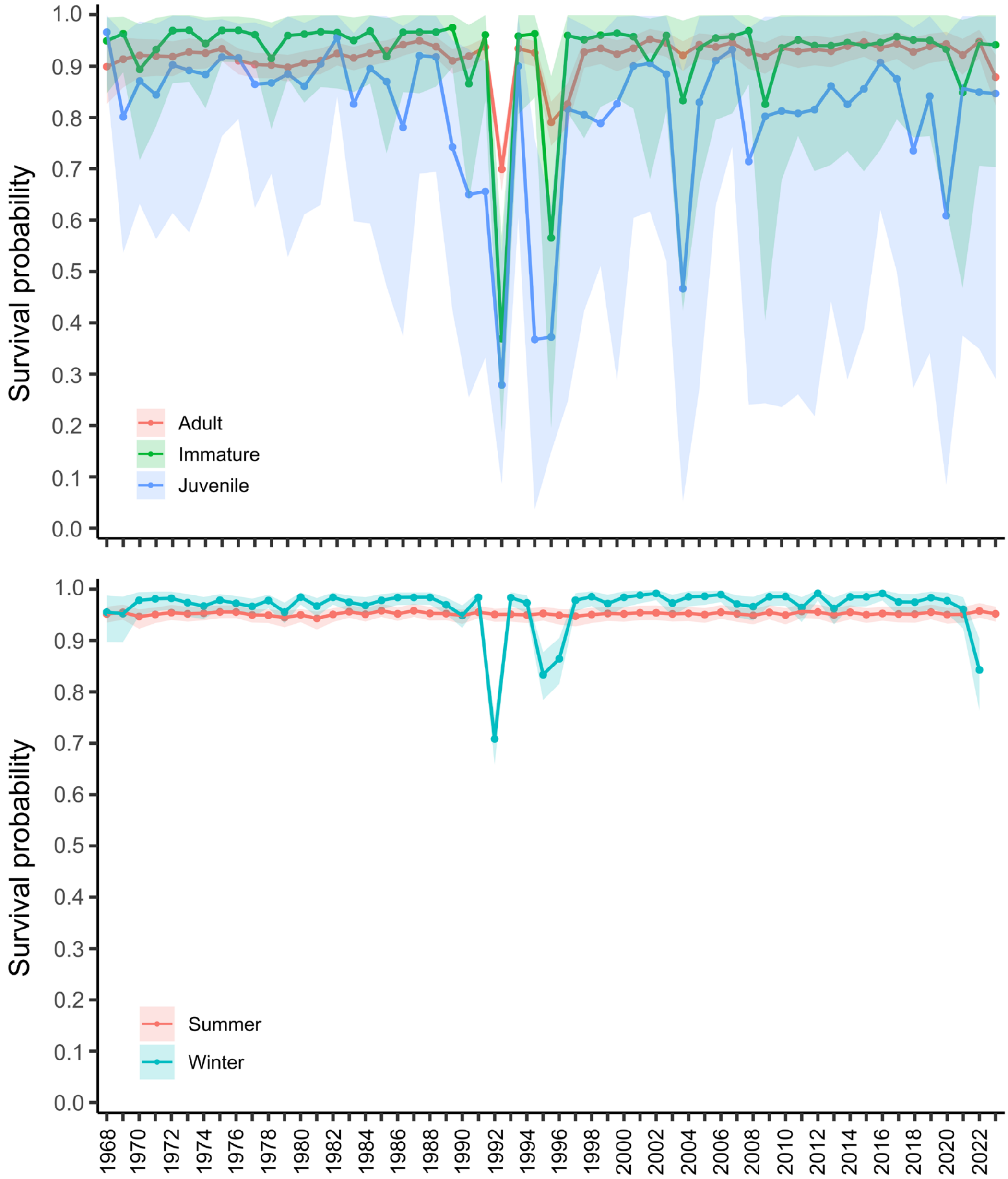


Table 2. Coefficient estimates (β) and 95% credible intervals (CI) from the six-monthly Oystercatcher survival models testing whether winter or summer survival is related to shellfish stocks, winter weather, and population size. Estimates in bold are those where the CIs do not cross zero.

