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Resilient protected area network enables species adaptation that mitigates the impact of a crash in food supply

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ABSTRACT: With coastal wader populations exhibiting long-term declines globally, understanding how they respond to changes in their preferred prey is important for future predictions, especially given the potential for warming seas to affect invertebrate populations. The cockle *Cerastoderma edule* population in the Burry Inlet Special Protection Area (SPA) in south Wales, UK, declined from 1997–2004 before an abrupt 'crash' in stocks between 2004 and 2010. While there has been some recovery since, stocks of larger cockles are still very low. Using survey data from the UK Wetland Bird Survey and analyses of apparent survival and biometrics from ringing, we investigated how the Burry Inlet SPA's wintering Eurasian oystercatcher *Haematopus ostralegus* population responded to this crash. Our analysis showed that both body condition and apparent survival of wintering adult oystercatchers were reduced in the years following the cockle crash but both recovered. The number of birds using the Burry Inlet SPA decreased through the course of the cockle stock decline whilst numbers of birds in the adjacent Carmarthen Bay increased, indicating the importance of adjacent sites for buffering the effects of such changes, i.e. protected secondary habitats can be a vital component of a resilient site network. Our findings are useful in understanding how a predator copes with a serious decline in its preferred food stocks. This study has wide applicability in planning the management of coastal wetlands and shellfisheries as well as the design of resilient protected area networks in the light of environmental change.

KEY WORDS: Shorebirds · Shellfish mortality · Foraging · Apparent survival · Capture–mark–recapture analysis · *Charadriiformes*

1. INTRODUCTION

Over the past decade, the significance of networks of ecologically important protected sites has gained attention from conservationists, researchers and policymakers (Lawton et al. 2010, Gormley et al. 2015). The maintenance of individual sites alone does not provide enough resilience for systems to cope with unexpected changes, be they anthropogenically induced or not, due to the multi-habitat use

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of species during the different stages of their life cycles (Aharon-Rotman et al. 2016, Piersma et al. 2016) and tidal cycles (Burger et al. 1977). Evidence of the importance of these 'resilient networks' has begun to be published (Johnston et al. 2013, Hopkins et al. 2016), but more studies are needed to help guide their conservation, not least in the overly exploited and 'squeezed' coastal zone (Gittman et al. 2016). Fishery stock collapses are not uncommon (Edgar & Samson 2004, Buestel et al. 2009, Dumbauld et al. 2011, Kamphausen et al. 2011, Pogoda et al. 2020); therefore, modelling relationships between these and higher trophic level protected species such as birds is important.

The 3-way relationship between waders, shellfish and shellfisheries has a long history. With the increase in coastal commercial fisheries spurred by increasing markets and aided by mechanical harvesting methods, competitive interactions between fishermen and birds have been antagonistic in the past (Davidson 1968, Prater 1974). More recently, however, the importance of many coastal sites for birds and other wildlife has been recognised globally through the RAMSAR Convention (Ramsar Convention Secretariat 2013) and in Europe through the designation of Special Protection Areas (SPAs) under the European Union Wild Birds Directive (2009/147/EEC) and Habitats Directive (92/43/EEC). Present management at such sites aims to ensure sustainability for both birds and fisheries by setting limits to catches (Stillman et al. 2010, Stillman & Wood 2013a, Herbert & Saunders 2017).

There are 9 species of oystercatchers (Haematopodidae) that are widespread around the coastlines of the globe's temperate zones (del Hoyo et al. 1998). The Eurasian oystercatcher *Haematopus ostralegus* L. (hereafter oystercatcher) is a characteristic bird of the UK's shorelines and among the most numerous species recorded by the UK's monthly National Wetland Bird Survey (WeBS; Frost et al. 2017). Although oystercatchers can exploit a range of prey resources, they predominantly feed on bivalve molluscs (Heppleston 1971, Goss-Custard et al. 2006). The oystercatcher has experienced population declines over recent decades, and in 2015 it was reclassified as Near Threatened on the IUCN's Red List (Birdlife International 2019) and vulnerable within Europe (Birdlife International 2015). It is also Amber-listed on the UK's Birds of Conservation Concern list (Eaton et al. 2015) due to its European status, the concentration of its wintering population in protected sites and the international importance of UK breeding and wintering populations. The causes of declines in oystercatcher populations are currently being investigated (van de Pol et al. 2014), but are likely to include combined effects across the breeding and non-breeding seasons (Bell & Calladine 2017).

Well-known for its highly productive cockle *Cerastoderma edule* fishery (Davidson 1968), the Burry Inlet SPA in south Wales, UK, faced an unprecedented economic issue when increased mortality in larger, older cockles led to a collapse in stocks in 2004 (Stillman et al. 2010, Murray & Tarrant 2015). Mass mortalities were first observed in 2002 and similar losses were seen in the neighbouring Three Rivers estuary (part of the Carmarthen Bay Special Area of Conservation [SAC] with the Burry Inlet) from 2005, with greatest losses occurring during warmer weather in dry sandy areas of high cockle densities (Otto et al. 2007). This mortality was occasionally thought to be compounded by sewage 'flushes' (Murray & Tarrant 2015). Since 2004, smaller (1 yr old) cockles have re-established themselves at numbers close to those seen in previous years, but these individuals are less valuable to the fishing industry and, as long as high levels of mortality persist in larger, older cockles, this means they are lower in numbers and harvesting is only viable for part of the year (Murray & Tarrant 2015). Ongoing mass mortalities are likely to be a multifactorial problem (see Callaway et al. 2013) that prevents definitive management and conservation measures from being put in place, and stocks of larger cockles have yet to recover.

