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Decline in the numbers of Eurasian Oystercatchers *Haematopus ostralegus* (L.) on the Exe estuary Special Protection Area

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Abstract: According to the monthly counts of the Wetland Bird Survey (WeBS), the numbers of Oystercatchers *Haematopus ostralegus* (L.) wintering in Great Britain has gradually decreased since the late 1980s/early 1990s. Although numbers also decreased in the South-West region of England, the decline was much steeper in the Exe estuary population, suggesting that site-specific pressures may have affected this species in this regionally-important Special Protection Area. By combining data from the WeBS with those from 45 years of research on Oystercatchers by the Centre for Ecology and Hydrology, we tested five hypotheses that could explain the relative decline on the Exe estuary: (i) a gradual improvement in estimating Oystercatcher numbers as counting methods were refined; (ii) a deterioration in the main food supply, the blue mussel *Mytilus edulis* (L.); (iii) disturbance from people on and alongside the estuary; (iv) disturbance from Peregrine Falcons *Falco peregrinus* (L.); and (v) an as yet unexplained increase in the frequency of stealing of mussels from Oystercatchers ('kleptoparasitism') by Carrion Crows *Corvus corone* (L.) and Herring Gulls *Larus argentatus* (L.). The data are consistent only with the fifth hypothesis. Individual-based modelling suggested that kleptoparasitism at the increased frequency that occurred on the Exe estuary could have reduced the foraging success of Oystercatchers sufficiently to have (i) reduced the overwinter survival of the numerically dominant mussel-eating adults and (ii) deterred prospecting immatures from choosing the estuary as their future wintering site.

Keywords: overwinter survival, inter-specific kleptoparasitism, population decline, food supply, individual-based model

Introduction

The coastal wetlands of Great Britain support large numbers of shorebirds of which wading birds, Charadriiformes, comprise a large and, in conservation terms, a highly significant part (Austin *et al.* 2000). As wetland habitats are subject to many pressures, the Wetland Bird Survey (WeBS) was started in the early 1970s to conduct monthly censuses on about 2000 coastal and inland wetland sites throughout Great Britain, including all the main estuaries (Woodward *et al.* 2019, Frost *et al.* 2021). Amongst other purposes, the data are used to monitor trends in particular sites to compare with regional and national trends to alert conservation authorities to any unusual, site-specific decreases in population. In such cases, 'Alerts' are announced. These are intended as advisory measures, triggering further investigation, and are interpreted with reference to the population dynamics and abundance of the species involved (Leech *et al.* 2002).

Of the six species assessed this way for the Exe estuary Special Protection Area (SPA) in South-west England, Alerts have been triggered for two species, the Eurasian Oystercatchers *Haematopus ostralegu* (L.), a near-threatened species (BirdLife International 2019) and the grey plover *Pluvialis squatarola* (L.) (Woodward *et al.* 2019, Frost *et al.* 2021). Further analysis suggested that only the Oystercatcher decline, which started in the late 1980s /early 1990s, may have been driven by site-specific factors (Woodward *et al.* 2019). As part of a broader management plan for the SPA, measures were taken to reduce the amount of disturbance from people, this being viewed as a likely reason for the relative decline in Oystercatchers (Liley *et al.* 2011).

It is scientifically challenging to identify, with confidence, the cause of a site-specific relative decline in a migratory species, like the Oystercatcher. One explanation is that the breeding success and survival on the breeding grounds and migration staging sites of the birds that winter there have decreased whereas those of birds wintering elsewhere in the region have not. Another explanation is that the conditions in some or all of the other wintering sites within the region have improved whereas those in the site in question have deteriorated: indeed, conditions may have improved in all wintering sites but to a lesser degree in the subject site. Accordingly, in order to identify the cause of a relative decline in one site, it is necessary to conduct a multi-site investigation during the winter as well as through the entire species range during the migration and breeding seasons (Runge *et al.* 2014, Bowgen *et al.* 2022, Morten *et al.* 2022). The difficulty of identifying the cause of a decline in bird numbers in one site when the causes may lie elsewhere and at other times of the annual cycle in a species that ranges over a large geographical area are well illustrated by red knots *Calidris canutus rufa* (L.) of Delaware Bay (Niles *et al.* 2008).

Even if factors elsewhere in the wintering, migration and breeding ranges are implicated in a relative decline, the possibility remains that a deterioration in the site itself has also contributed to the decline: that is, these explanations are not mutually exclusive. However, identifying the likely cause of a suspected deterioration is difficult because there are so many candidate explanations. Also, it is not enough just to show that a deterioration has occurred in the wintering conditions, it is also necessary to demonstrate that it has been sufficient to affect bird numbers through increased mortality, emigration or recruitment.

In the case of Oystercatchers on the Exe estuary, it is unlikely that factors on the breeding grounds and staging sites could explain the relative decline. Oystercatchers overwintering on that estuary migrate and breed over much of the species range in North-west Europe, including Scotland, the Netherlands and Norway (Goss-Custard *et al.* 1982c, Morten *et al.* 2022). It is most improbable that those wintering on the Exe experience very different conditions during the migration and breeding seasons to those to which other birds in the South-west region are subjected.

We cannot so readily dismiss the possibility that improved relative conditions in some estuaries in the South-west England attracted Oystercatchers away from the Exe. As our study illustrates, it requires intensive and long-term research to test even a few of the many potential explanatory hypotheses for just one estuary, let alone several. A minimal list of candidate hypotheses includes several anthropogenic activities (Lambeck *et al.* 1996) along with natural changes in food supply, predation and parasites (Goss-Custard *et al.* 1996a). For wintering Oystercatchers, investigating the food supply alone presents a formidable challenge because it comprises so many components. On the Exe, the diet varies between age-classes and sexes and includes a variety of intertidal macro-invertebrates as well as terrestrial prey, principally earthworms Lumricidae (Goss-Custard & Durell 1983, Morten *et al.* 2022). A change in the numerical density, size-distribution and/or flesh-content (Goss-Custard *et al.* 2006), or in its accessibility to the birds (Zwarts *et al.* 1996a, b), in any one of these food sources could affect Oystercatchers' intake rates and so their chances of obtaining their energy requirements in the time available. Despite years of research, numerous uncertainties about their foraging behaviour and ecology remain (Goss-Custard & Stillman 2022).

We tested five within-site hypotheses that could, at least partially, explain the relatively high rate of Oystercatcher decline on the Exe between the late 1980s/early 1990s and 2014, when the study ended. They were suggested by our local experience and the availability of data with which to test them: : (i) a gradual improvement in estimating Oystercatcher numbers as counting methods were refined; (ii) a deterioration in the main food supply, the blue mussel *Mytilus edulis* (L.); (iii) disturbance from people on and alongside the estuary; (iv) disturbance from Peregrine Falcons *Falco peregrinus* (L.); and (v) an increase in the frequency of stealing of mussels from Oystercatchers ('kleptoparasitism') by Carrion Crows *Corvus corone* (L.) and Herring Gulls *Larus argentatus* (L.). The data are inconsistent with the first four hypotheses but consistent with the kleptopasrasitism hypothesis. Individual-based modelling suggested that kleptoparasitism at the as yet unexplained increased frequency that occurred on the Exe estuary could have reduced the foraging success of Oystercatchers sufficiently to have (i) reduced the survival of those mainly adult, mussel-eating birds that wintered on the estuary and (ii) deterred prospecting immature Oystercatchers from choosing the estuary as their future wintering site.

METHODS

Study area and study period

Most Exe-ringed Oystercatchers occurred within the study area comprising the (i) Exe estuary (Figure 1), (ii) sandy and/or rocky shore along the adjacent coast within 5 km of the estuary, and (iii) fields and recreation grassland within 1-2 km of the coast and estuary (Goss-Custard & Durell 1983).

Research initiated by the Centre for Ecology and Hydrology (CEH) in July 1976 provided the data on foraging behaviour and ecology. In 1976, most overwintering Oystercatchers subsisted on blue mussels (Goss-Custard and Durell 1983). The remainder consumed clams *Scrobicularia plana* (da Costa, 1778), cockles *Cerastoderma edule* (L.), ragworms *Nereis diversicolor* (O.F. Müller, 1776) and winkles *Littorina* spp (Goss-Custard & Durell 1983, Boates & Goss-Custard 1992, Morten *et al.* 2022). Although many mussel-feeders sometimes fed along the coast at low water on spring tides, most fed within the estuary when the low-lying coastal beds were submerged by the receding and advancing tides and throughout low water on neap tides. Accordingly, mussel beds within the estuary provided mussel-feeders, and therefore the majority of the population, with most of their food.

This continued until 2014 when the usually abundant mussels within the estuary had disappeared in parallel with a rapid increase in the Pacific oyster *Magallana gigas* (Thunberg, 1793). Coastal mussels remained abundant, however, whereas mussels within the estuary have not recovered (Davies & Stephenson 2017, Thomas 2019). Oysters are seldom taken by Exe Oystercatchers (Morten *et al.* 2022). Accordingly, this paper considers the winters 1976/77 to 2013/14 during which mussels were the primary food source and most of the decrease in the relative abundance of Oystercatchers occurred.

Testing hypothesis (i): Gradual improvement in estimating Oystercatcher numbers

As accumulating experience and improving optical equipment may have gradually minimised errors in the WeBS counts, it is possible that the relative decline in Oystercatchers may in part reflect improving counting methods. This possibility was tested by comparing WeBS counts with the CEH counts made at low tide during the same spring tide series as the WeBS counts. Whether the magnitude of any difference between the CEH and WeBS counts had changed over time was tested by comparing the magnitude of the difference between them in 67 paired comparisons spread over 45 winters.

The monthly WeBS censuses are carried out throughout Great Britain by teams of volunteers using the methods referred to in (Woodward *et al.* (2019) and Frost *et al.*

(2021). The WeBS data were provided by the British Trust for Ornithology (BTO). They include all the WeBS Core count sites - estuaries, open coast and inland - other than for non-protected sites with less than 50% of available counts, which are routinely excluded from all WeBS indices (Woodward *et al.* 2019). For those sites that are retained, any missing counts are imputed using the algorithm developed by Underhill & Prŷs-Jones (1994).

On the Exe estuary, WeBS counts were made on the advancing tide when birds were in transit to high tide roosts and fields. Counts by different volunteers in different areas were co-ordinated to reduce the chances of double- and under-counting. As accumulating experience and improving optical equipment may have gradually minimised such potential errors, the relative decline in Oystercatcher numbers may in part reflect improving counting methods. This possibility was tested by comparing the counts made by the WeBS and those made by CEH at low tide during the same spring tide series.

All CEH censuses were carried out by the senior author using a x30-60 telescope. The study area was divided into easily-identified patches of habitat - such as a mussel bed, sandy ridge or field - within which all birds could be counted individually from one observation point. Censuses were made within ± 90 min of low water when Oystercatchers moved very little unless disturbed by people or birds of prey: any disrupted count was repeated next day. Recent GPS tracking confirmed that Exe Oystercatchers move least over this part of the exposure period (Morten *et al.* 2022). As one census took up to five days, the net movement of birds may have consistently biased the total either upwards or downwards, but this is unlikely. Counts in one area on adjacent days gave very similar numbers on successive tides. Colour-marked and radio-tracked individuals generally foraged for long periods in the same location

(Goss-Custard *et al.* 1982a, b, Morten *et al.* 2022). Finally, CEH counts at low tide compared very closely with CEH counts at high water at times of year when Oystercatchers congregated in a few easily counted roost sites (Goss-Custard 1981).

CEH counts were made monthly through the winters 1976/77 to 1983/84, called here 'period 1'. Subsequently, counts were made less regularly as other research priorities intervened. Counts were then conducted during two periods; at the beginning of the relative decline in 1989/90-1992/93 ('period 2') and towards the end in 2012/13 and 2013/14 ('period 3').

Testing hypothesis (ii): Decrease in the mussel food supply

This hypothesis is that the feeding conditions within the Exe estuary deteriorated from the late 1980s and early 1990s because of changes in the main mussel food supply. Mussel abundance on the main mussel beds within the estuary was estimated by CEH during a sample of Septembers from 1976 to 2013 using the methods described in McGrorty *et al.* (1990). Since 2012, the Devon and Severn Inshore Fisheries and Conservation Authority have sampled annually the abundance and size distribution of mussels as described by Gray (2012), Davies & Stephenson (2017) and Thomas (2019).

The Exe estuary version (ExeMORPH) of the individual-based model MORPH was used to investigate how the feeding conditions provided by mussels within the estuary changed over the study period. MORPH (Stillman 2008) represents individual birds that use optimisation decision rules to decide how to obtain most rapidly their daily energy requirements which, in the model as in reality, depend on the ambient temperature. Individuals vary in their competitive ability, and each bird takes into account the decisions made by competitors in deciding when (night or day), where (which shellfish bed) and on what (mussels or alternative prey species) it should feed. Because shellfish are particularly profitable for wintering Oystercatchers (Zwarts *et al.* 1996a), model birds first attempt to obtain their requirements from shellfish, but should they fail to do so, they eat other intertidal invertebrates or terrestrial prey, such as earthworms (Lumbricidae). Once an individual has obtained its current daily energy requirements, it stores subsequent consumption as fat up to a daily limit. A bird uses its fat reserves if it fails to obtain its requirement from current foraging. It starves to death if its body reserves fall to zero. Simulations ran from 1 September to 15 March when the numbers of birds that had starved was calculated.