	β (95% CIs)	
COVARIATE	Winter survival	Summer survival
Mussel stocks	1.156 (0.165, 2.092)	0.321 (-0.015, 0.659)
Cockle stocks	1.480 (0.457, 2.535)	0.387 (0.034, 0.738)
Population size	0.212 (-0.279, 0.717)	0.057 (-0.112, 0.226)
Winter severity	-0.064 (-0.525, 0.391)	0.076 (-0.060, 0.211)
Cockle x Mussels	-0.452 (-0.867,-0.013)	-0.101 (-0.250, 0.059)

Figure 3. Winter survival probabilities of adult Oystercatchers against (a) Mussel and (b) Cockle stocks. The red and blue lines indicate the effect of each shellfish stock when stocks of the other are high and low, respectively.

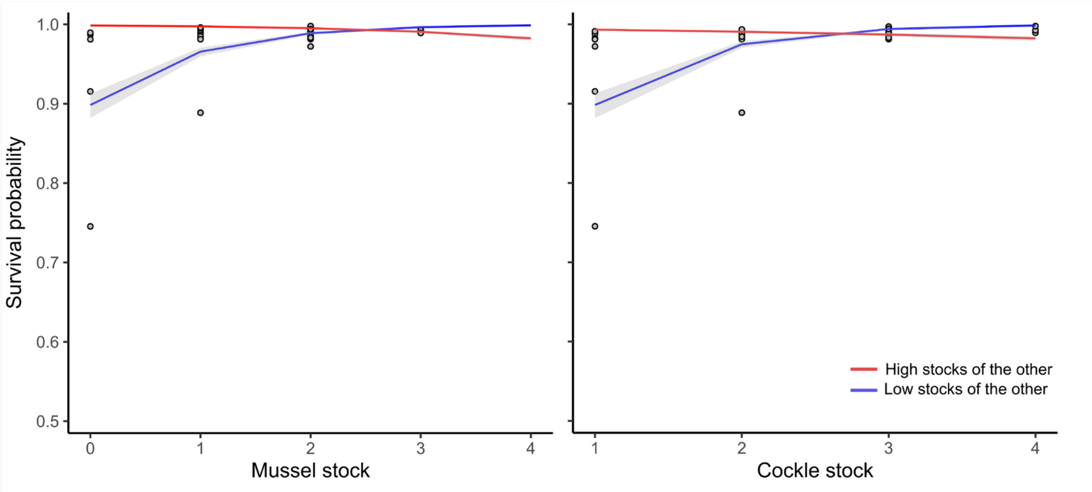


Figure 4. Expected ages of (a) Oystercatchers alive in The Wash in the winter of 2022/23 based on date of ringing and assuming survival for birds in their first year was 0.87 before 1991 and 0.82 thereafter, and that survival in later years of life was 0.92 (black bars) and those found dead in Jan/Feb 2023 (red bars). (b) Relative frequency by presumed age among birds found dead in the winter of Jan/Feb 2023 compared to the population, bars above the line indicate dead birds were over-represented in a given age-class.