As a primary prey species for waders like the oystercatcher, the loss of cockles in optimal size classes may also place significant pressure on oystercatcher populations (Goss-Custard 1996, Goss-Custard et al. 2006). Previous investigations have highlighted the associations between shellfish stocks and oystercatchers. In the Dutch Wadden Sea, numbers of oystercatchers declined severely in the early 1990s following losses of intertidal mussel beds combined with reduced spat-fall (Smit et al. 1998, Ens et al. 2004, Ens 2006); the slow recovery of the beds means that stocks remained below previous levels (Kraan et al. 2011, Blew et al. 2017). Similarly, on The Wash SPA in the UK, declines in shellfish populations resulting from poor recruitment after periods of overfishing in the 1980s have been associated with declines in oystercatcher survival and numbers due to increased vulnerability to mass-mortality episodes during years of low prey numbers (Atkinson et al. 2003, 2005). Predictive modelling can further our understanding of the relationships between shellfish stocks and oystercatcher populations (Stillman et al. 2001, 2014, Goss-Custard et al. 2004) and aid sustainable management (Caldow et al. 2004, Stillman & Wood 2013b, Goss-Custard et al. 2019), but direct studies during system-wide changes are still needed to verify and investigate repercussions from such changes.

Protected area networks have the potential to improve the resilience of populations of many species, including birds (Johnston et al. 2013, Virkkala et al. 2014), by providing productive refuge areas that they can take advantage of during different stages of their life cycles. The importance of protected area networks is most well-documented for waders on their migration routes (Matz et al. 2012, Li et al. 2019); however, the potential value of networks to benefit species at other times of year is less well-studied. The Three Rivers estuary and Burry Inlet (in south Wales, UK) lie adjacent to each other within the wider Carmarthen Bay SAC and, as such, may buffer one another for protected bird species affected on either site by events that affect prey.

The aim of the present study was to investigate the impact that the crash in cockle numbers in the Burry Inlet SPA had on the overwintering oystercatcher population at that site. We evaluated lethal and sublethal impacts on the birds after the cockle crash in the Burry Inlet shellfishery in 2004, using biometric and recapture information from ringing to calculate changes in oystercatcher body condition and survival. We also considered behavioural responses using survey data, and discuss the implications of our results for conservation management and the design of resilient protected area networks.

2. MATERIALS AND METHODS

2.1. Study site

The Burry Inlet SPA, the estuary of the River Loughor in south Wales, UK (Fig. 1), is designated for its international importance for non-breeding waterbirds of various species, including the Eurasian oystercatcher (JNCC 2015a, 2017a). The site contains around 2200 ha of saltmarsh, the largest continuous saltmarsh area in Wales, and extensive intertidal mudflats and sandflats (~4414 ha; JNCC 2015a, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m681p211_supp.pdf).

The Carmarthen Bay and Estuaries SAC encompasses the neighbouring estuaries of the Three Rivers (Taf, Tywi and Gwendraeth), the marine Carmarthen Bay SPA (designated for common scoter *Melanitta nigra*) and the Burry Inlet SPA (JNCC 2015b, 2017b). In the present study, we consider Carmarthen Bay as the site covered by the WeBS (see Section 2.2), which represents the coast of the SAC outside the Burry Inlet SPA (Fig. 1).

2.2. Data collection

2.2.1. Count data

Data on oystercatcher numbers in the Burry Inlet and Carmarthen Bay were obtained from the volunteer WeBS Core Count scheme between 1974–1975 and 2016–2017 (hereafter all winters will be referred to by the starting year, following Frost et al. 2017). WeBS is the monitoring scheme for non-breeding waterbirds in the UK where counts of all birds present on a site are made once per month, whenever possible on predetermined 'priority dates' to enable synchrony across count sectors at large sites, with counts at coastal sites usually made at high tide by around 3000 volunteer surveyors. Annual WeBS trends were used to provide

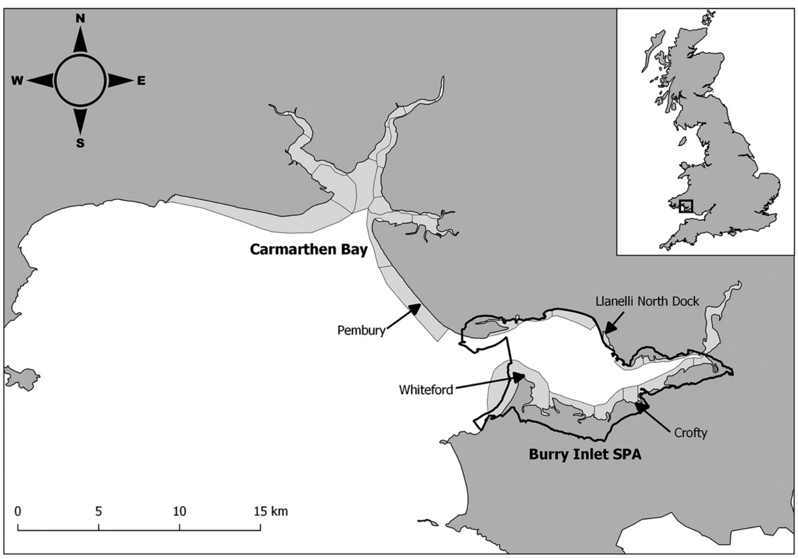

Fig. 1. The Burry Inlet Special Protection Area (SPA; solid black line) and Carmarthen Bay with locations of oystercatcher roost sites labelled (arrows) (JNCC 2017a). Light grey: British Trust for Ornithology Wetland Bird Survey count sectors (intertidal); dark grey: land; white: sea. Inset: map of UK, with box outlining study area within Wales

an assessment of the number of oystercatchers supported on the 2 sites in this study each year.

The WeBS Low Tide Count (Frost et al. 2017) scheme for the 2 estuaries in this study was provided with additional support (from the Countryside Council for Wales: CCW, now National Resources Wales: NRW) to enable an extended programme of annual counts at the Burry Inlet from winter 2003–2013 (with the exception of 2005) and at Carmarthen Bay from 2006–2013. Data were collected from November to February each year. These data provide density estimates of the distributions of birds feeding on subdivisions of the intertidal habitat across the sites (Fig. S2).

2.2.2. Biometric and ring–recapture data

Oystercatchers were caught on 40 occasions between 1990 and 2016 in the Burry Inlet or just outside its boundary at 4 locations (Fig. 1): Whiteford Sands (26 catches), Llanelli North Dock (11), Crofty (2) and Pembrey Sands (1). All catches were carried out using cannon nets at roost sites during the high-tide period, with catches predominantly made at the start of the winter (October–November). No catches were made in 4 winters (1992, 1998, 2006 and 2009). All birds caught were fitted with numbered metal rings (except 44 birds previously ringed elsewhere). In total, 5662 individual oystercatchers were caught during this period, 245 of which were subsequently recaptured (some multiple times, so total recapture events = 342).