The first version of ExeMORPH was calibrated to predict the observed overwinter mortality rate of mussel-eating adults for the ‘calibration’ winters 1976/77 to 1979/80 when there were, on average, 1550 Oystercatchers (Stillman *et al.* 2000a). It correctly predicted the increased mortality rate that accompanied the increase in population size over the ‘validation’ winters of 1980/81 to 1983/84 and 1988/89 to 1990/91. However, ExeMORPH did not accurately predict mortality rates in birds using different methods to open mussels. Accordingly, ExeMORPH was updated in two ways. First, some parameter values in ExeMORPH that described the foraging behaviour of Oystercatchers were changed to take into account research carried out since 2000. Second, a ‘calibration coefficient’ was introduced that adjusted the intake rates of model birds so that the predicted mortality rates during the calibration winters coincided with observed rates. The development of the calibration procedure and the revised parameter values used in ExeMORPH are detailed in the Supplemental Material 1. As well as better predicting the difference between age-classes and birds using different feeding methods, this version predicted that the overall mortality rate of adult birds – by far the largest age-class of birds in the population - over the validation years would be 1.94 times the rate during the calibration years. As this compared well with the observed increase of 1.88, it was believed that this new version of ExeMORPH could be used with increased confidence.

The quality of the main mussel food supply was measured in terms of the survival rate it enabled Oystercatchers to achieve taking into account their ability to supplement their mussel consumption with other prey species upshore and in fields when the mussel beds were submerged by the tide. Predictions were based on the September surveys of each of the ten main mussel beds of the numerical density and size distribution of mussels 30 – 60 mm long, the size range most consumed by Exe Oystercatchers (Cayford & Goss-Custard 1990). For period 1 (winters 1976/77 to 1983/84), ExeMORPH was parameterised with data averaged over all eight years (Stillman *et al.* 2000a). For period 2 (winters 1989/90 to 1992/93), data were available for only winter 1992/93: it is unlikely that mussel abundance varied much between the winters either side of that winter (Stillman *et al.* 2000c). For period 3 (2012/13 and 2013/14), mussels were sampled for winter 2013/14 (Stillman *et al.* 2015). As the purpose of the simulations was to measure the quality of the mussel food supply, kleptoparasitism did not occur in these simulations and Oystercatcher numbers were held constant at 1561 birds, the average size across the three periods. The population comprised 90% adults and 10% immatures in their second to fourth winters (Stillman *et al.* 2000a).

Testing hypothesis (iii): Disturbance by people

The hypothesis is that increasing disturbance from people on and alongside the estuary during the exposure period and at the roosts and foraging sites used over high tide increased the energy requirements of the birds while reducing the amount of time they had in which to obtain their food. Although seldom disturbed at night (Sitters 2000), Exe Oystercatchers can be disturbed by people at any time during the tidal cycle. People on the main mussel beds were routinely counted during the CEH censuses at low water but not in other intertidal habitats and at other stages of the tidal exposure period and alongside the estuary. However, an intensive study of disturbance in all habitats and at all stages of the exposure period on and alongside the entire estuary was carried out in daylight during the second half of the decline (winters 2009/10 to 2017/18). This allowed the energy and time costs resulting from disturbance to be estimated and the significance for Oystercatcher survival to be evaluated (Goss-Custard *et al.* 2020). Oystercatchers are also disturbed by people over high water at their main roosts on Dawlish Warren Nature Reserve at the mouth of the estuary. They can also be disturbed in fields and recreational grassland in a number of sites around the estuary. As systematic observations on the frequency of disturbance over high water were not made, we evaluated whether the gradual introduction of more conservation measures that reduced the frequency with which Oystercatchers were disturbed over high water affected the relative rate of decline in their numbers.

Testing hypothesis (iv): Disturbance by Falcons

Although no Oystercatchers were seen killed by Peregrine Falcons, the disturbance they caused when hunting on the estuary during the exposure period may have increased the energy requirements of Oystercatchers while reducing the amount of time they had in which to obtain their food. Peregrine Falcons were seldom seen over the estuary in the late 1970s. However, one or two overwintered over much of the period of the relative decline in Oystercatcher numbers. Accordingly, the frequency of 'scares' caused by raptors – which were always Peregrine Falcons in that majority of occasions when the raptor could be identified - was recorded during studies by Stillman & Goss-Custard (2002) for the winters 1994/95 and 1995/96 and by Goss-Custard *et al.* (2020) for winter 2013/14.

Testing hypothesis (v): Kleptoparasitism by Carrion Crows and Herring Gulls

A noticeable change in the Exe estuary since 1976 was the increase in Carrion Crows on the mussel beds and the greater frequency with which they attacked Oystercatchers to steal mussels (Stillman *et al.* 2015, Wood *et al.* 2015). Herring Gulls also kleptoparasited Oystercatchers but only in recent years. As the number of Gulls was not counted, the magnitude of the increase in kleptoparasite abundance can only be illustrated using Crows which were first included in the low-tide censuses during winter 1979/1980.

Using the methods described in Goss-Custard & Durell (1988), the percentage of mussels found by focal Oystercatchers stolen by kleptoparasites was estimated from samples of 5-minute observations on individual Oystercatchers. These data were obtained on some of the main mussel beds throughout the exposure period on spring and neap tides during the winters of 1982/83, 1983/84, 1993/94 and 1994/95 and so either within or close to periods 1 and 2 before the relative decline in Oystercatcher numbers had begun. For period 3, the frequency of kleptoparasitism was measured throughout the winter on all the main mussel beds during the winter 2013/14 (Wood *et al.* 2015).

ExeMORPH was used to test whether kleptoparasitism at the observed rates could have reduced the intake rate of mussel flesh by Oystercatchers sufficiently to have reduced their overwinter survival rates. Intake rate in shorebirds is measured as the biomass of flesh consumed per unit time, the usual metric being mgAsh-Free Dry Mass (AFDM)/s (Zwarts *et al.* 1996a). With no kleptoparasitism, the interference-free intake rate of an Oystercatcher (*IFIR*) in mgAFDM/s is:

$$IFIR = na/t_{nk} \qquad (1)$$

where n is the number of mussels opened and consumed over t_{nk} secs with no kleptoparasatism and a is the mgAFDM of the average consumed mussel.

In order to calculate the amount by which a given frequency of kleptoparasitism reduced the intake rate of Oystercatchers, we assumed that Crows and Gulls stole mussels immediately an Oystercatcher opened the mussel and so before it had begun to consume the flesh. This would be expected if the kleptoparasite attempted to gain the maximum reward from stealing a mussel and was also consistent with observation.

The reduction in average intake rate due to mussels being stolen from an Oystercatcher was calculated using data obtained by Sitters (2000) on bed 20 (Table 1), one of the main mussel beds within the Exe estuary. Sitters measured from video the time taken by an Oystercatcher to search for, open and successfully consume one mussel from the end of one handling time to the end of the next. This ‘search-handling sequence (SHS)’ included the aggregate of all the time spent on failed attempts to open mussels - the ‘waste handling time’ – as well as brief periods spent on other non-searching activity, such as preening and agonistic behaviour: these activities had also been included in the time intervals over which intake rate had been measured in all the studies of intake rate on the Exe estuary (Goss-Custard *et al.* 2006). The final phase of an SHS was the time taken by the Oystercatcher to extract the flesh, the ‘Gross Eating Time’ (*GET*), timed from the moment that the first piece of flesh was visible on the video until the handling time had finished and the bird had resumed searching. Accordingly, the time spent on an unsuccessful search-handling sequence (t_u) terminated by the theft of the mussel was the duration in seconds of the average successful SHS sequence (t_s) *minus GET*:

$$t_u = t_s - GET \qquad (2)$$

Intake rate when kleptoparasitism occurs (*IR*) is:

$$IR = (1 - p)na / t_k \qquad (3)$$

where p is the proportion of mussels opened by the Oystercatcher that were stolen by a kleptoparasite before the flesh could be swallowed, n is the number of mussels opened over t_k secs during which kleptoparasitism occurred and a is the mgAFDM of the average consumed mussel.

When kleptoparasitism occurs, t_k is:

$$t_k = (1 - p)\mathrm{nt}_\mathrm{s} + pnt_u \qquad (4)$$

Accordingly, when kleptoparasitism occurs, intake rate is:

$$IR = (1 - p)na) / ((1 - p)nt_\mathrm{s} + pnt_u) \qquad (5)$$

Which, by dividing by n throughout, simplifies to:

$$IR = (1 - p)a) / ((1 - p)t_\mathrm{s} + pt_u) \qquad (6)$$

Since $t_u = t_s - GET$, equation (6) simplifies to:

$$IR = (1 - p)a / (ts - p\ GET) \qquad (7)$$

In ExeMORPH, the intake rate of an individual Oystercatcher is calculated from a functional response based on a review of intake rates in shorebirds (Goss-Custard *et al.* 2006). An equation predicts the intake rate of the average bird on a given mussel bed at a given time step from the numerical density and mean AFDM of the mussels within the preferred size range of 30 - 60mm long. As birds differed in their foraging efficiency, each individual in the model is ascribed a baseline foraging efficiency (FE), in which the value 1 equates with the intake rate of an average bird predicted by the functional response in the absence of kleptoparasitism. Each bird is ascribed at random a value for its baseline FE from a range of ±15% in stabbers and ±10% in hammerers from the coefficient of variation established in field studies on the Exe estuary (Stillman *et al.* 2000a). In the absence of kleptoparasitism, therefore, the predicted intake of an individual bird in the model is the product of the predicted intake of an average bird obtained from the functional response equation and its FE. In the presence of kleptoparasitism, its predicted baseline intake rate is multiplied by the ratio IR/IFIR. Since:

$$IFIR = a / t_s \qquad (8)$$

$$IR/IFIR = (1 - p)t_s / (t_s - p\,GET) \qquad (9)$$

By dividing numerator and denominator by t_s, this simplifies to:

$$IR/IFIR = (1 - p) / (1 - p\,GET/t_s) \qquad (10)$$

This ratio measures the proportionate reduction in intake rate due to kleptoparasitism at a given rate of p: the mean of the (very similar) values for adults and immatures was 0.91, 0.82 and 0.73 for rates of stealing of 10%, 20% and 30% respectively. As interspecific kleptoparasitism was not seen during 74 h of observations on focal Oystercatchers at night (Sitters 2000), kleptoparasitism only occurred when model birds were foraging in daylight.

Statistical analyses

The statistical software used for linear regression, general linearised modelling (GLM) and t-tests was Minitab, release 13 (www.minitab.com).

RESULTS

Relative decline in Oystercatchers

WeBS indices for Oystercatchers for the Exe estuary and South-west region decreased from the late 1980s/early 1990s until about 2010 (Figure 2A). Over that time, the ratio between the WeBS annual indices for the Exe and the South-west also declined and may have continued to do so until 2017/18, the last winter for which indices were available (Figure 2B). Relative to the numbers in the South-west, Exe Oystercatchers decreased steadily from the late 1980s.

Hypothesis (i): Gradual improvement in estimating Oystercatcher numbers

The numbers of Oystercatchers recorded by WeBS were broadly similar to those recorded by CEH apart from the late 1980s and early 1990s when the CEH counts were consistently below the WeBS counts made in the same winters (Figure 3). This raised the possibility that the WeBS counts over-estimated numbers at the time of peak population. If so, it would have exacerbated the magnitude of the subsequent relative decline in Oystercatcher numbers measured by the WeBS.

This possibility was tested by comparing winter counts made by CEH and WeBS in the same month and winter. As described in Supplemental Material 2, several steps were made in reaching the key comparisons shown in Figure 4. These show that the percentage difference between the CEH and WeBS counts did not change either with population size (Figure 4A) or over the duration of the study period (Figure 4B). Accordingly, there is no reason to believe that the WeBS data either exaggerated or under-estimated the rate of decline in Oystercatcher numbers over recent decades.

Hypothesis (ii): Decrease in the mussel food supply

From winters 1976/77 to 1992/93 (periods 1 and 2) before the relative decline in Oystercatcher numbers occurred, 75 - 85% foraged on mussel beds over low tide (Table 2). By period 3, the surface area occupied by mussels 30 – 60mm long had decreased and, although their numerical density was not notably reduced, their average size had greatly increased (Table 3). The intake rate of mussel-feeding Oystercatchers depends more on the mean flesh-content, and therefore size, of the mussels than on their numerical density (Goss-Custard *et al.* 2006). Accordingly, ExeMORPH predicted that the starvation rate of Oystercatchers over the winter was marginally lower during period 3 than during period 2 and substantially lower than during period 1 (Table 4). (That it was the increase in the average length, and therefore average flesh-content, of mussels that mainly caused this improvement in the feeding conditions was tested with additional simulations with ExeMORPH, (Supplemental Material 3). The evidence suggests that, rather than deteriorating, the feeding conditions provided by mussels improved marginally over the period of the relative decline. Indeed, the improvement in feeding conditions may have been even larger than indicated in Table 4: in those simulations, the flesh-content of mussels of each length were assumed to be the same in all three periods yet, in fact, they may have increased (Supplemental Material 4).

Hypothesis (iii): Disturbance from people

During the exposure period

Foraging Oystercatchers were subject to disturbance in a number of places from people in the intertidal zone and on sea walls alongside (Goss-Custard *et al.* 2020).

The numbers of people at low water on the main mussel beds of the estuary – the main source of disturbance during the exposure period - increased 3.26-fold between the winters prior to the decline (period 1) and the winters over which the decline occurred (periods 2 and 3) (Table 5). Although this result is consistent with the disturbance hypothesis, intensive research during the second decade of the decline suggested that disturbance by people in the intertidal zone and alongside the estuary would have had a small impact on the birds: the total time and energy costs were equivalent to 0.21% and 0.05%, respectively, of the daylight foraging time and energy requirements of the average bird (Goss-Custard *et al.* 2020). Accordingly, the evidence suggest that it is most unlikely that disturbance over the tidal exposure period contributed to the relative decrease in Oystercatcher numbers.