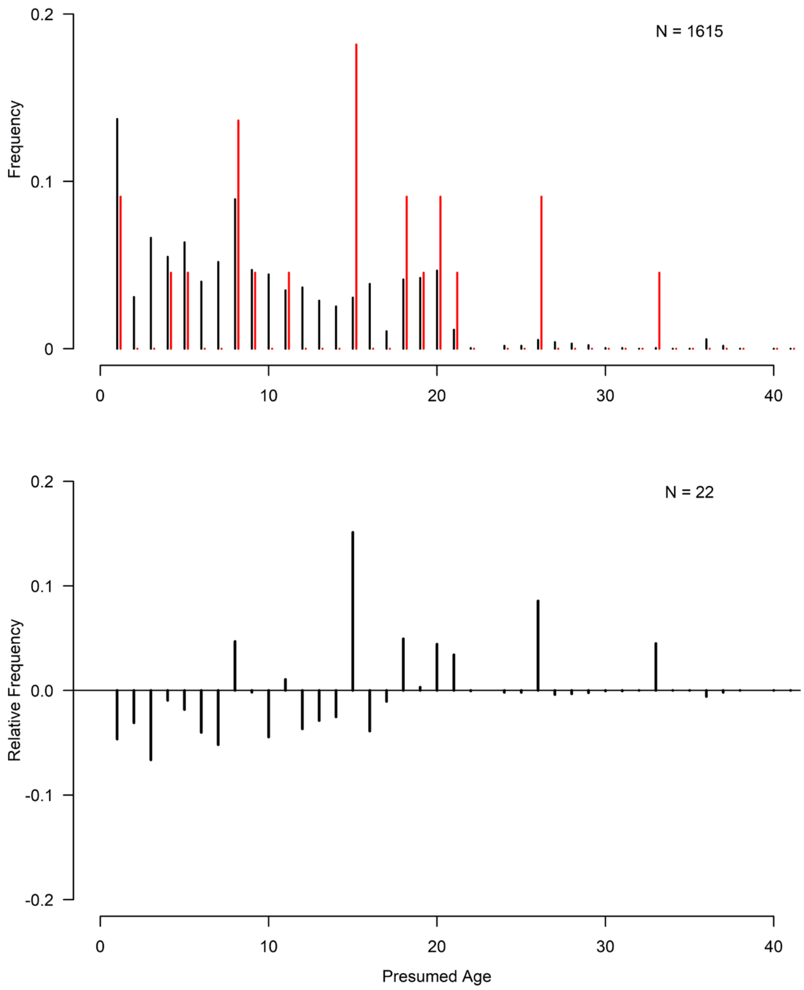


Figure 5. Weight distribution of oystercatchers caught on the east shore of The Wash by month. Grey bars indicate the frequency distribution in catches between 1990 and 2022, and the heavy black line, the mean weight. Red bars (and line) are for catches made in that month in 2023, dashed lines indicate means for the previous month (and the dotted line in the March panel, the mean for January) for easy comparison. In March an additional catch was made on saltmarsh on the south shore, the weights from this catch are shown in blue).

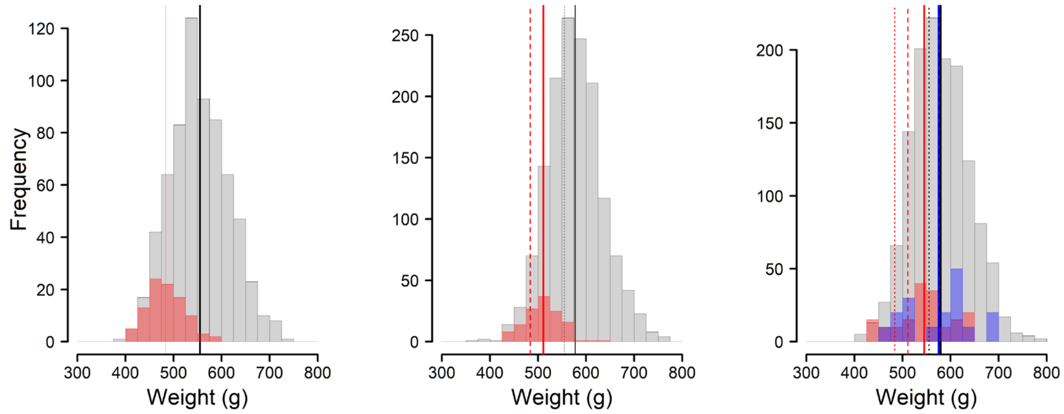
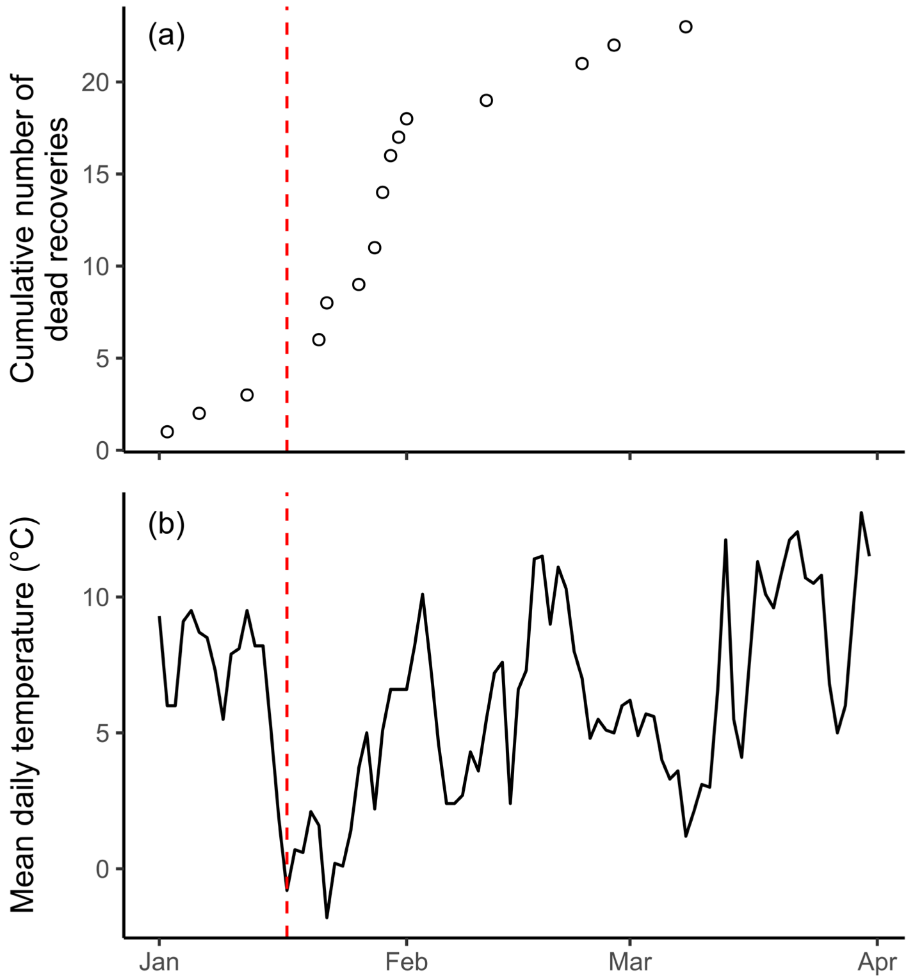