Biometric data were available from 27 of these catches (1993–1996, 2002–2016) (Table S1). The following biometrics were recorded: weight (to 5 g, i.e. ±1%), wing and total head lengths (all to 1 mm), bill depth (to 0.1 mm) and primary moult score (a score of the growth stages of each of 10 primary feathers following Ginn & Melville 1983). Birds were classified as adults (n = 4269, 75%), sub-adults (birds in their second winter; n = 726, 13%) or juveniles (birds in their first winter; n = 664, 12%) based on eye and leg colour, plumage and moult (Baker 2016).

Burton et al. (2010) previously reported analyses of survival and biometrics based on these ring–recapture data covering the winter periods 1989–2008; the present study extends that preliminary assessment to include 7 additional years of data. The extra catches were all carried out at Whiteford Sands, mainly during October (see Fig. 1, Table S1). Full data on numbers of recaptured individuals were only available from winter 2001 onwards; thus, calculated apparent survival and recapture estimates (see Section 2.3) are restricted to these later years.

2.2.3. Cockle data

Estimates of cockle biomass recorded in November each year from 1993–2008 were obtained from annual surveys of the Burry Inlet undertaken by the Centre for Environment Fisheries & Aquaculture Science (CEFAS) and as reported in Stillman et al. (2010). More recent data (to 2016) were obtained from NRW reports (Vanstaen 2009, Firmin 2010, Moore 2011, 2012, Grubb et al. 2014, Clarkin & Grubb 2015, Smith 2016). Data on cockle numbers and biomass were collected each autumn from a grid of sample sites (maximum of 388 accessible depending on tide height, 317 accessed on average) set 250 m apart and extrapolated to the entire estuary using inverse distance-weighted interpolation (Moore 2011, Smith 2017). Based on these data, it is apparent that cockle stocks declined for a period from 1997–2004, but that there was a 'crash' in stocks between 2004 and 2010 (Fig. 2). Estimates are available for total cockle biomass in the Burry Inlet and also on the total biomass of cockles of >25 mm (a larger size class that oystercatchers preferentially

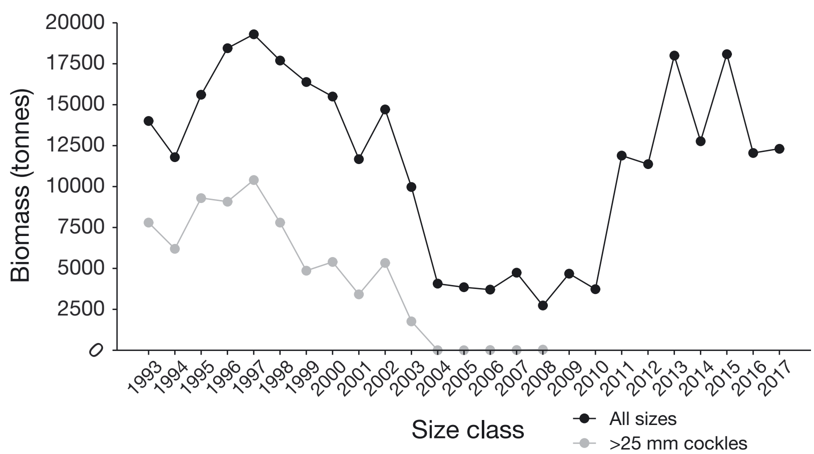

Fig. 2. Autumn (Oct/Nov) biomass estimates of cockles on the Burry Inlet Special Protection Area, Wales, measured each year between 1993 and 2016 (data from CEFAS/NRW). Tonnage of all cockle sizes is listed for each year whilst cockles >25 mm were only specifically estimated up until 2008 (CEFAS/NRW)

select; Sutherland 1982, Goss-Custard et al. 2006). Due to a change in field methods, data on the biomass of cockles >25 mm were not available after 2008. However, the subsequent surveys report that very few cockles >25 mm in size were present following the recovery in 2011 even though these were not specifically measured/weighed.

2.3. Data analysis

2.3.1. Oystercatcher body condition on the Burry Inlet SPA

Individual residuals from a linear model (using R v.4.0.1; R Development Core Team 2020) of body weight against wing length, expressed as a proportion of the expected body weight for each individual, were used as an index of body condition (Schulte-Hostedde et al. 2005). This index was used as the response variable in a generalized linear mixed model (GLMM, 'nlme' package; Pinheiro et al. 2018) to assess how body condition varied according to age (juvenile, sub-adult, adult), time to high tide (minutes, specified as a fixed covariate), moult status (moulting or not, based on moult score), sex (male or non-male [non-male comprised individuals classed as female and those that were unsexed due to limitations of sexual discriminatory function]; Durell et al. 1993) and total cockle biomass. The best model was selected based on the lowest Akaike's information criterion (AIC) value (Burnham et al. 2011). Observations from the same individuals were treated as a repeated measure (random effect), and 'un-aged' birds were dropped from the analysis (n = 5). Waders tend to lose mass (and thus body condition) over the high tide period when they are generally not feeding (Goede & Nieboer 1983); the model included a measure of the time interval between high tide and time of weighing. Unfortunately, data on time of weighing were only available for the catches undertaken between 2001 and 2014 and one catch at Whiteford from winter 1994. Initial models considered data from all sites; however, the data from Crofty and Pembrey were strongly biased by large numbers of moulting birds and thus were removed from this analysis (final model sample size = 2208).

The relationship between the resultant body condition indices and total cockle stocks in a given year was assessed using linear regression in R v.3.5.0 and 'ggplot2' (Wickham 2009). Annual mean (±SE) values were also plotted to further assess relationships with the crash in cockle stocks.

2.3.2. Apparent survival of oystercatchers on the Burry Inlet SPA

Apparent annual survival rates ('φ') were estimated from ring–recapture data using Cormack-Jolly-Seber models in Program MARK v.8.2 (White & Burnham 1999). The program U-CARE v.2.3.4 (Choquet et al. 2009) was used to estimate goodness-of-fit for recapture histories and indicated that no model assumptions were violated (Tables S2 & S3).