Over high water

The time- and energy-costs of disturbance over high water when Oystercatchers occur inland have not been estimated. However, conservation measures were introduced which, in effect, provided an experimental test of the hypothesis that disturbance over high water contributed to the relative decline in Oystercatcher numbers. In 1976, disturbance regularly caused Oystercatchers to leave Dawlish Warren to roost on a military firing range 4.5 km eastwards along the coast. This and similar disturbances prompted the establishment of a nature reserve on Dawlish Warren in 1980, and the appointment of a reserve warden, part of whose job was to discourage visitors from disturbing roosting shorebirds. Over subsequent years, a series of additional measures were introduced: (i) restricting access to the principal roosting sites with signs and fencing; (ii) constructing an elevated and well-protected roost site and associated hide in 1986, and (iii) appointing in 1993 a warden whose main task was to prevent people from disturbing roosting shorebirds, particularly in winter. One of the main sites for winter terrestrial foraging by Oystercatchers, a mini-golf course alongside the west side of the estuary, was also converted to a winter refuge for shorebirds and has subsequently been much used by Oystercatchers. Despite all these measures, the relative decline in Oystercatchers on the Exe estuary continued (Figure 2B). Accordingly, the data are inconsistent with the hypothesis that disturbance of Oystercatchers over high water contributed to their relative decline.

Hypothesis (iv): Disturbance by Peregrine Falcons

Oystercatchers were disturbed into flight – ‘scares’ - by over-flying Falcons when foraging on the mussel beds at low water and on the upshore flats at the beginning and end of the exposure period when the mussel beds were submerged. No data are available for the number of scares that occurred inland over high water. The details of the calculations of the frequency of disturbance caused by Peregrines over the exposure period are given in Supplemental Material 5.

The foraging time lost and extra energy expended by Oystercatchers when responding to Falcons was not measured but, as with disturbance by people, both would have been trivial. For an Oystercatcher to lose just 1% of its potential foraging time in the intertidal zone during a 24 h period, its flight response would have to have been 16 times longer than that caused by human disturbance (Table 6). To have increased the energy requirements per 24 h by just 1%, the cost of a single disturbance would have to have been 32 times higher than that caused by a human disturbance (Table 6). Even if (i) the frequency of disturbances by Peregrines Falcons did indeed increase during the years of the relative decline – which is not known – and (ii) even if overflying Falcons did reduce the foraging efficiency of Oystercatchers as hypothesised by

Quinn (2008), the costs in energy and time would have to have been very much higher to have had a significant impact on Oystercatchers.

Hypothesis (v): Kleptoparasitism by Carrion Crows and Herring Gulls

The best predictor of the frequency of kleptoparasite attacks is the number of kleptoparasites/Oystercatcher (Wood *et al.* 2015). This ratio increased 3.8-fold in period 3 compared with periods 1 and 2 (Table 7). The percentage of mussels stolen by kleptoparasites increased 30-fold between periods 1 and 2 and period 3 (Table 8). Exe Oystercatchers were most likely to starve during November-March (Stillman *et al.* 2000a). During those months in 2013/14, 15% - 36% of the mussels opened by Oystercatchers on the main mussel beds during daylight were stolen by kleptoparasites (Wood *et al.* 2015). Simulations with ExeMORPH suggested the starvation rate of Oystercatchers would increase over the kleptoparasitism range of 0 – 30% in all three periods modelled (Figure 5A) by 3.47-fold ($se = \pm 0.41$, $n = 3$) in immatures and 3.50-fold ($se = \pm 0.11$, $n = 3$) in adults (Figure 5B). The mortality rate was density-dependent in both immatures and adults (Figure 6). Interspecfic kleptoparasitism therefore had the potential to increase the winter mortality rate of Oystercatchers over the years of their relative decline in numbers.

DISCUSSION

The numbers of Oystercatchers wintering on the Exe estuary has declined since the late 1980s at a rate that exceeded the South-west regional rate of decline. Simultaneously, they decreased as a proportion of the region’s total from approximately 60% to 35% (Woodward *et al.* 2019). This implies a decrease in carrying capacity, *sensu* Goss-Custard (2017), relative to sites elsewhere in the region.

Although the capacity of Exe may have remained constant while improving elsewhere in the region, we could not test this hypothesis. We could only test whether changes in the condition of the estuary itself might have contributed to the relative decline, and many such changes can be postulated.

From Goss-Custard *et al.* (1996a) and Goss-Custard & Stillman (2022), a minimal list for the feeding conditions alone includes: (i) a deterioration due to changes in the accessibility, numerical density, mean body size, calorific density, nutrient content and digestibility of one or more of the several prey species consumed by primarily shellfish-eating Oystercatchers; (ii) an increased risk from damaging internal or external parasites obtained from one or more prey species, and (iii) an increased frequency of being disturbed or taken by predators on the estuary and fields. Based on experience since 1976, four hypotheses emerged as contenders: (i) deterioration in the main blue mussel (*Mytilus edulis* (L.) food supply; (ii) disturbance from people; (iii) disturbance from Peregrine Falcons,and (iv) increase in kleptoparasitism of mussels by Carrion Crows and Herring Gulls. The empirical evidence was strongly *contra* to the first three hypotheses but consistent with the fourth.

Individual-based modelling suggested that kleptoparasitism at the frequency occurring during the winter 2013/14 could have reduced the foraging success of mussel-eating Oystercatchers sufficiently to have reduced their winter survival. Indeed, the impact could have been even greater for two reasons. First, in intra-specific kleptoparasitism, the intake rate of subdominant Oystercatchers is suppressed partly because they lose mussels to dominant individuals but mainly because they capture fewer mussels in the first place (Ens & Cayford 1996). Stealing accounts for only 20% of the reduction in intake rate in sub-dominants, the remaining 80% probably being due to sub-dominants avoiding dominants and being displaced from feeding spots. This is very likely to be true of inter-specific kleptoparasitism because most Oystercatchers lost most encounters against Crows and Gulls and were therefore sub-dominant to them (Wood *et al.* 2015). Accordingly, the effect of inter-specific kleptoparasitism on Oystercatcher survival could have been much greater than the simulations suggest. This could not be tested by modelling because there are no estimates of the parameters of the interference functions relating intake rate in Oystercatchers to the densities of Crows and Gulls. Second, and again by analogy with intra-specific kleptoparasitism, it is likely that much of the inter-specific kleptoparasitism was directed at particularly vulnerable individuals, in the same way that intra-specific interference particularly disadvantages sub-dominants (Stillman *et al.* 2000b). If so, the impact of kleptoparasitism on the mortality rate of that vulnerable section of the Oystercatcher population would be much higher than current simulations suggest.

Individual-based modelling is highly appropriate for testing hypotheses on the cause of such population declines because it yields quantitative predictions in novel circumstances based on tested assumptions derived from evolutionary thinking on how birds respond to environmental change (Goss-Custard & Sutherland 1997; Stillman *et al.* 2000a, Stillman & Goss-Custard 2010). Although the simulations suggest that the rates of kleptoparasitism before the mussel population collapsed in 2014 was sufficient to have reduced the overwinter survival in both adult and immature Oystercatchers by up to three or four-fold, we cannot estimate its impact at different stages of the relative decline: all we know is that it was low at the start and high towards the end. The potential impact of kleptoparasitism on Oystercatcher survival was actually greatest during period 1, before the relative decline had begun, because the feeding conditions were at their least favourable then and Oystercatcher densities were high: however, kleptoparasitism was infrequent at that time. The simulations predicted that, in period 2, at the start of the relative decline, losing 30% of mussels to kleptoparasites would have increased the winter mortality rate by about 1.85% in adults and 6.55% in immatures but, on the one mussel bed studied at that time, the rate of kleptoparasitism was low and the rates elsewhere are unknown. By period 3, much of the decline in Oystercatchers had already occurred and the improved feeding conditions on the mussel beds led to the prediction that losing 30% of mussels to kleptoparasites would have increased the winter mortality rate by only 0.54% in adults and 2.44% in immatures. It is therefore not at all self-evident that kleptoparasitism would have had a significant impact on Oystercatcher survival at every stage of the relative decline.

On the other hand, the increase in mortality would not have to be large to cause a relative decline in numbers. First, the wintering population decreased between periods 2 and 3 by 491 birds from 1835 to 1344 (Table 7). Across the 25 winters from 1989/90 to 2013/14, the average annual reduction was 19.6 birds, equivalent to 1.23% of the average population over the decline of 1590 birds per winter. As the regional index decreased by 10% from 118 in period 2 to 106 in period 3, the extra decline on the Exe amounted to 1.1% per year. Second, population size in long-lived birds can be reduced by even small absolute increases in the mortality rate of adults (Croxall & Rothery 1991; Goss-Custard *et al.* 1996b, Atkinson *et al.* 2003, Saether & Bakke 2000, Sandercock 2003, Miles *et al.* 2015). For example, just a 2% increase from 6% to 8% in the adult annual mortality rate of Oystercatchers could reduce equilibrium population size to 30% or 62% of its previous level, depending whether the density dependence in recruitment in summer is, respectively, weak or strong (Goss-Custard *et al.* 1996b).

There are no data to establish at which point during the relative decline that kleptoparasitism began to increase significantly. It would have depended on the quality of the mussel food supply, on the density of Oystercatchers and on the numbers of kleptoparasites and on their behaviour at each stage of the decline, none of which are known. The numbers of Crows on the mussel beds increased approximately three or four-fold from periods 1 and 2 to period 3. Assuming the numbers of Crows in the vicinity of the Exe estuary reflected the approximately 40% increase in the England breeding population over this period (BTO's Trend Explorer: https://data.bto.org/trends_explorer/?species=Carrion+Crow), the 10-fold increase in the rate of mussel-stealing on the Exe mussel beds may suggest that individual Crows – and presumably Herring Gulls - increasingly employed theft to obtain mussels. Currently, we cannot explain how this increase occurred in either species. Nor are the data available with which to test our implicit assumption that the rate of kleptoparasitism of Oystercatchers was particularly high on the Exe estuary compared with other estuaries in the South-west region of England. This uncertainty is another reason why the kleptoparasitism hypothesis advanced in this paper should be regarded as a tentative suggestion at this stage in our knowledge.

It is also very likely that the relative decline was not primarily caused by an increased mortality rate but by increased emigration or by decreased immigration. MORPH does allow for birds to emigrate, with a starving bird leaving the population when its fat reserves reach 8% of its total body weight (Goss-Custard *et al.* 1996c), the value at which Oystercatchers leave the Wadden Sea in severe winter weather (Hulscher 1989, 1990). However, it makes little difference to predicted carrying capacity whether it is achieved through starvation or emigration (Goss-Custard & West 1997), so emigration and mortality are inter-changeable in our simulations.

It is much more likely, however, that the relative decline was partly, perhaps largely, caused by a reduction in the recruitment of young birds to the Exe. The recruitment of prospecting sub-adults seems to be the most likely means by which the numbers of waders adjust to any changes in the relative feeding conditions across wintering sites (Goss-Custard *et al.* 1977, Sutherland 1982, Gunnarson *et al.* 2005). In support of this notion, GPS tracking revealed that sub-adult Oystercatchers on the Exe had larger home ranges and were more likely to explore areas outside of the estuary than mature individuals and therefore seem more likely successfully to find alternative foraging and wintering areas (Morten *et al.* 2022). Accordingly, young and inexperienced Oystercatchers prospecting for an area in which to spend their future winters would be less likely to settle on a site where they had difficulty in meeting their food requirements and would move on to find a site with better feeding conditions.

Inter-specific kleptoparasitism has not previously been identified as a factor likely to affect the numbers of a wader species wintering in an area. Ens & Cayford (1996) conclude that the amount of food lost to kleptoparasites differs widely between studies and that, in many, the amount of food lost is very low or not even reported, implying that it was negligible. Whereas the potential significance of kleptoparasitism for the population size of target species of seabirds has been realised for many years (Phillips *et al.* 1996), most attention in waders has focussed on the efficacy of kleptoparasitism as a foraging strategy (Thompson 1983, 1986, Thompson & Barnard 1984, Thompson & Lendrem 1985, Flower *et al.* 2012). We present our findings on the possible significance of inter-specific kleptoparasitism to the over-winter survival of Oystercatchers as no more than an interesting and potentially very credible hypothesis to which other researchers might give further consideration.

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TABLES

Table 1. The duration of the search-handling sequences (SHS) and gross eating time (GET) in Oystercatchers opening mussels with the three techniques predominating on the Exe estuary. Unsuccessful SHS = successful SHS *minus* GET From Sitters (2000).

Mussel-opening method	Successful SHS (s)			GET (s)			Unsuccessful SHS (s)
	Mean	± *se*	*n*	Mean	± *se*	*n*	
Stabbing	311	30.0	29	34	3.4	39	277
Ventral hammering (VH)	284	25.9	35	39	3.9	40	245
Dorsal hammering (DH)	269	25.0	20	56	4.0	23	213
Average of VH and DH	276.5			47.5			229

Table 2. The total numbers of Oystercatchers recorded in *n* monthly winter (late September to January) counts during periods 1 and 2, with the percentages occurring along the coast and on the mussel beds within the estuary. The final column is the sum of the preceding two columns.

Period	*n*	Oystercatchers	± *se*	% within estuary	± *se*	% on coast	± *se*	% on mussels
1 (1976/77 to 1988/89)	22	2580.1	49.3	66.8	1.94	8.9	1.19	75.7
2 (1989/90 to 1992/93)	6	2841.8	97.4	71.7	2.85	10.7	2.67	82.4

Table 3. The mussel food supply within the Exe estuary during periods 1, 2 and 3 and the predicted rate of starvation in a population of 1561 of Oystercatchers, of which 90% were adults. *n* is the number of Septembers in which the mussels were sampled; *Area* is the combined surface area of all the mussel beds; *Density* is the total numbers of all the mussels 30 - 60mm long on all beds combined divided by the total area of mussels; *Size* is the total length-related ash-free dry weight (g) of all the mussels 30 - 60mm long on all beds combined divided by the total number of mussels. The starvation rates are the percentages of the population in September that starve by March 15th.

Period	*n*	Area (ha)	Density (mussels/m^2)	Size (gAFDM)	Adults (%) ± se	Imms (%) ± se (2nd – 4th winter)
1	8	61.2	342.9	0.575	2.26 0.067	7.55 0.429
2	1	94.8	275.4	0.647	0.51 0.034	1.88 0.233
3	1	47.4	318.6	0.809	0.27 0.027	1.18 0.186

Table 4. General linear model of the winter starvation rates for period 1 in adult and immature Oystercatchers as predicted by ExeMORPH. The surface area covered by mussels on all the main mussel beds combined, the numerical densities of each 5 mm length-class and the flesh-content of mussels 30 – 60 mm long on each mussel bed were varied, one at a time, by a factor ranging from 1.0125 to 1.25. Bird age was represented by a dummy 0/1 variable, with immatures = 0.