Figure 6. (a) Cumulative number of recoveries of dead Oystercatchers on The Wash and (b) the mean daily temperature at the Holbeach weather station (Meteorological Office 2006) between January and end of March 2023. The vertical red dashed line indicates a drop in temperature to below 0°C.



RESULTS

Survival

Between the summer of 1968 and the winter of 2022, 38,385 Oystercatchers were ringed at The Wash. The majority (n = 28,117) of birds were ringed as adults; 6,361 were ringed as immature birds, and 3,907 were ringed as juveniles. Of these, 1,558 were subsequently recovered dead (Table 1). The probability of recovering a dead individual ranged from 0.025 to 0.085, declining over time (β = −0.013, CIs from -0.019 to -0.007). On average, annual Oystercatcher survival was high (ϕ_{ad} = 92.4%, CIs = 91.3–93.5%; ϕ_{im} = 96.4%, 95% CIs = 93.6–98.6%; ϕ_{juv} = 87.8%, CIs = 79.7–94.5%). However, survival of juvenile and immature birds varied more than adult survival. Among each age class, survival was particularly low in two years: 1992/1993 (ϕ_{ad} = 69.9%, CIs = 65.7–73.8%; ϕ_{im} = 36.9%, CIs = 18.7–56.9%; ϕ_{juv} = 27.9%, CIs = 8.6–53.5%) and 1995/1996 (ϕ_{ad} = 79.1%, CIs = 74.5–83.1%; ϕ_{im} = 56.5%, CIs = 19.6–88.0%; ϕ_{juv} = 37.2%, CIs = 14.9–62.7%), and adult survival remained low in 1996/1997 (ϕ_{ad} = 82.6%, CIs = 78.3–86.6%) (Fig 2a). Following the period of low survival, juvenile survival appears to have remained at a lower level, averaging 81.9% from 1996 onwards, compared with 86.7% in the years prior to 1991/1992 winter. The six-monthly survival model revealed declines in adult winter survival in the same years as the annual model: 1992/1993 (ϕad = 70.8%, CIs = 65.8–75.4%), 1995/1996 (ϕ_{ad} = 83.3%, CIs = 78.4–87.7%), and 1996/1997 (ϕ_{ad} = 86.4%, CIs = 81.5–90.5%) (Fig. 2b). This model also revealed 2022/2023 as a winter in which adult survival was unusually low (ϕ_{ad} = 84.3%, CIs = 76.3–90.3%). Summer survival was high (95.3%) but, on average, slightly lower than in winter (97.6%), and did not show the same sharp annual decreases as winter survival.