As no recapture data were available prior to the winter of 2001, the recapture rate ('*p*') was fixed to 0 in these years; ringing data from these years were retained as they nevertheless provided information on apparent survival through recaptures after that point. The recapture rate was also fixed to 0 in the winters of 2006 and 2009 when no catches were made. Initial model comparisons, with survival held constant over time but varying between age classes, assessed the effects of time and age class on recapture rates (Table S4). These comparisons indicated that recapture rates were low (varying between 1 and 3%). Whilst a model with time-dependent recaptures proved the best in terms of the quasi-likelihood adjusted AIC ($QAIC_c$), the need to reduce parameters given the sparsity of the data meant that we applied blocked average values for recaptures before and after winter 2001 for each age class; given the small range of variation in recapture rates, there was likely to be a minimal effect of fitting constant recapture rates on the final survival estimates.

Foraging efficiency and social dominance increases with age in oystercatchers (Goss-Custard et al. 1982, Marchetti & Price 1989), and thus, as has been shown in previous studies (e.g. Atkinson et al. 2003), we predicted that apparent annual survival rates would differ between age classes. Considering this difference, we initially used models that assessed whether apparent annual survival and recapture estimates varied between adults (birds at least 3 winters old), subadults (birds between their second and third winters) and juveniles (birds between their first and second winters). However, the limited data available for subadults indicated that consideration of 2 age-class models with adults and 'young birds' (birds between their first and third winters previously called juveniles and subadults) was necessary. Models specifically investigated whether apparent adult survival rates from winter 2001 either (1) varied fully between years for each age class; (2) were constant over time; or (3) differed before, during and after the period in which cockle stocks crashed, considering either the entire 2004–2010 period of the crash or 2004–2005, the year immediately following the crash. Young birds' survival rates were held constant in these models as there were insufficient data to estimate annual variation accurately. We also considered models in which (4) the apparent survival rates of adults or both adults and young birds varied in relation to a scaled value of total cockle biomass on the Burry Inlet. The scaled value of total cockle biomass is taken as the difference from the mean value of cockles seen in the years outside the crash period of 2004–2010 divided by 1000 to improve the performance of models (ensuring a mean closer to zero improves estimations by the optimization algorithm; Cooch & White 2019).

Analyses considered the full data set with overdispersion parameters of *c* estimated to adjust the final selected model's AIC_c values to $QAIC_c$ values (Burnham & Anderson 2002). Models were selected on a basis of $QAIC_c$ (where a lower value indicated a better model fit), number of parameters and biological significance. All apparent survival estimates are given with 95% confidence intervals. All plots are displayed post-2000, as the values before that were held constant.

2.3.3. Winter population recruitment

The change in recruitment between years was calculated by comparing the ratio of juvenile to adult oystercatchers for all years where a catch was made (Atkinson et al. 2003). Counts of adults and juveniles were taken from the ringing data sets each year, and ratios were calculated and plotted using R and 'ggplot2', respectively.

2.3.4. Regional population dynamics

To better understand birds' responses to changing cockle stocks and the reasons behind apparent changes in survival, additional investigations were made using count data from the Burry Inlet and neighbouring Carmarthen Bay. Indices of bird population size for each winter between 1974 and 2016 were calculated following the approach of Underhill & Prys-Jones (1994) (the 'Underhill Index'). Counts from November–March are traditionally used in the UK to calculate national indices for waders to avoid passage periods (when there is a higher, unquantified degree of turnover; Musgrove et al. 2007); we followed this approach. The Underhill Index is calculated by summing the number of bird months for each winter and scaling the summed counts so that the last period equals 100. Values for counts that were of poor quality or missing were imputed by modelling the counts as a function of site, year and month factors in a generalized linear model (GLM) with a log-link function and a Poisson error distribution (Underhill & Prys-Jones 1994, BTO 2017). Given that there is a great deal of inter-annual variation shown in annual indices, and trends are better observed with smoothed data, generalized additive models (GAMs) were used to model counts. These models were carried out as a smooth function of year, month and site factors to reveal underlying trends in the index data (Atkinson et al. 2000a, Fewster et al. 2000, Atkinson & Rehfisch 2006). The amount of smoothing applied is controlled by the degrees of freedom associated with each year parameter in the GAM model; we applied degrees of freedom to the year factor equivalent to 0.3 times the number of years, following Fewster et al. (2000) and Atkinson et al. (2000a). Further details of WeBS methods for assessing count completeness and the production of indices are provided in Frost et al. (2017).

We then assessed whether average winter numbers of oystercatchers in Carmarthen Bay were related to those in Burry Inlet and whether both were related to cockle stocks, using linear models in R v.3.5.0 and 'ggplot2' (Wickham 2009). Further to this analysis, data from the WeBS Low Tide Count scheme were used to provide summary representations of the foraging distributions of birds across the sites. Mean sector-level counts for the winters of 2003–2013 are presented to illustrate foraging distributions in years during the cockle crash and after the recovery in stocks (Fig. S2). These dot density maps were created in ArcGIS (ESRI 2018) and randomly distribute dots to represent the total number of birds seen in a sector (3 birds dot^{-1}). Note that no low tide counts were available for Carmarthen Bay before winter 2006, meaning that data were only available from incomplete surveys of Burry Inlet in the years preceding the cockle crash.

3. RESULTS

3.1. Oystercatcher body condition on the Burry Inlet SPA

The linear regression of body weight against wing length showed a strong significant relationship (β =

3.44 ± 0.16, $t_{1,1742}$ = 20.85, p < 0.0001). The residuals extracted from these to provide an index of body condition were then used as the response variable in the GLM, where the final model (body condition index ~ total cockle biomass + time to high tide + sex + age, individual as repeated subject) indicated that the body condition indices of adults were significantly greater than those of sub-adults and juveniles (t = 9.58, p < 0.001), were negatively related to the time after high tide (t = −7.06, p = 0.0047) and were slightly greater in females (t = −5.64, p < 0.0001). Based on this final model, analysis indicated no significant relationships between body condition index and total biomass of cockles available in a given winter (adults: t_{11} = 0.168, p = 0.870; subadults: t_{11} = 0.721, p = 0.486; juveniles: t_9 = 0.835, p = 0.425). The analysis of this relationship did not show any significant trend (t_{11} = 0.131, p = 0.898) in body condition with an increase in cockle biomass (Fig. S3).