Source	*df*	*F*	*P*
Age	1	354.93	<0.001
Area (ha)	1	1.10	0.300
Density (mussels/m^2)	1	7.97	0.007
Size (gAFDM)	1	84.32	<0.001
Error	41		
Total	45		

Table 5. The mean number of people on the main mussel beds over low water on spring tides during the winter periods 1, 2 and 3. The period 2 and 3 means are not significantly different (t = 1.52, P = 0.163) but their combined mean differs from that in period 1 (t = 4.17, P = 0.000).

Winters	Number of counts and winters		Mean people	se
Period 1 1976/77 to 1983/84	30	8	2.13	0.49
Period 2 1989/90 to 1992/93	16	4	7.50	1.24
Period 3 2012/13 & 2013/14	4	2	4.75	1.31
Periods 2 and 3 1989/90 to 2013/14	20	6	6.95	1.05

Table 6. The costs in foraging time and energy to Oystercatchers disturbed by over-flying Peregrine Falcons. The percentage costs per 24 h in foraging time and energy from disturbance by people are from Goss-Custard *et al.* (2020). The average daily costs incurred because of Falcons disturbances is 1.76 times those caused by people and are shown in column 3. The final column shows by how much the costs caused by a Falcon scare would have to exceed that caused by a person if the time available for foraging per 24 h was to be reduced by 1% and the bird's daily energy requirements per 24 h was to be increased by 1%; *i.e.* 1 over column 3.

Cost of being disturbed	By people (%)	By Peregrines (%)	Factor needed to reach 1%
Foraging time lost by the average bird as a % of two 9 h exposure periods per 24-h	0.0356	0.0627	16
Energy spent flighting as a % of 24-h requirements	0.0177	0.031	32

Table 7. The mean numbers of Oystercatchers, Carrion Crows and Carrion Crows per Oystercatcher on the main mussel beds at low water on spring tides. The difference between periods 1 and 2 in the mean numbers of Crows/Oystercatcher was not significant ($t = 0.70$, $P = 0.487$) but their combined mean ± *se* of 0.0419 ± 0.0039 ($n = 35$) was significantly different from the means for period 3 ($t = 4.27$, $P = 0.005$).

Winters	Period	*n*	Oystercatchers ± *se*		Carrion Crows ± *se*		Crows/Oystercatcher ± *se*	
1979/80 to 1983/84	1	19	1502.8	44.4	56.6	7.39	0.0394	0.0057
1989/90 to 1992/93	2	16	1835.4	67.4	77.2	7.79	0.0449	0.0052
2012/13 and 2013/14	3	7	1344.0	102.0	204.1	33.2	0.1527	0.0256

Table 8. Percentage of mussels found by focal Oystercatchers that were stolen by kleptopartasites, mainly by Carrion Crows in periods 1 and 2, but also by Herring Gulls in period 3. In periods 1 and 2, so few mussels were stolen by Herring Gulls that the occasional theft by Gulls was included with those stolen by Crows. The difference between the total percentages stolen during the two groups of winters was significant: *t* = 5.64, *P* = 0.011.

Winters	Closest period	Mussel beds	Mussels found	% stolen by Crows	% stolen by Gulls	Total % stolen
1982/83 & 1983/84	1	3 & 4	768	<0.65	Negligible	0.65
1982/83 & 1983/84	1	3 & 4	674	<0.74	Negligible	0.74
1993/94 & 1994/95	2	20	245	<0.41	Negligible	0.41
1993/94 & 1994/95	2	20	1207	<0.33	Negligible	0.33
Mean (± *se*)	1 and 2					0.53 (± 0.10)
2013/14	3	3 & 4	315	13.0	8.3	21.3
2013/14	3	20	129	15.5	3.9	19.4
2013/14	3	22 - 28	81	7.4	1.2	8.6
2013/14	3	30 & 31	187	8.0	8.0	16.0
Mean (± *se*)	3					16.3 (± 2.8)

FIGURES

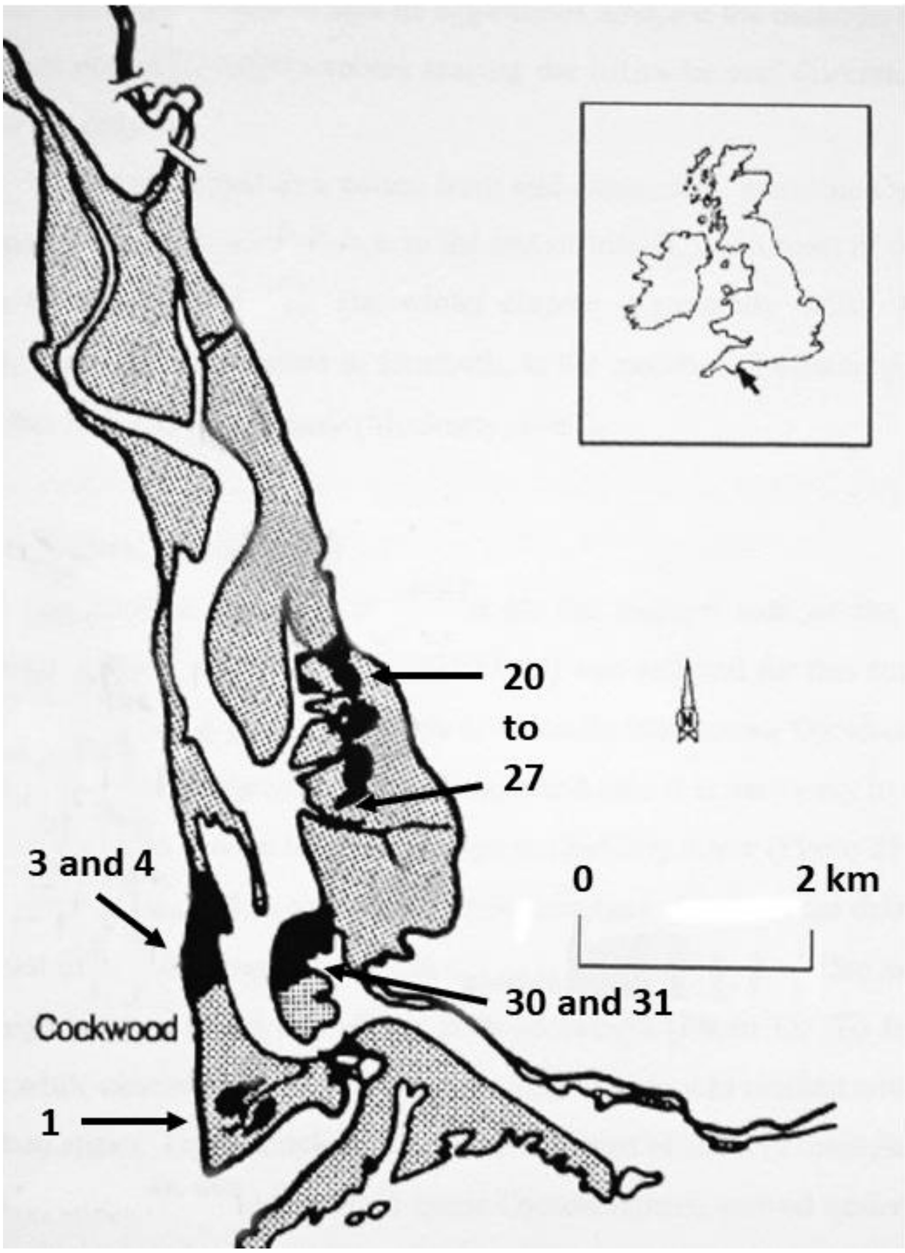

Figure 1. The Exe estuary and the adjacent coast showing the main features mentioned in the text. The black areas are the main mussel beds within the estuary, their individual idenification numbers being shown by the arrows. The shaded area shows the intertidal zone exposed at low water on spring tides. The locations of the

main high water roost on Dawlish Warren at the mouth of the estuary is shown by the star.

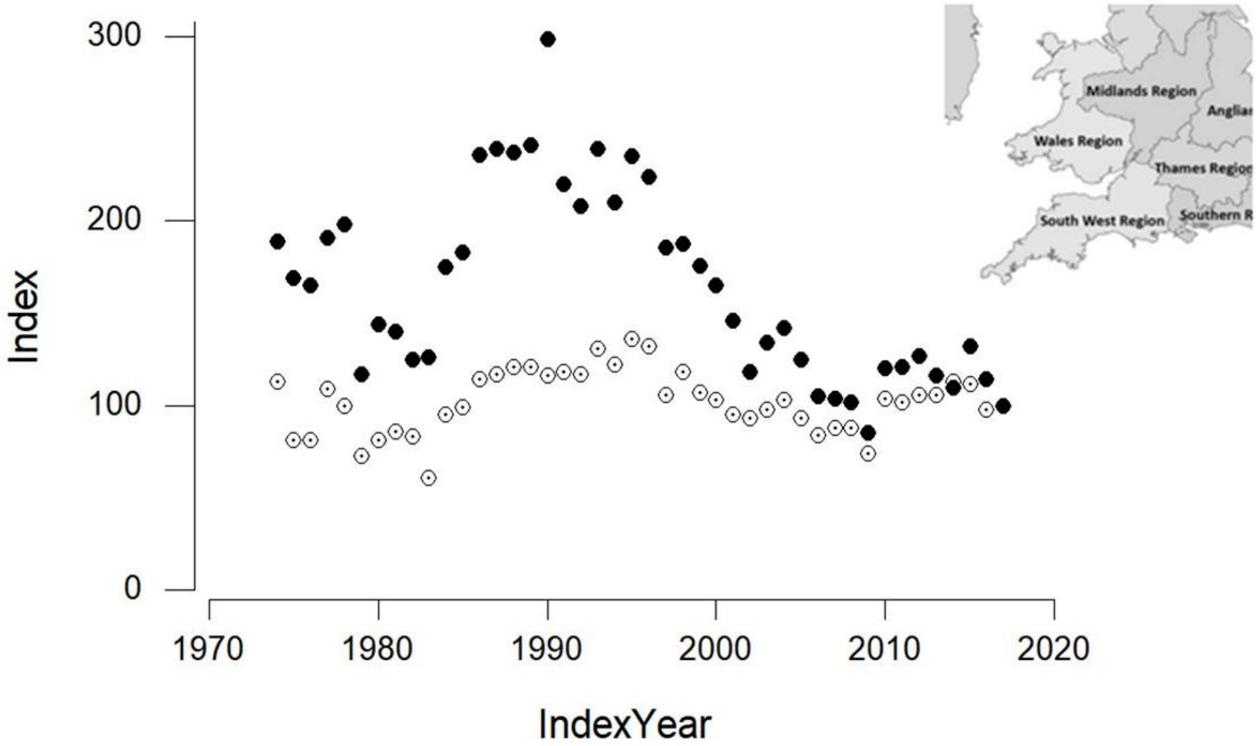

Figure 2A. The WeBS annual indices for Oystercatchers on the Exe estuary (closed symbols) and for the South-west region as a whole (open symbols). The index year is 2017. The polynomial expressions for the 44 years are: for the Exe index ± *se*: 64525365 ± 27002134 + 96693Year ± 40596 – 48.30Year^2 ± 20.34 + 0.008041Year^3 ± 0.003398, R^2(adj) = 50.1%, P = < 0.001, and for the South-west region index ± *se*: -168244 ± 65981 + 168.59Year ± 168.59 – 0.04221Year^2 ± 0.01657, R^2(adj) = 10.5%, P = 0.038. The inset shows the area included within the South-west region, as defined by the Environment Agency (2014).

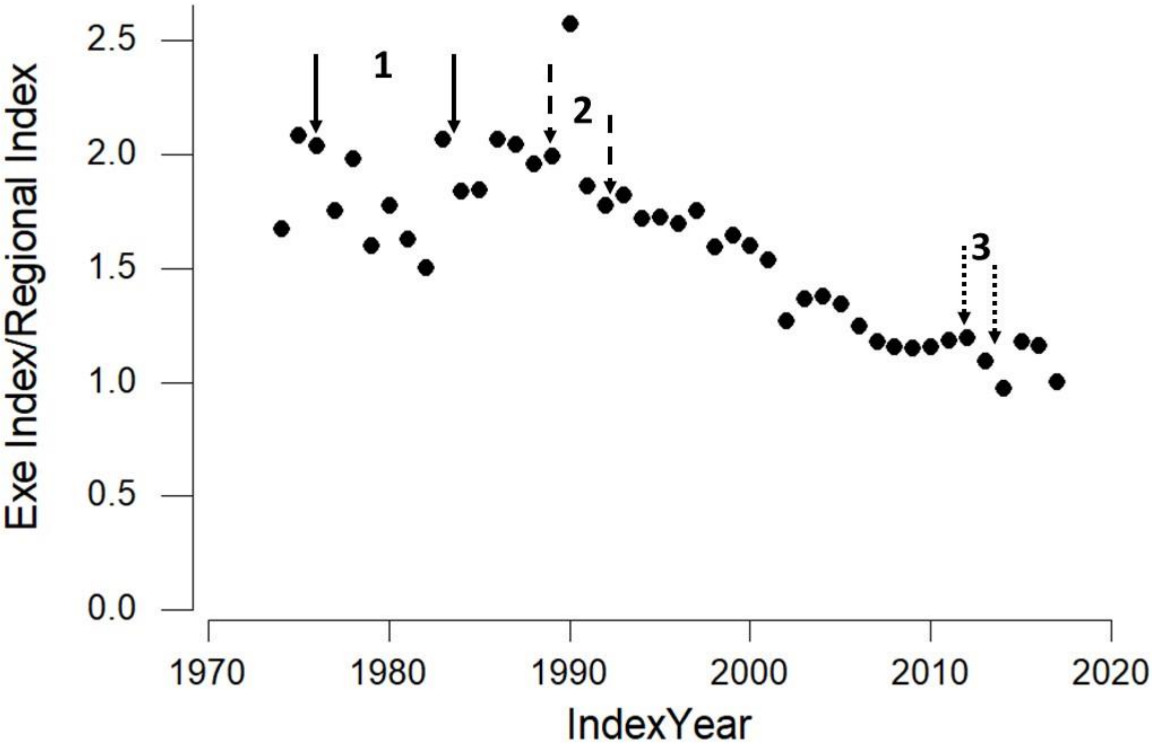

Figure 2B. The ratio between the WeBS annual index for Oystercatchers on the Exe estuary and the WeBS annual index for the South-west region as a whole. The polynomial expression ± *se* for the trend is: 15.7 ± 1.84 + 0.003967Year ± 0.000454 – 0.00000372 Year^2 ± 0.000000454: $R^2(adj.)$ = 87.1%, P = < 0.001. The vertical arrows show the first and last year of periods 1, 2 and 3.