The only covariates to have an influential effect on adult winter survival between 1982 and 2020 (the years for which data were available for all covariates) were Mussel and Cockle biomass (Table 2). The interaction term was significant for the winter period, indicating high survival when either Cockle or Mussel stocks were high, and lower survival when both Mussel and Cockle stocks were low (Fig. 3). The effect of Cockle stocks was slightly greater than that of Mussels. When Mussel biomass dropped to its lowest in 1992 (~1,000 tonnes), adult survival also dropped to its lowest level (Fig. 2). Our measure of winter severity and Oystercatcher population size did not explain variation in adult survival (95% CIs crossed zero).

Recoveries of dead birds

The low survival in the winter of 2022/23 was associated with a large number of dead birds being found on the east shore (only) of The Wash in late January and early February 2023. No reports were received from the west shore and few from the south shore although, since the level of public access is lower (and the number of marked birds fewer), it is hard to say whether this was due to lower mortality, or simply dead birds not being found. A systematic search of the beach between Heacham and Snettisham yielded up to 30 corpses counted over 3 dates (28 Jan – 5; 1 Feb – 10; 11 Feb – 15), although as corpses were not removed, some double-counting may have occurred. This coincided with a period of unusually cold weather (Fig. 6). Although the precise cause of death could not be established directly, all birds showed signs of emaciation (e.g. lack of breast muscle) that suggested starvation as a likely contributing factor.

Among the dead birds found, a number bore rings having previously been captured and marked by WWRG. In total 22 individuals were identified and, as the date of ringing was known, an estimate of minimum age could be determined; dead birds were on average older than the estimated age of the population as a whole (Fig. 4).

Condition of birds caught

Condition of birds feeding primarily on the east shore was assessed through cannon-net catches of roosting birds at high tide on Heacham beach on five occasions during the 2022/2023 winter: cannon-netted on 26 November 2022 (199 birds), 21 January 2023 (97), 25 February 2023 (130), and 11 March 2023 (34), with an additional sample of birds mist-netted on the south shore on 11 March 2023 (18).

Previous ringing by WWRG indicates that adult birds caught on The Wash typically weighed between 500 g and 700 g, but the lowest mass recorded in the 2022/23 winter was a bird at 365 g which must have been on the edge of starvation, and the heaviest was 780 g. The lowest weights tend to be recorded in the summer, with weights increasing through the late autumn to reach a peak in spring, just before they leave for their Norwegian breeding grounds (the 780 g bird was caught in mid March). This is demonstrated by the grey bars in Fig. 6, which show how many individuals have been caught at each weight across the years in each month. The bars shift a little to the right each month, indicating a greater number of heavier birds in February and March. The thick black line on each graph indicates the mean adult weight in each month (January: 555 g; February: 577 g; March: 579 g); birds in February/March have, on average, 20 g more weight – mostly fat as fuel for their migration – than in January.

In November 2022, the weights of individuals caught (1st to 3rd quartile: 480–526 g) were broadly similar to those caught in November in previous years (1991–2021, 490–570 g). By January (Fig. 6a), however, the weights were well down on where we would expect them to be. Almost all birds weighed less than the historical average and the mean weight in January 2023 (484 g) was 75 g (or about 15%) below where it should have been (559 g). By February (Fig. 5b), the mean mass was closer to the long-term mean but presumably mostly because the lightest birds had already died of starvation, as evidenced by a high number of corpses found washed up on the tideline (above). The mean weight had increased to 512 g, but most of the birds caught still weighed less than the mean weight of caught in past years in February (the black line).

In March (Fig. 5c), two catches were taken on the same day, one cannon-netted on Heacham beach on the east shore, and one mist-netted on Terrington Marsh on the south shore. The interesting thing is that the birds at Terrington are likely to feed to a larger extent on worms, rather than Cockles and Mussels, which is reflected in individuals having longer, pointier bills (WWRG, unpubl. data). These birds therefore would be expected to have largely escaped the effects of low shellfish numbers and the blue bars are roughly where we would expect them to be (allowing for the fact that relatively few birds were caught). The birds caught on Heacham, however, were still relatively underweight.