Mean annual body condition indices showed considerable variation, but were lower in 2005 (the winter following the crash in cockle stocks) and improved the following year the same as they did following the cold winter of 2010 (Fig. S4).

3.2. Apparent survival of oystercatchers on the Burry Inlet SPA

The 2 best-fitting models for the recapture data (i.e. those with the lowest $QAIC_c$ value, 2518.90) were ones where apparent survival post-2000 was correlated with total cockle biomass and had a combined model weight of 82% (Table 1). In the best model, adult survival dropped from an average of 99.3% (range: 98.3–99.9%) to 78.5% (68.5–84.3%) during the years following the crash in cockle stocks in winter 2004, before rising back to 99.5% (99.0–99.9%) (Fig. 3a). Although survival was poorly estimated using the fully time-dependent model, a regression with cockle biomass (Fig. 3b) had a substantially lower AIC value than either the fully time-dependent or time-constant model (Table 1). Furthermore, a model in which survival was estimated separately pre-, during and post-crash had a similarly lower AIC value and estimated survival in the crash year of 0.78 compared to a survival probability pre- and post-crash of >0.90.

Extremely high survival estimates for oystercatchers are not unusual (Duriez et al. 2009), but with the

Table 1. Comparison of models of apparent survival rates of oystercatchers on the Burry Inlet Special Protection Area based on recaptures of ringed individuals. Except in the second model, young bird survival rates were held constant in all models, as there were insufficient data to accurately estimate annual variation; adult survival rates were held constant up to 2000, and beyond 2001 they varied either with the cockle biomass coefficient or between specified blocks of time; recapture rates were held constant pre and post 2001 though different in each age class. The model in **bold** is the best fitting when comparing quasi-likelihood adjusted Akaike's Information Criterion ($QAIC_c$) (c = 1.24)

Model	$\Delta QAIC_c$	Parameters	Model deviance	Model weight
Young bird φ(.); adult φ(.) up to 2000 then correlated to total cockle biomass	0	7	388.68	0.53
Adult and young bird φ(.) up to 2000 then correlated to total cockle biomass	1.20	8	387.88	0.29
Young bird φ(.); adult φ(.) up to 2000 then blocked into pre-crash, crash (winters 2004–2010) and post-crash years	2.79	8	389.46	0.13
Young bird φ(.); adult φ(.) up to 2000 then blocked into pre-crash, crash (winter 2004) and post-crash years	5.08	8	391.75	0.04
Young bird φ(.); adult φ(.) correlated to total cockle biomass	9.01	6	399.69	0.01
Young bird φ(.); adult φ(.) up to 2000 then blocked into pre-crash and crash onwards (winter 2004)	14.66	7	403.34	0.00
Young bird φ(.); adult φ(.) blocked into pre-crash, crash (winters 2004–2010) and post-crash years	15.14	6	405.83	0.00
Young bird φ(.); adult φ(.) blocked into pre-crash, crash (winter 2004) and post-crash years	17.15	6	407.84	0.00
Young bird φ(.); adult φ(.) blocked into pre-crash and crash onwards (winter 2004)	18.33	5	411.02	0.00
Young bird φ(.) and adult φ(.) pre-2000 and post-2000	18.81	6	409.50	0.00
Young bird φ(.) and adult φ(.)	26.61	4	421.30	0.00
Young bird φ(time) and adult φ(time)	64.49	56	355.07	0.00