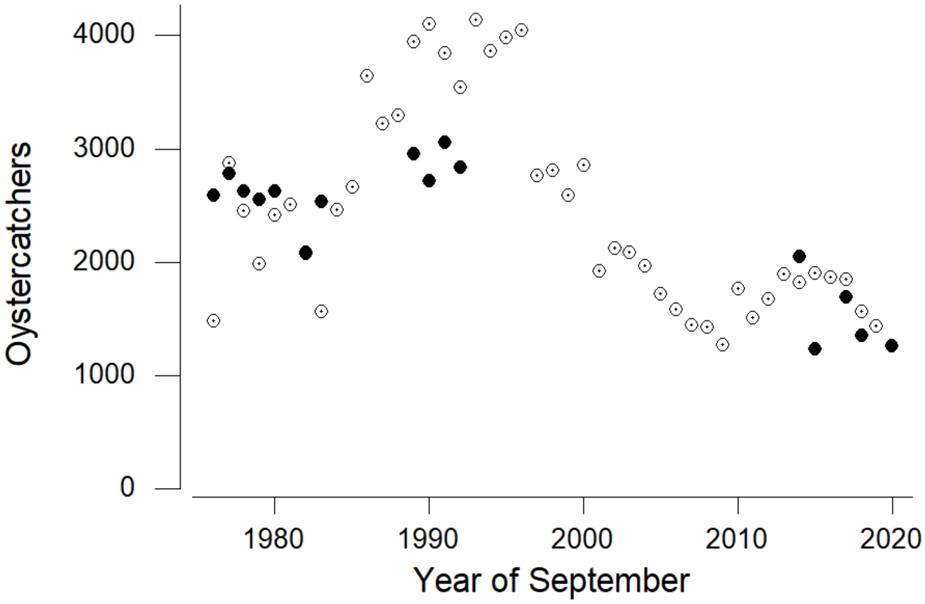

Figure 3. The mean numbers of Oystercatchers counted each winter on the Exe estuary since the winter 1976/77 by WeBS (open symbols) and CEH (closed symbols). CEH counts were from late September – January inclusive and WeBS from October to January inclusive.

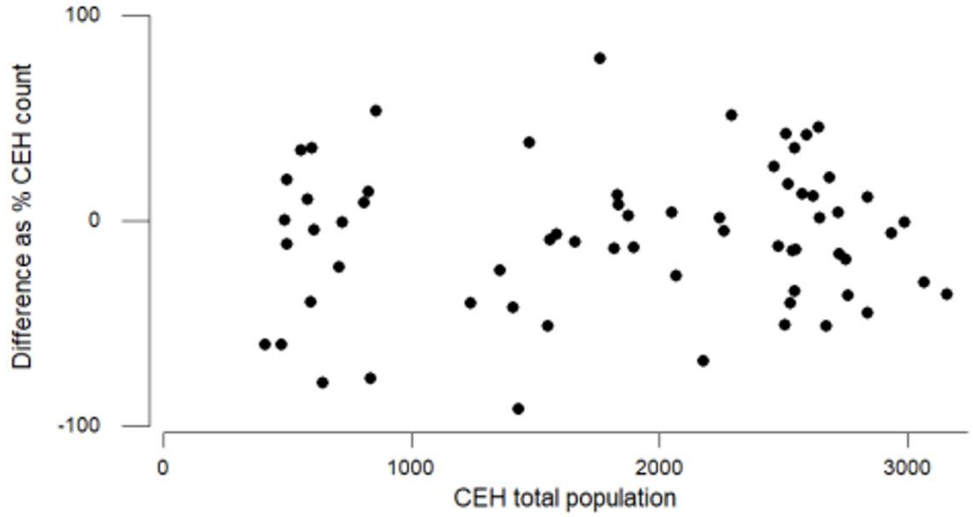

Figure 4A. The magnitude of the difference between the WeBS counts and the CEH counts in relation to the numbers of Oystercatchers recorded by CEH. The difference = 100(CEH count – WeBS count)/CEH count). R^2 *(adj.)* = 0.0, P = 0.534.

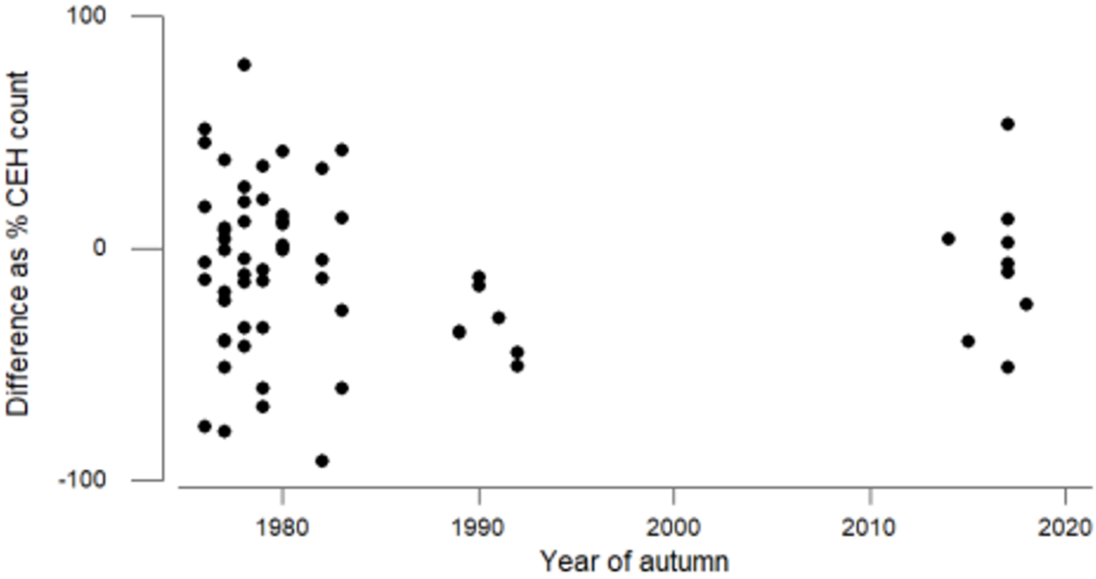

Figure 4B. The magnitude of the difference between the WeBS counts and the CEH counts in relation to the year: for winter 1990/91, the 'Year of autumn' is 1990. The difference = 100(CEH count – WeBS count)/CEH count. R^2 *(adj.)* = - 0.048, *P* = 0.699.

Figure 5A. Percentage of adult (solid circles) and immature (open circles) Oystercatchers predicted to starve by 15 March as the percentage of mussels they opened in daylight that was stolen by kleptoparasites increased. Separate predictions are shown for periods 1, 2 and 3. Each symbol shows the mean of 20 simulations with the model ExeMORPH.

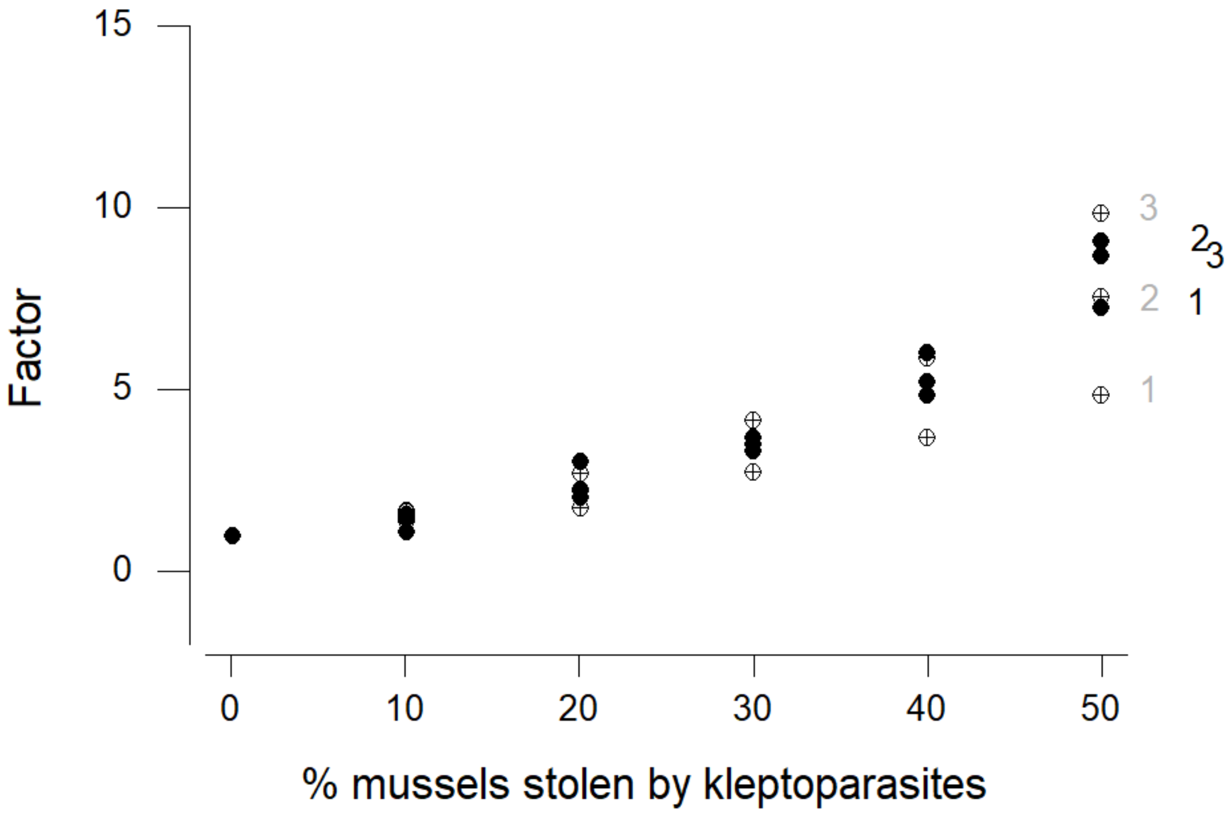

Figure 5B. The factor by which the percentage of adult (solid circles) and immature (open circles) Oystercatchers predicted to starve by 15 March as the percentage of mussels they opened in daylight that was stolen by kleptoparasites increased from the baseline rate in the absence of kleptoparasitism. Separate predictions are shown for periods 1, 2 and 3. Each symbol shows the mean of 20 simulations with the model ExeMORPH**.**

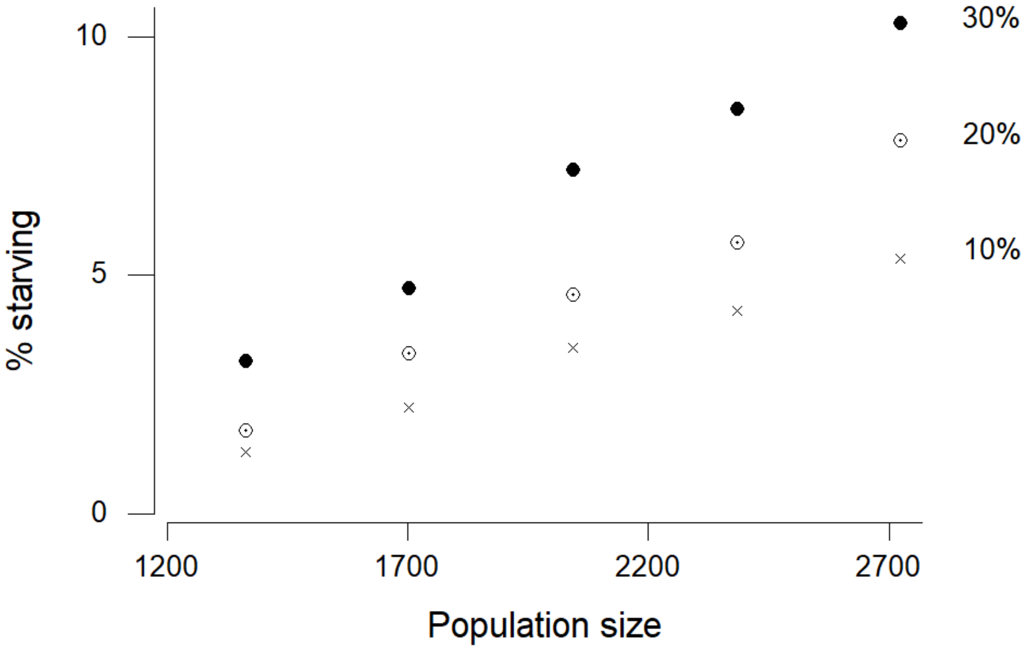

Figure 6A. The predicted overwinter mortality rate of immature Oystercatchers in relation to population size over the range of the actual size (1362 birds) to twice the actual size (2724) with frequencies of kleptoparasitism of 30%, 20% and 10%. Each point is the mean of 20 simulations with ExeMORPH.