DISCUSSION

We have shown that, in general, Oystercatchers on The Wash experience little variation in mortality rates between years. The estimated overall annual mortality of adult and immature Oystercatchers on The Wash is, at ~9%, broadly in line with the previous estimate of ~11% obtained from an earlier study on The Wash (Atkinson et al. 2003), and close to figures obtained from other regions, e.g. ~12% in the Wadden Sea (Camphuysen et al. 1996) and ~11% in the Exe estuary (Durell et al. 2000). Slightly higher survival rates were found among immature birds, which have not reached breeding age, so largely remain on The Wash in summer, compared with adults, perhaps reflecting that immature birds are not subject to the mortality risks associated with migration, such as predation and anthropogenic threats, e.g. cars. Likely for the same reason, average mortality (~5%) of adults was higher during the summer period, which includes migration to and from the breeding grounds in Norway, compared with winter mortality (~2%), when birds are largely resident on The Wash. While winter mortality rates are comparable to figures obtained from previous studies carried out on British wintering Oystercatcher populations, summer mortality in the Norwegian breeding grounds appears to be lower than in the breeding grounds of northern Britain (~8%), where Oystercatchers wintering on the Exe estuary tend to breed (Durell et al. 2000). Despite relatively stable survival over time, there were several mass mortality events in The Wash Oystercatcher population between 1991 and 1997, and more recently in 2022. These events were evident in annual survival of adult Oystercatchers, as well as adult winter survival. The adult survival during the winters of 1992/1993, 1995/1996, and 1996/1997 estimated for this study were very close to previous estimates using the same data (Atkinson et al. 2003), and comparable to those found in another study on the Burry Inlet in South Wales (79%), where shellfish numbers crashed (Bowgen et al. 2022).

Although observations from the Wadden Sea indicate that mortality is higher in periods of severe weather (Camphuysen et al. 1996, Durell et al. 2001), no effect of winter severity on survival was found in this study. Winters tend to be relatively mild on The Wash, which is reflected in a relatively low winter mortality compared with the ~8% calculated for the Wadden Sea. Furthermore, many birds found dead during severe weather are juveniles or birds with deformities or injuries, such that cold winter weather may be hastening mortality of already susceptible individuals, rather than increasing mortality overall (Atkinson et al. 2000). Oystercatcher survival on The Wash also remained apparently unaffected by population size, despite Mussel-feeding Oystercatchers showing density-dependent survival on the Exe estuary (Durell et al. 2000). It is possible that the model was unable to detect the effect of population size from WeBS counts, as there are issues with estimation (The Wash is a large area and challenging to survey), and the relatively coarse resolution of the counts (a single whole estuary midwinter peak), where density-dependence may act at smaller scales, e.g. in clusters of particular beds. There may also have been too few years of higher bird densities to explore whether mortality increases once the population crosses a certain threshold density. Following a rapid decrease in The Wash Oystercatcher population in the 1990s, the population has remained at approximately a quarter of this peak population size (Fig. 1b).

The updated survival analysis undertaken here indicates that survival of Oystercatchers on The Wash is driven more by food availability, than winter weather or density-dependent factors. The results of the six-monthly survival model revealed a positive effect of Mussel and Cockle stocks on winter survival among adults. Indeed, the mass Oystercatcher mortality events occurred during winters when Cockle stocks were low and Mussel stocks crashed as a result of overfishing (Dare et al. 2004). Even in severe cold winters, Oystercatchers do not tend to move to other estuaries in search of food, unlike more mobile species such as Red Knot *Calidris canutus*, making them particularly susceptible to food shortages (Atkinson et al. 2003). In winter with poor shellfish stocks, Oystercatchers have been observed feeding in amenity grassland in areas surrounding The Wash, including parks but also roundabouts. There may be inadequate alternative food sources, such terrestrial earthworms, due to the lack of substantial areas of permanent pasture around The Wash and, during severe weather the grassland will freeze, thus making earthworms inaccessible (Atkinson et al. 2000). Our study confirms that Mussel stocks, which tend to be relatively stable, unless overfished, may be crucial to preventing mass mortality events on The Wash (more so than Cockle stocks, which normally vary much more (Atkinson et al. 2003)). However, the drop in Oystercatcher survival in the 2022/2023 winter was associated with relatively abundant stocks of Mussels and Cockles (~13,000 tonnes each, although the larger, adult, Cockles made up a relatively small proportion of this) and an increase in dead recoveries following a cold period where temperatures dropped below 0°C (Fig. 6).