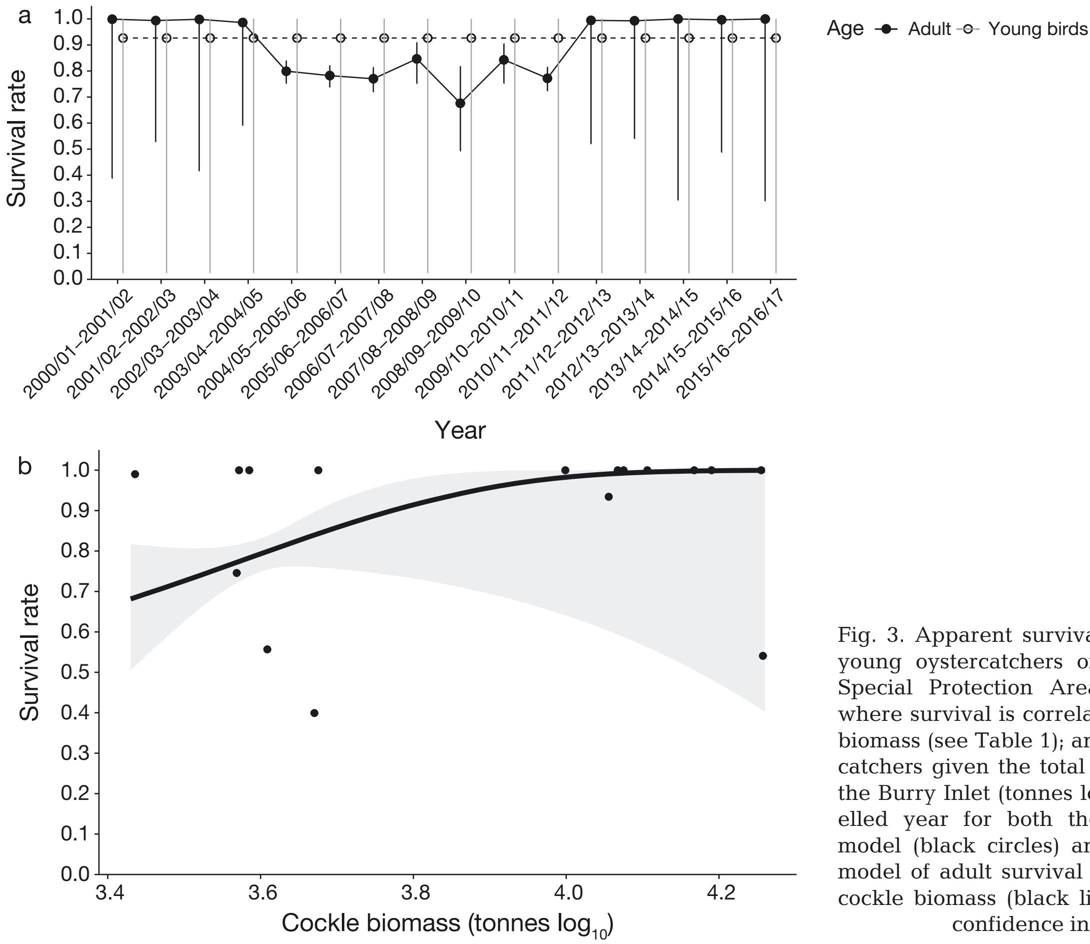

Fig. 3. Apparent survival of (a) adult and young oystercatchers on the Burry Inlet Special Protection Area using a model where survival is correlated to total cockle biomass (see Table 1); and (b) adult oystercatchers given the total cockle biomass of the Burry Inlet (tonnes $\log_{10}$) in each modelled year for both the time-dependent model (black circles) and the best fitting model of adult survival correlated to total cockle biomass (black line and grey 95% confidence intervals)

low numbers of recaptures across the whole study (216 adults and 45 juveniles and subadults), there are some boundary effects pushing predictions potentially higher than previously reported.

3.3. Winter population recruitment

Recruitment, as indicated by the ratio of juveniles to adults in catches of oystercatchers, varied widely between years, from 0.01–0.57 juveniles per adult (displayed per 100 adults in Fig. 4). Recruitment increased between the winters of 2001–2004 but was lower thereafter. There was no statistically significant relationship between the recruitment index and average winter temperatures, either directly ($\beta = -1.071 \pm 2.469$, $t_{26} = 0.434$, $p = 0.668$) or when offset by 1 yr ($\beta = 1.189 \pm 2.424$, $t_{25} = 0.490$, $p = 0.628$), which both allow for the years with missing information (when no captures were made) and an abnormally large catch in winter 1995.

3.4. Comparing wintering populations in the Burry Inlet SPA and Carmarthen Bay

WeBS Core Count data showed a significant long-term decrease in the population of oystercatchers wintering in the Burry Inlet ($t_{1,41} = -3.76$, $p = 0.0005$) and a long-term increase in the population in Carmarthen Bay ($t_{1,41} = 11.8$, $p < 0.001$) (Fig. 5). The wintering oystercatcher population in Carmarthen Bay was significantly negatively related to that in the Burry Inlet ($t_{1,41} = -5.295$, $p < 0.001$; Fig. 6a). The wintering oystercatcher populations in the Burry Inlet and Carmarthen Bay showed weak positive ($t_{1,16} = 1.705$, $p = 0.108$) and significant negative ($t_{1,16} = -2.430$, $p = 0.027$) relationships, respectively, with total cockle biomass in the Burry Inlet (Fig. 6b).

Lack of data from the Low Tide Count surveys before the crash and spatial autocorrelation prevented formal analysis, but visual inspection of the dot density maps (Fig. S2) highlights changes in foraging distributions that are consistent with the

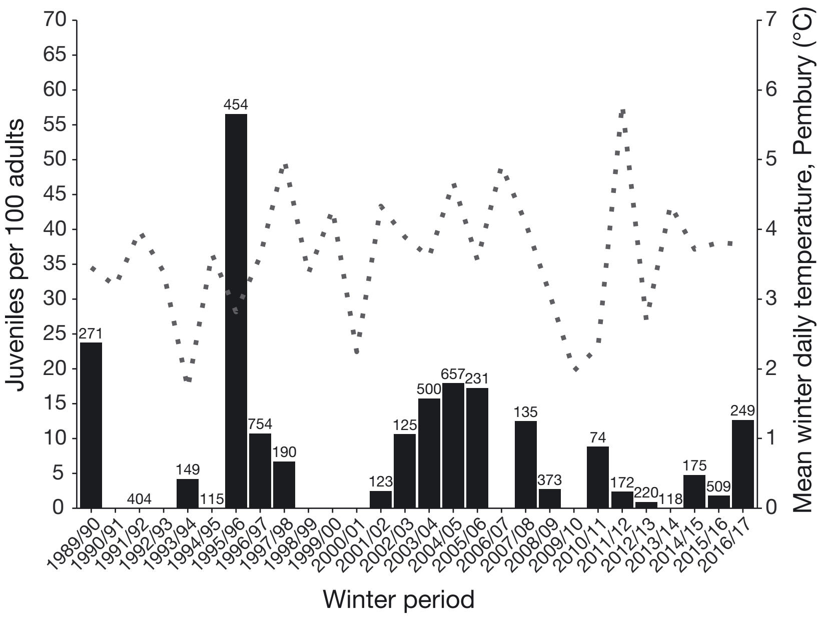

Fig. 4. Number of juvenile oystercatchers per 100 adults for all catches on the Burry Inlet Special Protection Area where oystercatchers were aged. Sample size is displayed for each year; average winter temperature October–March (for Cardiff Bute Park/Pembury Sands, dotted line) is displayed for each winter (Met Office 2012, 2018)