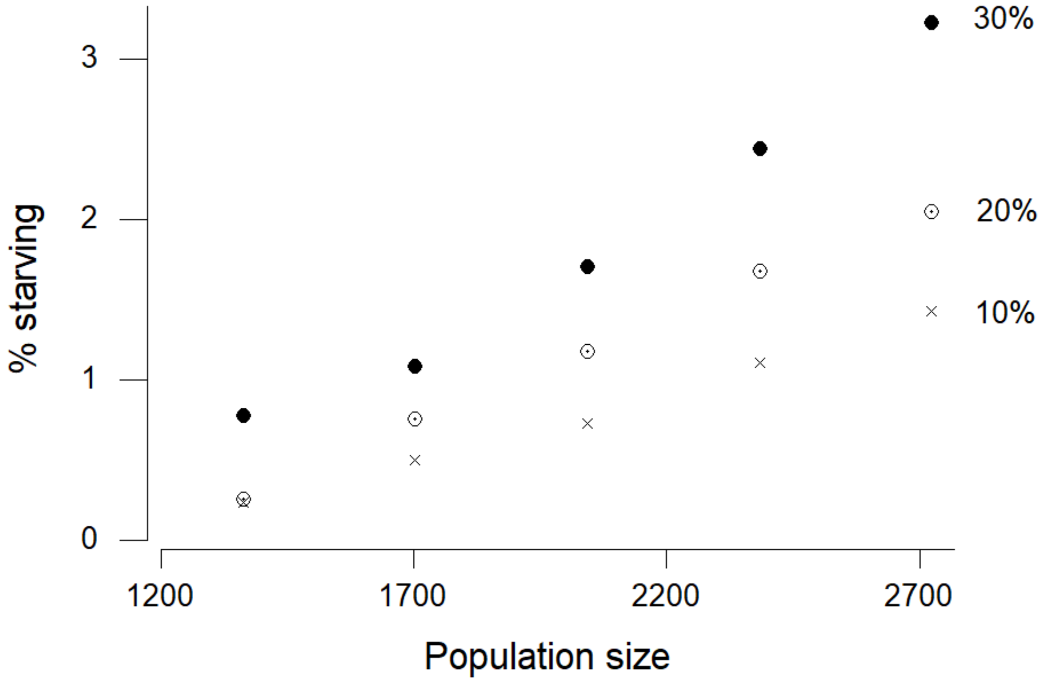

Figure 6B. The predicted overwinter mortality rate of adult Oystercatchers in relation to population size over the range of the actual size (1362 birds) to twice the actual size (2724) with frequencies of kleptoparasitism of 30%, 20% and 10%. Each point is the mean of 20 simulations with ExeMORPH.

SUPPLEMENTAL MATERIAL

Supplemental Material 1: Calibration and validation of ExeMorph

This Supplement extends and renders out-of-date the summary of the calibration and validation previously given in https:// figshare. com/ articles/ Goss-Custard _ J _ D _ 2018 _ Calibration _ of _ the _ individual-based _ model _ MORPH _ for _ mussel-eating _ Oystercatchers _ of _ the _ Exe _ Estuary _ / 7259105.

Development of the calibration method

ExeMorph is the individual-based model for the Exe estuary Oystercatchers that eat mussels and use upshore areas and fields for supplementary feeding when they cannot meet their requirements from mussels alone.

The first version was published by Stillman et al. (2000). This version was set-up to predict the observed within-winter mortality rate of adults for the winters (September 1 to March 15) 1976/77 to 1979/80 when there was an estuary-wide density of Oystercatchers on the mussel beds of 18/ha. This first version correctly predicted the increased mortality rate amongst adults that accompanied the increase in population density over the winters 1980/81 to 1990/91: see Figure 3 in Stillman et al. (2000). The density of Oystercatchers increased to 25/ha in the winters 1980/81 to 1983/84 and 31 in the winters 1988/89 to 1990/91 over which winters the mortality rate had been estimated. These winters (September 1 to March 15) are referred to here as the Calibration winters of 1976/77 to 1980/81, the Validation 1 winters of 1980/81 to 1983/84 and the Validation 2 winters of 1984/85 to 1991/92.

This model predicted the increased adult mortality rate in Validation winters 1 and 2 quite well (Stillman et al. 2000). However, it did not accurately predict the mortality rates of the four classes that comprised the Oystercatcher population: *i.e.* immature hammerers, immature stabbers, adult hammerers and adult stabbers.

It was also considered unsatisfactory that it was necessary to include the ‘Aggregation factor’ (AF) in order to calibrate the model successfully. The AF was included in ExeMORPH to capture the widespread tendency of Oystercatchers to aggregate in particular parts of each mussel bed, the principal foraging habitat patch in the model. For example, with 100 adult stabbing Oystercatchers on a mussel bed of 10ha, the density of Oystercatchers in ExeMORPH would be increased from 10 to 80 birds/ha by the AF for stabbers of 8 (Stillman et al. 2000). This frequently increased bird densities in the model well above the interference threshold density of 65.4 stabbing Oystercatchers/ha (Stillman et al. 2000), and thus increased the difficulties the birds had in obtaining all their food requirements from mussels alone.

The major concern about using the AF was that the degree of aggregation of Oystercatchers probably varies greatly between mussel beds, through the exposure period, through the winter and with population size, yet there was available only a very limited number of measurements that had only been made over low tide. The AF was retained in ExeMORPH for over a decade, however, because it acted as a calibration factor and without it no Oystercatchers in the model starved.

Bowgen (2016) devised an alternative parameter to capture the tendency of Oystercatchers to aggregate in limited parts of many mussel beds which she termed ‘Regulated Density’ (RD). The basic idea was that birds tend to aggregate - either by mutual attraction or by being drawn to the best localities within a patch – but would spread out if interference began significantly to reduce their intake rate. This ‘attraction-avoidance’ idea coincided with the concept arising from recent work on waders in the Wadden Sea (Folmer et al. 2011). Research on the Exe suggested that, for mussel-eating Oystercatchers, the value of RD is 45 birds/ha: this is the maximum density typically occurring when the population size is high and there is a large area of mussels over which the birds are able to spread out. In the model, RD serves to spread the birds out more widely over the available area of mussel beds and, in Bowgen's individual based model for Poole Harbour, its inclusion improved the match between the predicted and observed distribution of birds at low tide (Bowgen 2016).

Bowgen created a version of ExeMORPH in which AF was replaced by RD. But still no Oystercatchers starved: without AF increasing foraging density and suppressing intake rate, all individuals were able to obtain their food requirements in the time available and to survive the winter. However, RD had been measured at low tide when large areas of mussel beds were accessible whereas, in nature, RD would probably be much higher when Oystercatcher densities were high, as at the beginning and end of the exposure period. Therefore, the value of RD was gradually increased in ExeMORPH in a series of calibration simulations. This increased the mortality rate above 0% once RD had exceeded the interference threshold density. It appeared that the original calibration factor in ExeMORPH of AF could be replaced by RD.

But this proved not to the case. In the model, hammerers were predicted to have a higher mortality rate than stabbers whereas, in nature, hammerers have a lower mortality rate than stabbers. Many attempts were made to rectify this discrepancy between model predictions and reality, but without success. For example, the 10 mussel bed patches in ExeMORPH were sub-divided into 30 sub-patches, each with its own shore-related mussel flesh-content and size-distribution but hammerers still starved at a much higher rate than stabbers.

It was clear that, without AF in ExeMORPH, the only way to calibrate the model was to change the values of one or more parameters that are specific to age-class and feeding-method groups. Although it is possible that stabbers and hammerers, adults and immatures differ in their post-consumption efficiency at assimilating energy - for example, through different gut parasite infestation loads - there was no reason to believe it. Accordingly, the only option for re-calibrating the model without AF was to reduce the gross intake rates and/or the intensity of interference by different amounts in the different age-class and feeding method groups of Oystercatchers.

Interference is represented by three coefficients in ExeMORPH: (i) the threshold density of Oystercatchers at which interference starts to depress the intake rate; (ii) the subsequent rate at which intake rate declines as competitor density increases, and (iii) the increasing intensity of interference as the winter progresses (Stillman et al. 2000). The number of combinations of these three coefficients which could be used to re-calibrate the model across four age-class/feeding-method groups was therefore very large. Accordingly, the simpler option of varying the ‘efficiency’ with which the average bird in an Oystercatcher group consumed food was adopted instead.

The chosen calibration factor adjusts the value of the interference-free intake rate (IFIR) of all individual Oystercatchers within one group by the same amount but its value differs between groups. In ExeMORPH, a functional response equation is used to predict the intake rate in mg ash-free dry mass (AFDM)/s of the average Oystercatcher feeding in a given place at a given time: the equation does this from the numerical density, flesh-content and size-distribution of the mussels present at that time and place. The predicted average interference-free intake rate is then multiplied by an individual’s ‘foraging efficiency’ (FE), the value for which is drawn at random from an empirically-determined normal distribution with SD = 0.125 and a mean of 1

(Stillman et al. 2000). An individual’s FE remains constant throughout the winter and, in the early versions of ExeMORPH, only applied to birds when feeding on mussels. The ‘Calibration Coefficient’ differed between immatures and adults and between hammerers and stabbers but was the same for all individuals within each of these groups. The calibration coefficient was used to vary the IFIR of the average bird within one group in a given place at a given time, as predicted by the functional response. For example, assume the functional response predicted an average intake rate of 500mgAFDM/s and the calibration coefficient for immature stabbers was 0.6, the average immature stabber would then have an IFIR of 300mgAFDM/s (0.6x500). If an individual’s FE was, 1.10, it would have an IFIR at that time and place of 1.1x300=330mgAFDM/s. If the density of competitors where the individual was feeding exceeded the interference threshold density, this IFIR would be further reduced by interference by an amount that depended on the density of competitors and on the stage of the winter when the model bird was foraging.

Initially, the calibration coefficient was applied to mussel-eating Oystercatchers only. However, in ExeMORPH, the birds can survive in normal winter weather without consuming any mussels at all. They can do this by taking alternative prey, such as clams and cockles on the estuary and earthworms in the fields, at the empirically-determined average rates that were used in the model (Stillman et al. 2000). Accordingly, the untested assumption was made that individual birds consumed these alternative prey species with the same efficiency with which they took mussels. That is, the calibration coefficient was applied to all diets. The IFIR of the average bird on the upshore flats and in fields was also multiplied by the calibration coefficient and by an individual’s FE. Accordingly, it was assumed that a bird that was inefficient when feeding on mussels was equally inefficient when feeding on upshore prey and earthworms in fields: there is no evidence that either is the case but the idea does have the merit of being testable. And by introducing this assumption, some individuals now starved.

It was then possible to calibrate ExeMorph so that it replicated the observed and different winter mortality rates of immature hammerers, immature stabbers, adult hammerers and adult stabbers as had been estimated by Durell et al. (2001). However, the predicted mortality rates were too high at the higher bird densities during the validation winters 1 and 2.

Sitters (2000) found that interference might be much reduced, even absent, at night in mussel-eating Oystercatchers. Accordingly, the next step in the development of the calibration procedure was to reduce the intensity of night-time interference. This was achieved by raising the night-time interference threshold and thus reducing the number of hour-long time-steps in ExeMORPH during which interference occurred. Although the predicted mortality rates did fall in the validation years by a substantial amount, they were still too high. Accordingly, interference at night was removed completely from ExeMORPH, whereupon the predicted and observed mortality rates, averaged over validation winters 1 and 2, coincided almost exactly.

Across the four Oystercatcher groups, CC varied between 0.53 and 0.71. Both represent a substantial reduction in the empirically-determined estimates of IFIR that had been obtained over several winters. As there was good evidence that the functional response equations used in ExeMORPH predicted IFIR quite well (Goss-Custard et al. 2006), it seemed that this particular calibration coefficient was unsatisfactory. Accordingly, an alternative was sought.

As the key feature of MORPH is individual variation, the suggestion was made that the coefficient of variation (CV) of the individual variation in foraging efficiency (FE) might be used to calibrate the model. The thinking was that, with larger CVs, there would be more inept birds at the low end of the distribution of FE and so a greater proportion of the birds would starve.

This possibility was explored by varying the CV for each Oystercatcher group separately: attempts to use a single value across all groups failed. Individuals had the same FE when feeding upshore and in fields as they did when feeding on mussels. Depending on the group, the CV had to be increased across all diets from its field-estimated value of 0.125 to as much as 0.3625. So, as was the case when calibrating ExeMORPH by varying the average IFIR, using the CV to calibrate the model necessitated a substantial departure from the estimates that had been made in the field. However, using the CV as the calibrator gave predictions for the validation years that were less good than those obtained when using IFIR as the calibrator. Accordingly, and as an interim measure, ExeMORPH is calibrated by varying IFIR and by equal amounts across all prey species within one age-class/feeding method group of Oystercatchers.

The magnitude of the calibration coefficients, however, do provide a measure of just how much more we still have to learn about the foraging, and perhaps physiology, of over-wintering Oystercatchers (Goss-Custard 2017); indeed, many uncertainties remain (Goss-Custard & Stillman 2022).

Winter mortality rates used for calibrating ExeMORPH

As most Oystercatchers in the wintering population were adults, only small samples of immature birds could be ringed and their survival monitored between autumn and spring. The estimates of the winter mortality rate from September 1st to March 15th was therefore most precise in adult birds, as shown in Figure 2 of Stillman et al.

(2000). Accordingly, the calibration of the model was largely guided by the accuracy with which it predicted the mortality rates of adults.

The data used to calculate the winter mortality rate of each age-class/feeding method group are shown in Tables SM1 1 to SM1 3:

Table SM 1. From Figure 2 in Stillman et al (2000), and excluding the 18.8% of deaths caused by accidents, the observed mortality rates were:

	Adults (%)	Immatures (%)
Observed mortality	2.01	10.43

As so few Oystercatchers in their first winter (‘juveniles’) foraged on mussels, this age group was not distinguished in the analysis. Their small numbers were included as immatures, using the stabbing technique to open mussels.