Given that juvenile Oystercatchers tend not to feed on Cockles and Mussels but mostly feed on marine worms and other small bivalves (Goss-Custard & Durell 1983), and juvenile survival has remained low compared with the years before these mass mortality events, there may have been a general deterioration in the health of The Wash ecosystem, which not only affected Mussels but other species as well. Furthermore, reduced shellfish available for older birds might have forced them to feed on worms or alternative foods, thereby increasing competitive pressure on juveniles. Little is known about the impacts of the past dredging operations in The Wash on non-target benthic invertebrates, but under intense dredging conditions that cause substantial changes in sediment types and physical disturbance of the sea floor (Ens et al. 2004), some invertebrate communities may not yet have recovered. High and fluctuating nutrient levels, which are often associated with shellfisheries, can favour filter-feeding shellfish over deposit-feeding worms (Philippart et al. 2007), potentially reducing food availability for juvenile Oystercatchers and other shorebird species that rely on worms.

Recognizing the importance of shellfish for the Oystercatcher population, management measures were developed in 2008 in line with The Wash SSSI conservation objectives, which stipulate that the target total stock of Cockles and Mussels in The Wash should not fall below a certain value per Oystercatcher at the start of the winter, to ensure there is sufficient food resources (Jessop 2019). Fishing restrictions put in place by the then Eastern Sea Fisheries Joint Committee (now EIFCA) led to the recovery of wild Mussel stocks. The Wash Fishery Order (1992) also explicitly allowed for areas to be leased for aquaculture, leading to increased farmed Mussel stocks, which provide a food source when wild Mussel stocks are low, and reduced pressure on the wild Mussel beds, helping them to recover (Atkinson et al. 2010). The management measures put in place as a result (EIFCA 2017), have allowed shellfishing to continue in The Wash without adversely impacting Oystercatcher survival, which remained high and relatively stable since the measures were put in place prevented further mass mortality events like those seen in the early 1990s.

In the winter 2022/23, a higher than expected winter mortality was observed. While not as extreme as the mass mortality observed in the 1990s, it was significantly higher than would normally be expected. There was a period of cold weather in January 2023 and the bulk of the dead ringed birds were found during or immediately after that period, suggesting that cold weather was an issue. However, birds had been in poor body condition throughout the winter suggesting that when food became limiting they had few reserves to buffer them. Die-offs have been observed in spawning-age Cockle in The Wash, possibly linked to parasite, *Marteilia* which has only recently been recorded in The Wash, and this could have the potential to change the way Oystercatchers interact with their prey. Oystercatchers preferentially take Cockles of particular, optimum, size and the die offs could reduce the majority of the Cockle stock to below this optimum. This has implications on the birds' intake of energy and it will be important to explore various scenarios further using the full estuary individual-based models of bird foraging (Stillman 2008) to fully assess the likely impacts on bird numbers.

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How effective has the management of Cockle and Mussel fisheries on The Wash estuary been in ensuring that there is sufficient food for birds?

The Wash is England's largest Special Protection Area (SPA) with Oystercatchers *Haematopus ostralegus* being a designated feature. During the winter, Oystercatchers rely heavily on Cockles *Cerastoderma edule* and Blue Mussels *Mytilus edulis* for their food requirements, creating the potential for conflict with the human fisheries for these species. During the 1980s, high fishing mortality of the Blue Mussel (hereafter Mussel) stocks led to an almost complete disappearance of Mussel beds in The Wash, with the Mussel fishery closing in 1994. Cockle stocks also collapsed due to a long run of poor recruitment that followed high fishing rates in the 1980s. During that same period, the number of wintering Oystercatchers on The Wash declined by 75%, which was linked to increases in adult mortality.

We use a long-running volunteer-collected dataset to quantify the relationship between survival and winter climatic conditions and Mussel stock data to determine how much of the variation in survival is due to these factors. We also characterise a period of high mortality in the latter part of the 2022/23 winter.

The 1992 Wash Fishery Order led to strengthened management of the shellfisheries in The Wash, allowing a harvest without adversely impacting Oystercatcher survival, which has remained high and relatively stable since these measures were put in place. However, the recent bout of high mortality suggests careful management of stocks is required going forwards.

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