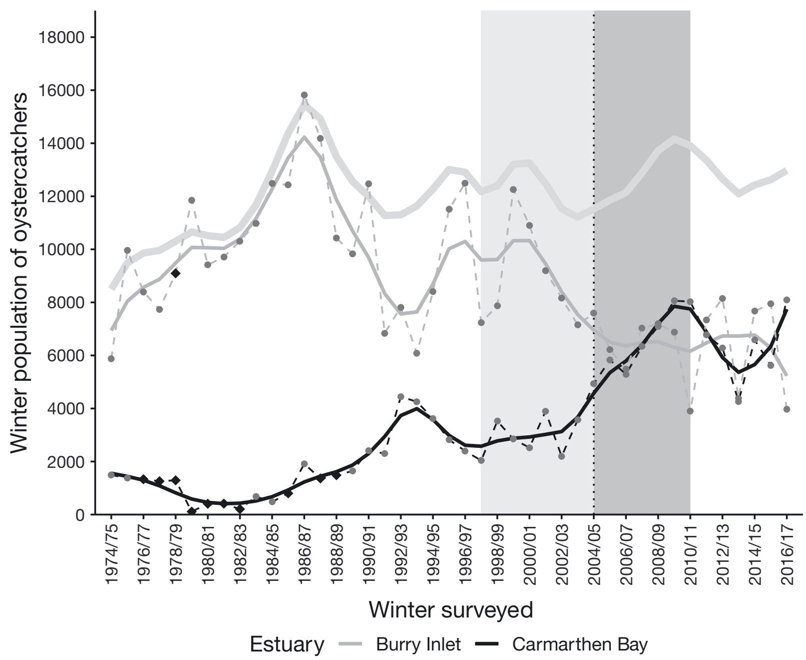

Fig. 5. Average winter populations of oystercatchers in the Burry Inlet (grey line) and Carmarthen Bay (black line) Wetland Bird Survey sites between 1974–1975 and 2016–2017 (thicker grey line: combined trend across the 2 locations). Light grey shaded area: the period of decline (1997–2004) in the cockle stocks on the Burry Inlet; darker grey: the years following the crash in stocks (dotted vertical line) until their partial recovery (data from CEFAS/NRW). Mean counts (circles and dashed line) are for November–March each winter; values for missing or poor quality counts (black diamonds) are imputed using the Underhill method; a smoothed trend (solid lines) is provided by a generalized additive model (see Section 2.3.4 for further details)

changes in numbers indicated by the WeBS Core Counts. Notably, during years immediately following the cockle crash (from 2004), densities of oystercatchers in the southern part of the Burry Inlet were reduced, while densities in Carmarthen Bay increased. Subsequently, after the initial recovery in cockle stocks (from 2010), densities in Carmarthen Bay fell.

4. DISCUSSION

The crash in Burry Inlet cockle stocks reduced the number of birds using the area and was matched by a concurrent increase in the number of birds using nearby Carmarthen Bay, although recruitment of juveniles into the local population was not affected. Despite the sparse recapture data, quantifying survival rates enabled us to show that apparent survival was reduced in the years of low cockle biomass, indicating either additional mortality as a result of reduced food supplies or that birds permanently emigrated from the site. Either way, habitat suitability was reduced, which may have been a result of birds experiencing poor body condition in the year of the crash.

Interestingly, this effect was weaker than was observed in a preliminary analysis (Burton et al. 2010) in which a shorter period of time was analysed (1989–2008 winters) when comparing a similar model (effect of a single crash year). In open biological systems such as that studied here, the ability of individuals to emigrate from the study site reduces the chance of observation and may thus increase apparent mortality during events of interest (Schaub & Royle 2014). In this study, the WeBS Core Counts indicated that oystercatcher populations increased in nearby Carmarthen Bay as the Burry Inlet population fell. It is probable that some birds that moved from the Burry Inlet during the period of

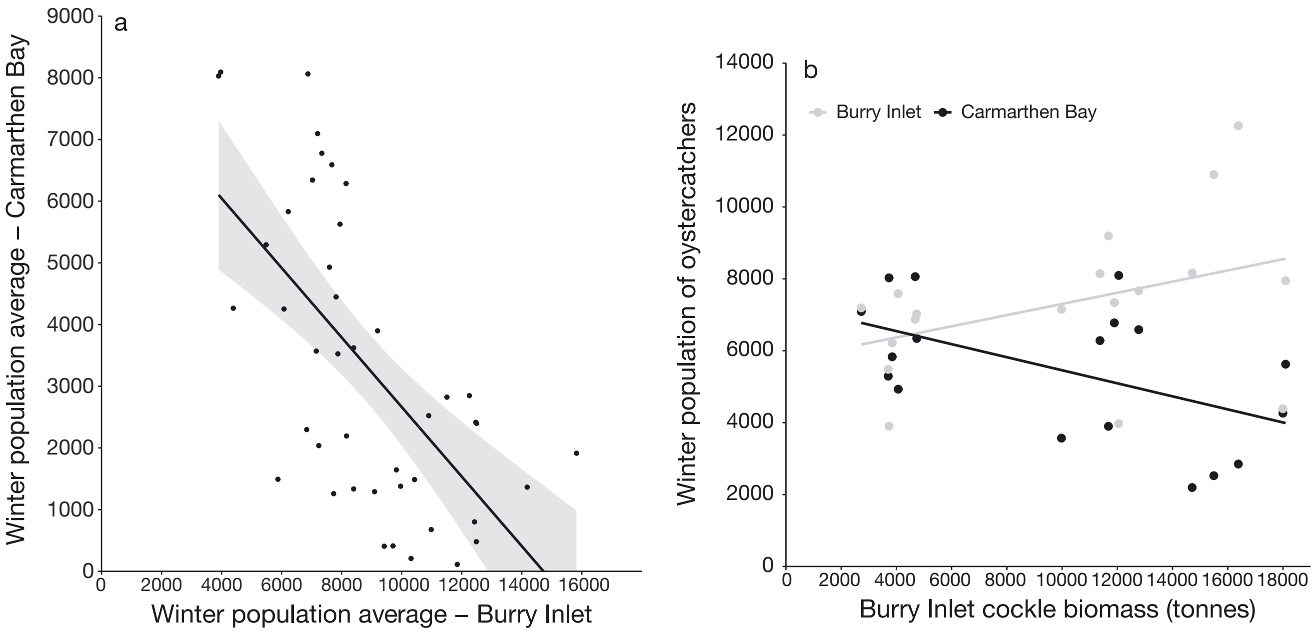

Fig. 6. Relationship between average winter populations of oystercatchers (Frost et al. 2018) in the Burry Inlet and Carmarthen Bay Wetland Bird Survey (WeBS) sites (Frost et al. 2018) correlated against (a) each other and (b) total biomass of cockles on the Burry Inlet for Carmarthen Bay and Burry Inlet WeBS sites (data from CEFAS/NRW)

the cockle crash subsequently returned — as evidenced by the changing distributions shown by the WeBS Low Tide Counts. This consequently meant that they were unavailable for recapture, and thus the reduction in apparent survival during the crash shown by the present analysis provided a closer reflection of changes in actual survival. While many waders are site-faithful, oystercatchers have previously been shown to move foraging areas and change to alternative diets (Evans 1976, Duriez et al. 2009); the shift back to the original feeding area is not always a quick process. The previous study (Burton et al. 2010) is therefore likely to have been, in part, showing the movement of oystercatchers away from Burry Inlet rather than an increased mortality rate. It should be acknowledged at this point that the low recapture probabilities resulted in unexpectedly high survival rate estimates in the earlier and later years of the study. Although these points do not alter our conclusions, they do highlight the need for sufficient capture effort when quantifying changes in survival.