Table SM1 2. From Durell et al. (2001), the winter mortality rates of the four age-class/feeding method groups over all the winters for which estimates were available were:

	Observed mortality (%)
Adult hammerers	1.4
Adult stabbers	2.3
Immature hammerers	3.7
Immature stabbers	7.8

Ratio stabbers/hammerers: adults 1.64 Immatures 2.11

Table SM1 3. From Figure 3 in Stillman et al. (2000), and excluding the 18.8% of deaths caused by accidents, the observed adult mortality rates during the calibration and validation winters were:

	Observed mortality of adults (%)	
1976/77 to 1979/80	1.32	Calibration winters
1980/81 to 1983/84	1.44	Validation winters 1
1988 to 1990/91	3.52	Validation winters 2

In combination, the data in Tables SM1 1, 2 and 3 enabled the mortality rate of each age-class/feeding method group to be estimated for each of the three periods of years as follows:

Adult mortality rate: Figure 2 in Stillman et al. (2000) gives the observed adult mortality as 2.01% over the calibration winters of 1976/77 to 1979/80 (Table SM1 1) whereas Figure 3 gives it as 1.32% (Table SM1 2). There is no detectable explanation for this difference. But as Figure 3 was used to test the model for the validation winters 1 and 2, the adult mortality rate of 1.32% from that Figure was used to test the model's predictions.

Immature mortality rate: Figure 2 in Stillman et al. (2000) gives the immature rate is 5.2 times higher than adults (Table SM1 1) whereas in Durell et al. (2001) it is only 3.9 times higher. As the latter was based on larger sample sizes, the value of 3.9 times the adult mortality rate was chosen as the target mortality rate for immatures. For the calibration winters, the value was 5.16%.

Feeding method and mortality rate: From Durell et al. (2001), the ratio between the mortality rate of stabbers and hammerer was 1.643 in adults and 2.108 in immatures (Table SM1 2).

Parameters

All the values for the parameters used in these calibration simulations for the ambient temperature, daylength, tidal cycle, food supply, size and composition of the Oystercatcher population and the foraging behaviour and physiology of the birds were the same as those detailed in the Appendix in Stillman et al. (2000) except for the following:

The times of exposure and covering of the mussel beds and upshore foraging habitats were based on their height on the shore and the times for which they were exposed and so accessible to Oystercatchers calculated from the height of the water, as determined by the tidal curve on each tidal cycle throughout the winter.

No interference at night.

No aggregation factor (AF = 1)

Regulating density (RD) = 45 birds/ha

Energy density of prey flesh = 22.5kJg^{-1}

Over winter non-Oystercatcher mortality = 5% removed at a constant proportional rate each day

Decrease in ash-free dry mass = 45% less at end of winter than at start

Table SM1 4. The numbers of each age-class/feeding method group in each period.

	Calibration winters	Validation winters 1	Validation winters 2
Immature hammerers	28	38	45
Immature stabber	112	152	181
Adult hammerer	804	1089	1296
Adult stabber	606	821	977
Total	1550	2100	2498

Calibration coefficients

The average IFIR of all individuals in an age-class/feeding method group was multiplied by the following coefficients. The values in brackets refer to foraging at night, and are based on Sitters (2000) data for mussel-feeding Oystercatchers on mussel bed 20: in hammerers, intake rate in winter was 16% lower at night than during the day whereas it was 17% higher in stabbers:

Table SM1 5. Daytime and night-time (in brackets) IFIR calibration coefficients for each age-class/feeding method group.

Hammerers:	adults	0.7125 (0.5985)	immatures	0.6568 (0.5517)
Stabbers:	adults	0.570 (0.6675)	immatures	0.5275 (0.6177)

Number of simulations required to reach stability

From Figure SM1, the number of simulations used in the above analyses to explore alternative calibration coefficients was 40:

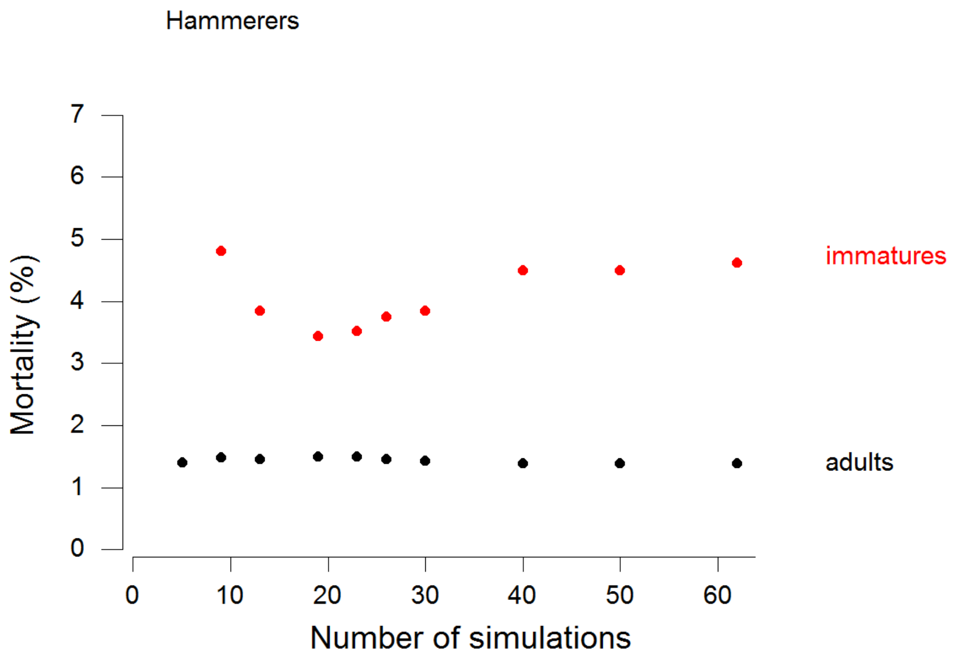

Figure SM1 A: Predicted mortality rate for the calibration winters in adult and immature hammerers in relation to the number of simulations run with ExeMORPH.

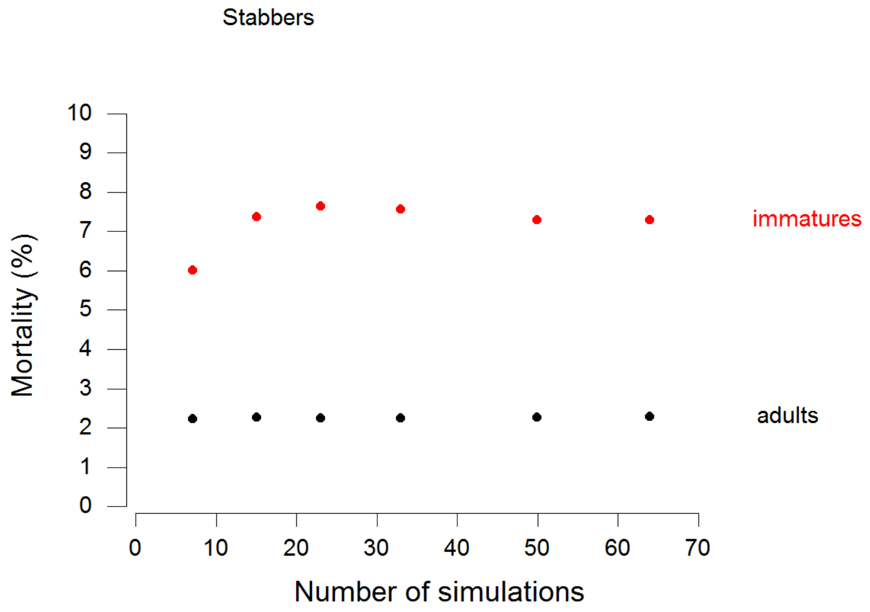

Figure SM1 B: Predicted mortality rate for the calibration winters in adult and immature stabbers in relation to the number of simulations run with ExeMORPH.

Validation

In order that the predictions of the four age-class/feeding method groups for the validation winters could be compared and combined, the predicted mortality rates for each group are expressed as the percentage change in the mortality rate during the calibration winters. Thus, a doubling in the predicted mortality rate from the calibration winters to the validation winters 1, for example, would be expressed as a 100% increase.

Compared with observed values, the predicted increase in the winter mortalities predicted by ExeMORPH were high in stabbers and hammers in validation winters 1 and low in validation winters 2 (Figure SM1 2). But when averaged, the predictions for stabbers and hammerers were both much closer to the observed values (large, crossed circles). The large solid show the results for stabbers and hammerer adults combined, weighted by their representation in the population. Observed = 88% increase over the calibration years; predicted = 94%.

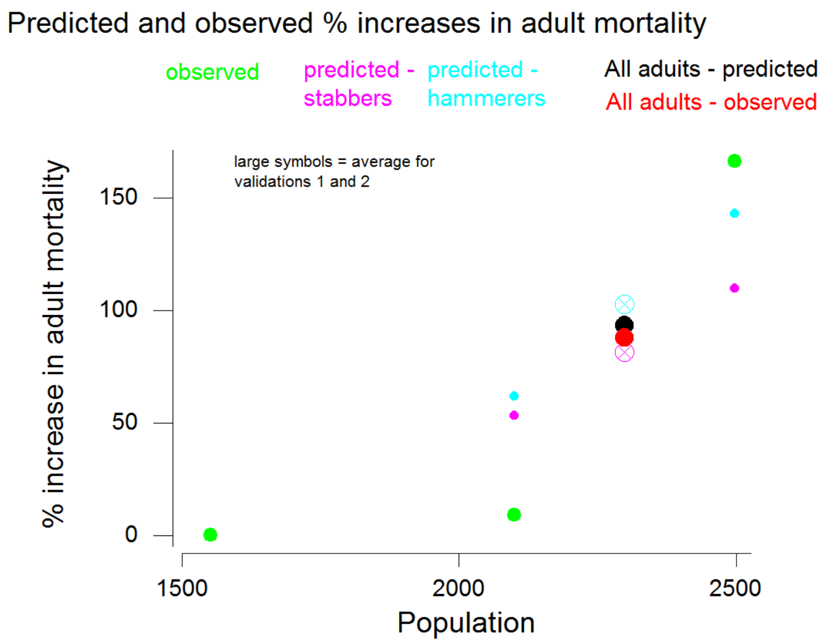

Figure SM1 2. The predicted and observed percentage increases in the mortality rate of adult Oystercatchers during the validation winters 1 and 2. The data show the percentage increase above the adult mortality rate during the calibration winters. The small green symbols show the observed rates for adult hammerers and stabbers combined. The small mauve symbols refer to stabbing adults. The small blue symbols refer to hammering adults. The large, solid symbols refer to the values for stabbing and hammering adults over the two validation periods combined, with the red symbol showing the observed value and the black symbol the predicted value. The large open symbols refer to the combined values for adult stabbers (mauve) and hammerers (blue) separately.

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Supplemental Material 2: Comparing the WeBS counts with CEH counts

The comparison between the CEH and WeBS winter counts made in the same month and winter involved several steps, as described here.

The CEH counts appear quite stable over the winters 1976/77 to 1983/84 (*sd* = ± 9.1%) compared with the WeBS counts (*sd* = ± 30.2%) (Figure SM2 1). On average, the CEH counts exceeded the WeBS counts: CEH mean ± sd = 2577.4 ± 234.9; WeBS: mean ± sd = 2186.0 ± 660.0). Although every precaution was taken by the increasingly experienced WeBS teams, under-counting and double-counting may have been very difficult to avoid, thus increasing the variability in the WeBS counts and raising the possibility that, at times, consistent biases were introduced. It is possible, of course, that the numbers of birds on the Exe really did vary much more than was revealed by the CEH low-tide counts but this would be incompatible with (i) the finding on the Exe estuary that there was little or no turn-over in colour-marked birds through the winter months (Goss-Custard *et al.* 1982; Morten *et al.* 2022), and (ii) the known reluctance of Oystercatchers to change wintering area, even when feeding conditions deteriorate (Atkinson *et al.* 2003, Verhulst *et al.* 2004).

There was, on average, a close correlation (R^2 *(adj.)* = 66.8%, P = < 0.001) between the 67 estimates made in all months (June to May) by the WeBS and CEH teams from 1976/77 to 2019/20 (Figure SM2 2). The WeBS mean ± *se* count of 1968 ± 136 was 6.84% higher than the CEH mean ± *se* count of 1842 ± 106 but the difference was not statistically significant (t = 0.73, P = 0.466, df = 124). As the slope ± *se* of the regression of the WeBS counts against the CEH counts of 1.0551 ± 0.0912 was not significantly different from 1 (P = 0.471) and the intercept ± *se* of 25.1 ± 185.4 was not significantly different from 0 (P = 0.893).

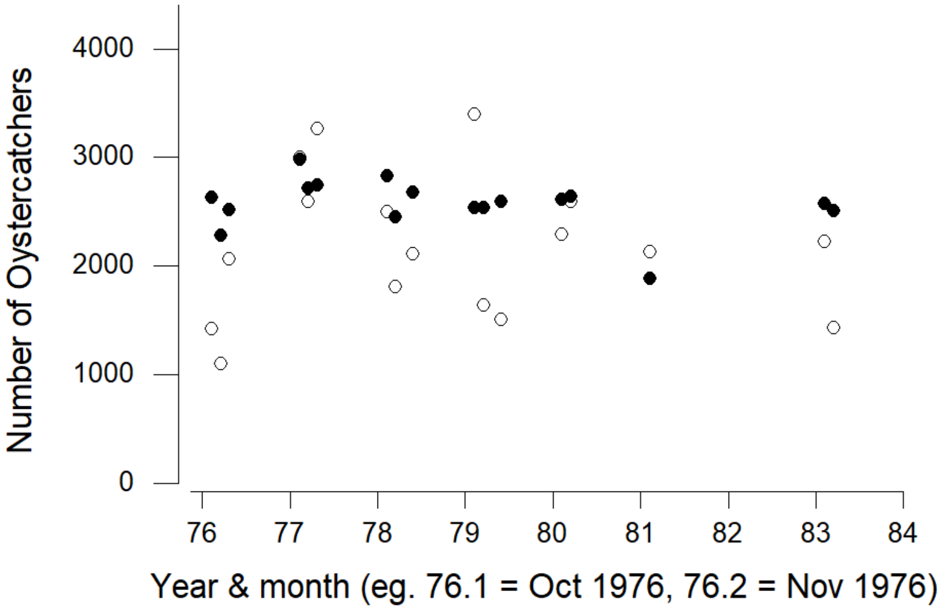

Figure SM2 1. CEH (closed circles) and WeBS (open circles) monthly counts of the Exe estuary Oystercatcher population during the winters (October to January) 1976/77 to 1983/84. The 17 paired counts of the Exe estuary Oystercatcher population were made during the same spring tide series.

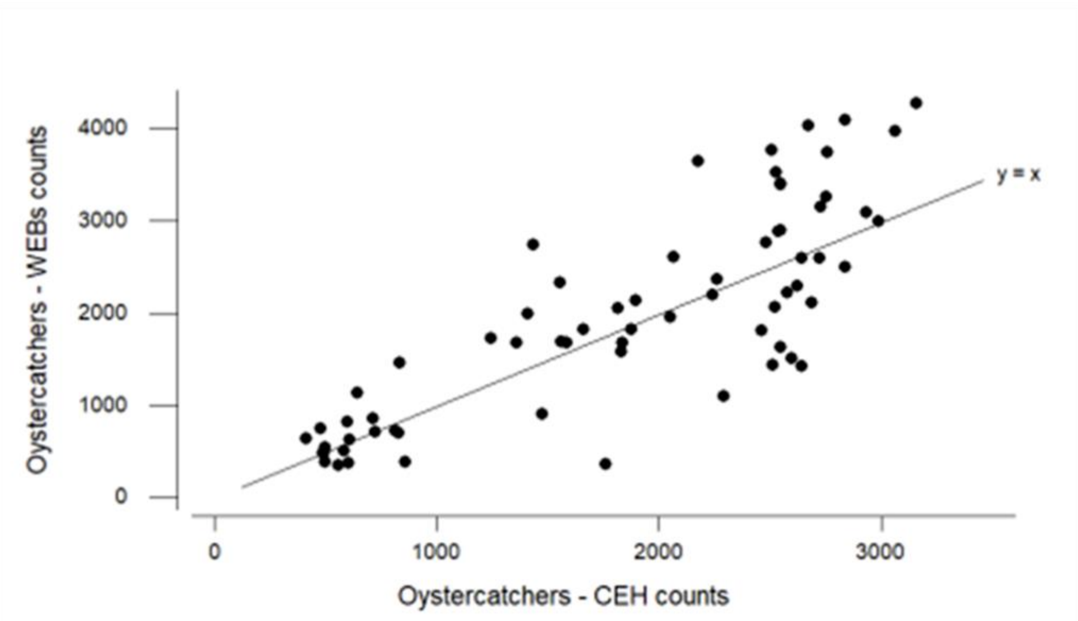

Figure SM2 2. Comparison between the WeBS and CEH counts made in the same month and year 1976/77 to 2019/20.

References for Suplemental Material 2

Atkinson P.W., Clark, N.A., Bell M.C., Dare P.J., Clark J.A. & Ireland P.L. 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. Biol. Conserv. 114: 127-141.

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Supplemental Material 3: Improvement in the mussel food supply over the period of the Oystercatcher population decline.

That it was the increase in the average length, and therefore average flesh-content, of mussels that mainly caused the improvement in the feeding conditions was tested with additional simulations with ExeMORPH.

There are three components of the total food supply provided by mussels 30 – 60 mm long: the surface area of all the beds combined and their mean numerical density and their mean flesh content across all beds. In the following simulations, the values of each of these components in period 1 were varied, one at a time, by multiples of 1.0125, 1.025, 1.0375, 1.05, 1.1, 1.15 and 1.2: the other two components remained at their period 1 value. This provided 25 combinations with which to explore by GLM the relative importance of surface area, numerical density and flesh-content in determining the starvation rate in 1561 adult and immature Oystercatchers. The high values of the F-statistic in Table SM3 1 suggest that, in addition to the age of the birds, mortality rate was most influenced by the mean flesh-content of mussels. This confirmed the significance of the increase in mean mussel size over the years of the relative decline.

Indeed, the improvement in feeding conditions may have been even larger than indicated in Table SM3 1: in those simulations, the flesh-content of mussels of each length were assumed to be the same in all three periods yet, in fact, they may have increased (Supplemental Material 4).

Table SM3 1. General linear model of the winter starvation rates for period 1 in adult and immature Oystercatchers as predicted by ExeMORPH. The surface area covered by mussels on all the main mussel beds combined, the numerical densities of each 5 mm length-class and the flesh-content of mussels 30 – 60 mm long on each mussel bed were varied, one at a time, by a factor ranging from 1.0125 to 1.25. Bird age was represented by a dummy 0/1 variable, with immatures = 0.

Source	*df*	*F*	*P*
Age	1	354.93	<0.001
Area (ha)	1	1.10	0.300
Density (mussels/m^2)	1	7.97	0.007
Size (gAFDM)	1	84.32	<0.001
Error	41		
Total	45		

Supplemental Material 4: Changes in the flesh-content of mussels over the study period

The improvement in the feeding conditions provided by blue mussels *Mytilus edulis* (L.) may have been even larger than suggested by the simulations with ExeMORPH. This is because in the simulations, the same values were used in all three periods for the flesh-content of each of the 5mm length-classes of mussels that defined the mussel population on each mussel bed (Stillman *et al.* 2000): this was necessary as the flesh-content of mussels was not measured during period 3. However, the flesh-content of mussels ranging in length between 20 mm and 65 mm was measured on beds 1, 3, 4, 20, 22, 25, 26, 27, 30 and 31 in the Septembers of 1976, 1981, 1992 and 1997. A GLM analysis with mussel bed and year as the model and the length of the mussel as covariate revealed that, over this period, there was a tendency for the flesh-content of mussels to have varied significantly over the 21 years covered by the analysis (Table SM4 1).

Table SM4 1. General linear modelling of the flesh-content of mussels in mgAFDM on the same 10 mussel beds of the Exe estuary during September in 1976, 1981, 1992 and 1997. The model was the mussel bed and the year and the only covariate was the length of the mussel. As the flesh-content depends strongly on the length of a mussel, and as the relationship of the logarithm of flesh mass is non-linear (Goss-Custard *et al.* 2002), the logarithm of mussel length is described by the quadratic expression.

Source	*df*	*F*	*P*

Mussel bed	9	11.02	<0.001
Year	3	500.9	<0.001
$Log_{10}length$	1	251.8	<0.001
$Log_{10}length^2$	1	84.7	<0.001
Error	2015		
Total	2029		

Repeating the analysis with the year as a covariate suggested that, on average, the flesh-content of mussels of a given length increased over the study years: regression coefficient ± *se* = 0.010384 ± 0.000570, *P* <0.001. As a further test, the flesh-contents of mussels in 1992 and 1997 - at the beginning and approximately the mid-point of the relative decline in Oystercatcher numbers – were compared in a multiple regression analysis in which the two years were represented by a dummy 0/1 variable. This confirmed that the flesh-content of mussels increased from 1992 to 1997 (Table SM4 2) and that the feeding conditions improved, rather than deteriorated, over the years of relative decline in Oystercatcher numbers.

Table SM4 2. Regression analysis comparing the flesh-content of mussels, in mgAFDM, on the same 10 mussel beds in September 1992 and September 1997.

Predictor	Coefficient	± *se*	*P*	%
Constant	-7.1058	0.6382	<0.001	
$Log_{10}length$	8.7289	0.8053	<0.001	
$Log_{10}length^2$	-1.7255	0.2528	<0.001	

1992 = 0; 1997 = 1	0.2980	0.0091	<0.001	
R^2 (adjusted)			<0.001	88.1

References for Suplemental Material 4

Goss-Custard, J.D., Clarke, R.T., McGrorty, S., Nagarajan, R., Sitters, H.P. & West, A.D. 2002. Beware of these errors when measuring intake rates in waders. Wader Study Group Bull. 98: 30-37.

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Supplemental Material 5. The amount of human disturbance caused by Peregrine falcons.

Upshore scares

The frequency with which Oystercatchers foraging upshore were flighted by Falcons was recorded in the seven areas where most Oystercatchers occurred at the beginning and end of the exposure period. The number of disturbances was unrelated to the area where, or the month when, the observations were made or whether the tide was receding or advancing (Table SM5 1). The mean ± *se* number of disturbances across the seven areas on receding and advancing tides was 0.139 ± 0.039 (n = 79). Accordingly, on most winter days, Oystercatchers were flighted 0.278 (0.139 x 2) times over a tidal exposure period; that is, approximately every four days.

Downshore scares

All disturbances of birds feeding on the mussel beds occurred within ± 1.5 h of low tide. The number of disturbances was unrelated to winter month and year but differed significantly between areas of the estuary but according to the year and month (Table SM5 2).

The frequency with which Oystercatchers on mussel beds were flighted during a typical exposure period in winter was calculated from the product of the number of times the birds were flighted and the proportions of Oystercatchers on each of the mussel-bed groups, as shown in Figure 1 of the main paper (Table SM5 3). On the precautionary assumption that all mussel-feeding Oystercatchers occurred on upshore areas at the beginning and end of the exposure period, the rate of flighting upshore was then added to the rates of flighting over low water (Table SM5 4). For example, Oystercatchers on mussel beds 20 – 27 were flighted 1.3 times per low water period and, upshore, 0.278 times per exposure period. During a complete exposure period, therefore, the 46% of mussel-feeders that fed on mussel beds 20 – 27 were flighted 1.578 (1.3 + 0.278) times. Across the whole estuary, mussel-feeding Oystercatchers were flighted 1.094 times per exposure period of 12.4 h duration, an hourly rate of 0.088/h. This is equivalent to 1.76 times the hourly rate of disturbances of 0.05/h by people (Goss-Custard *et al.* 2020).

Although these calculations refer to the 75 – 85% of Oystercatchers that fed on mussels within the estuary over the period of the relative decline, they reflect the frequency of disturbances of Oystercatchers on other habitats, many of which were very close to mussel beds. For example, Oystercatchers on the mud and sand flats in the middle reaches of the estuary were almost certainly subjected to a similar frequency of disturbance from Falcons as were those feeding on the nearby mussel beds 20 – 27.

Table SM5 1. General linear modelling of the number of disturbances caused by overflying Peregrine Falcons of Oystercatchers foraging upshore of the main mussel beds at the beginning (tide receding) and end (tide advancing) of the tidal exposure during the winters (November – March) of 2009/10 to 2017/18. Observations were made either on the receding tide or advancing tide in these areas of the estuary: Bite, Powderham, Lympstone, Bay, Promontory, South-east corner and Cockle Sand (see Figure 2 in Goss-Custard *et al.* (2020). In the analysis, tide receding = 0; tide advancing = 1; November = 1, December = 2 through to March = 5.

Source	*df*	*F*	*P*

Area	3	0.63	0.597
Tide receding = 0; tide advancing = 1	1	0.46	0.501
Month	4	0.28	0.889
Error	70		
Total	78		

Table SM5 2. General linear modelling of the number of disturbances caused by overflying Peregrine Falcons of Oystercatchers foraging on the main mussel beds. Whether the observations were made during the two winters of 1994/95 and 1995/96 or the winter of 2013/14 was represented by 0/1. In the analysis, November = 1, December = 2 through to March = 5. The mussel bed groups were: 1 = beds 1-4; 2 = beds 30 and 31, and 3 = beds 20 – 27 (Figure 1 in main paper). The mean number of disturbances per 100 min ± *se*, including before and after low tide, were: beds 1 - 4, 0.000 ± 0.000 (*n* = 17); beds 20 - 27, 0.667 0.153 (*n* = 57)**;** beds 30 and 31, 0.273 ± 0.141 (*n* = 11).

Source	*df*	*F*	*P*
Area	2	5.26	0.008
Year	1	0.86	0.358
Month	7	0.85	0.551
Error	61		
Total	71		

Table SM5 3. The mean proportion of mussel-feeding Oystercatchers during periods 1 to 3 on the mussel beds in the south-west of the Exe estuary (beds 1 – 4), on the east side (beds 20 – 27) and by its mouth (beds 30 and 31). Over periods 2 and 3 during which the relative decline in Oystercatcher numbers occurred, only the proportion of Oystercatchers on the beds in the south-west and mouth of the estuary differered significantly between the two periods: beds 1 – 4, *t* = 3.73, *P* = 0.001: mean of the two means is 0.125. The proportions did not differ on beds 20 – 27 (*t* = 0.08, *P* = 0.936) or on beds 30 and 31 (*t* = 1.93, *P* = 0.075). *n* = the number of counts

Mussel beds	Period 1: n = 42	±se	Period 2: n = 16	±se	Period 3: n = 9	±se	Period 2 + 3: n = 25	±se
1 - 4	0.247	0.010	0.156	0.012	0.094	0.012		
20 - 27	0.429	0.008	0.459	0.020	0.461	0.028	0.460	0.016
30 & 31	0.324	0.008	0.385	0.017	0.445	0.026	0.407	0.015

Table SM5 4. The number of times Oystercatchers were flighted by Peregrine Falcons during the exposure period in winter on, and upshore of, the main mussel beds of the Exe estuary. The total per Oystercatcher is calculated in thefinal column.

Mussel beds	Flights on mussel beds	Flights upshore	Total flights per exposure period	Proportion of Oystercatchers	Product of columns 4 and 5

1 - 4	0	0.278	0.278	0.133	0.037
20 - 27	1.300	0.278	1.578	0.460	0.726
30 and 31	0.536	0.278	0.814	0.407	0.331
Total per Oystercatcher					1.094

References for Suplemental Material 5

Goss-Custard J.D., Hoppe C.H., Hood M.J. & Stillman R.A. 2020. Disturbance does not have a significant impact on waders in an estuary close to conurbations: importance of overlap between birds and people in time and space. Ibis 162: 845-862.