This comparison between the 2 studies highlights the importance of long-term studies to fully understand the implications of different events (Clutton-Brock & Sheldon 2010, Lindenmayer et al. 2012, Taig-Johnston et al. 2017); in particular, it has been highlighted in other fields that long survey periods are needed to distinguish true effects from misleading trends (Somerfield et al. 2014, Cusser et al. 2020). Eurasian oystercatchers typically live for 12 yr but can live as long as 41 yr (Robinson 2005), so a small decrease in annual survival can have an important effect on population levels in such long-lived birds. This is of particular significance, as studies indicate that adult survival is key to understanding population growth in longer-lived species (Sæther & Bakke 2000). Whilst we might have expected there to be some influence of winter temperature on recruitment, there is also a significant influence of conditions on the breeding grounds — which were not possible to measure due to the varied breeding origins of birds wintering at the study site (Robinson et al. 2020).

Assessment of body condition and survey data provided an understanding of how the Burry Inlet's oystercatchers were able to regulate their energetic reserves under serious conditions of food depletion. However, body condition can be both positively and negatively correlated with fitness (Cresswell 2009). Adult birds were in better body condition than subadults and juveniles during the study period (Atkinson et al. 2000b); possibly due to their abilities to support themselves through either alternative resources, moving between foraging areas (Evans 1976, Duriez et al. 2009) or social dominance over younger individuals (Marchetti & Price 1989). Changes in mean annual body condition suggested an initial impact on birds in the year following the crash, although there was considerable variation in these indices across the study period, which could have been due to a shift in diet. Oystercatchers are known to also feed on other bivalves and soil invertebrates (Smit et al. 1998), and there are many invertebrates other than cockles available in the Burry Inlet system and Carmarthen Bay area (Countryside Council for Wales 2005, 2009). Fieldwork carried out by the Welsh Government has found that in addition to these other invertebrates, small cockles (first year) were eaten by oystercatchers in the Burry Inlet system (M. Murphy pers. comm.). Such resources could have provided buffering for lower levels of their preferred prey in the years following the crash, and the WeBS count data combined with the oystercatcher's adaptability suggest they may have taken advantage of alternative prey and feeding areas. This adaptation, though, requires time to learn the best locations and prey to feed upon (Bernstein et al. 2006, Hand et al. 2010).

Cockle mass mortalities are an example of a multifactorial problem (Stillman et al. 2010, Elliott et al. 2012), the underlying cause of which remains unresolved despite some of the several possibilities having been eliminated (Callaway et al. 2013, Burdon et al. 2014). Mass mortality events in cockle populations have been recorded in northwest Europe for more than a century, but the number of unexplained bivalve mortality events is apparently increasing (Elliott et al. 2012, Malham et al. 2012). Cockle management responses are constrained at the site level by the lack of positively identified causes, but the present study indicates that conservation objectives can still be met if protected area networks provide alternative sites and prey species for the duration of the events — i.e. are functionally resilient. Portions of the cockle stock have been held back from harvesting in reserve for birds on the Three-River system of Carmarthen Bay (South Wales, <10 km west of the Burry Inlet), which may help to explain the attractiveness of this alternative area for the oystercatchers that would normally use the Burry Inlet (Otto et al. 2007). Elsewhere, similar reductions in cockle stocks have had severe consequences for oystercatcher populations (Smit et al. 1998, Atkinson et al. 2005, 2010), and oystercatcher populations have taken many years to even partially recover (Frost et al. 2019). In the present study, an apparently previously less-utilised area within the Carmarthen Bay SAC for oystercatchers became a vital resource that mitigated the effects of a collapse in the birds' preferred food resource within the neighbouring Burry Inlet SPA.

Understanding how birds can respond to changing food resources is important given the changing climate shifting the distribution of invertebrate prey stocks (Beukema et al. 2009, Schückel & Kröncke 2013) and pressures to change fisheries quotas (Murray & Tarrant 2015). The ongoing cockle decline in the Burry Inlet is of concern for both the fishermen reliant on the stocks and conservation managers monitoring bird populations. Whilst this study suggests that oystercatchers may be adaptable during periods of stress, the consequences for their fitness will be dependent on the availability of alternative foraging areas and the levels of intraspecific competition that individuals will face (cf. Burton et al. 2006, Goss-Custard et al. 2006). This study demonstrates an example of site-resilience in a protected area network. Including protected 'secondary habitats' as vital components of a resilient site network can facilitate foraging adaptation and minimise the impact of environmental changes on protected species (McLeod et al. 2009, McCook et al. 2010, Johnston et al. 2013, Hopkins et al. 2016).

The analysis of long-term data sets allows more accurate understanding of incidents such as the cockle crash investigated here and improves our abilities to manage their effects on longer-lived species such as waders. Only through long-term monitoring is it possible to fully understand the consequences of major changes in species' resources and how individuals might adapt to mitigate impacts. Coastal zones are facing increasing developmental and environmental pressure, with over 38% of the world's human population and more than 60% of the Welsh population living in them (Shi & Singh 2003, WWF Cymru 2012). Global pressures in the marine environment have consequently escalated, and are now widespread (e.g. Halpern et al. 2008, McCauley et al. 2015). Understanding how species adapt to pressure will allow the development of more sophisticated and resilient protected networks; the present study suggests that these networks should promote the inclusion of alternative foraging areas, over and above what might have been used in the recent past.

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