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Report

Shellfish Fishery Severely Reduces Condition and Survival of Oystercatchers Despite Creation of Large Marine Protected Areas

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ABSTRACT. Fisheries and other human activities pose a global threat to the marine environment. Marine protected areas (MPAs) are an emerging tool to cope with such threats. In the Dutch Wadden Sea, large MPAs (covering 31% of all intertidal flats) have been created to protect shellfish-eating birds and allow recovery of important habitats. Even though shellfish fishing is prohibited in these areas, populations of shellfish-eating birds in the Wadden Sea have declined sharply. The role of shellfish fisheries in these declines is hotly debated, therefore, we investigated the effectiveness of MPAs for protecting oystercatcher (*Haematopus ostralegus*) populations. Shellfish stocks (cockles, *Cerastoderma edule*) were substantially higher in the MPAs, but surprisingly this has not resulted in a redistribution of wintering oystercatchers. Oystercatchers in unprotected areas had less shellfish in their diet and lower condition (a combined measure of mass and haematological parameters), and their estimated mortality was 43% higher. It is likely, therefore, that shellfish fishing explains at least part of the 40% decline in oystercatcher numbers in recent years. Condition and mortality effects were strongest in males, and the population sex ratio was female biased, in agreement with the fact that males rely more on shellfish. The unprotected areas apparently function as an "ecological trap," because oystercatchers did not respond as anticipated to the artificial spatial heterogeneity in food supply. Consequently, the MPAs are effective on a local scale, but not on a global scale. Similar problems are likely to exist in terrestrial ecosystems, and distribution strategies of target species need to be considered when designing terrestrial and marine protected areas if they are to be effective.

INTRODUCTION

The efficiency of the fishing industry and its potential ecological impact on marine environments have increased dramatically in recent decades as a result of technical innovations (Collie et al. 2000, Jackson et al. 2001). Marine protected areas (MPAs) are becoming increasingly popular as a protection tool to reduce these effects. The possibilities and limitations of MPAs are therefore an important research topic, to evaluate their effectiveness and aid the development of effective "design rules" for them (Lubchenco et al. 2003, Gell and Roberts 2003).

A well documented example of increased exploitation of the marine environment as a result of technical innovation is the manifold increase in cockle (*Cerastoderma edule*) landings from the Dutch Wadden Sea since the introduction of suction dredging (Ens 2003). To protect shellfish-eating birds and to

restore important habitats (e.g., eel grass (*Zostera* sp.) and mussel (*Mytilus edulis*) beds), MPAs were created in 1993 in which shellfish fishing was prohibited (Department of Agriculture, Nature Conservation and Food Quality 1993). These MPAs initially comprised 26% of the area of tidal flats in the Dutch Wadden Sea; a further 5% was protected in 1999. In addition, it was stipulated that the shellfish present after fishing in the whole Wadden Sea had to be at least 60% (70% since 2001; cockles and mussels combined) of the estimated food requirements of shellfish-eating birds, most notably the European oystercatcher, *Haematopus ostralegus*, (for the remaining 30–40%, birds were assumed to rely on other food sources such as worms and baltic tellin, *Macoma baltica*). As food reservation was independent of shellfish distribution, an implicit assumption was that birds would redistribute themselves over the Wadden Sea following an ideal free distribution (Fretwell and Lucas 1970). This assumption was later justified in court by the

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observation that birds can fly and can, therefore, be expected to exploit resources anywhere in the Wadden Sea.

Populations of shellfish-eating birds have declined in recent years, despite the presence of large MPAs. Winter mortality of eider ducks (*Somateria mollissima*) reached unprecedented levels in recent years and all available data indicate that this was due to food shortage (Camphuysen et al. 2002). Numbers of knots (*Calidris canutus*) wintering in the Dutch Wadden Sea have declined sharply in recent years, but little is known of the causal factors (van Roomen et al. 2002). Both the breeding population (Hulscher and Verhulst 2003) and the number of oystercatchers wintering in the Wadden Sea have steadily declined in recent years. In winter, oystercatchers eat mainly cockles and mussels (Ens et al. 1996, Zwarts et al. 1996b), and eiders and knots also rely on shellfish. Food shortage caused by shellfish fishing has been suggested as the cause of the population declines of all three bird species, but direct support for this hypothesis is lacking.

We used the creation of MPAs in the Dutch Wadden Sea to investigate the effect of the shellfish fishery on oystercatchers, and to test the assumption that, for birds, it is sufficient to protect resources without taking into account their spatial distribution. We first investigated whether oystercatcher numbers in MPAs have increased relative to unprotected areas, as would be expected if birds were to track the changes in cockle abundance. Even when relative bird numbers have increased in MPAs, such a change in distribution may not be sufficient to equalize conditions. Therefore, we also investigated the effect of MPAs on condition and mortality, using three condition indices: mass, hematocrit, and buffy coat (the latter two are the proportion of blood volume taken by red and white blood cells, respectively). Each of these condition measures has its merits and limitations, but our data on condition-dependent mortality (see below) show that birds with high mass, high hematocrit, and low buffy coat have higher survival rates, which is in itself sufficient justification for the purpose of this study. There are few studies that have evaluated the correlations between physiological parameters and fitness components, but the available studies support our use of these measures as condition indices (Gustafsson et al. 1994, Ebbinge and Spaans 1995, Piersma et al. 1996, Moreno et al. 1998, Verhulst et al. 2002).

The creation of MPAs was not intended as a scientific experiment. Nevertheless, we assume that, on average, the only difference between protected and unprotected areas is the possibility to legally harvest shellfish. With respect to the original distribution of the cockles, this seems reasonable because protected sites were selected without regard to cockle stocks (van der Have 2003) and fishing intensity was identical in all areas before the creation of the MPAs (de Vlas, *unpublished*). A large difference in cockle stocks between protected and unprotected areas has developed, both as a direct effect of removing cockles and an indirect effect of cockle fishing on cockle recruitment (Piersma et al. 2001). For example, in September 2000, there was an estimated 9775 tons of cockle meat in the unprotected 69% of the area and an estimated 27 000 tons in the protected 31% (a sixfold difference in cockle stocks between areas). The fishing industry was given a license for autumn 2000 to catch all remaining stock in the unprotected areas (Department of Agriculture, Nature Conservation and Food Quality 2000), further increasing this difference. (We use the cockle stocks of autumn 2000 as an illustration because they are closest in time to our bird captures. See Kamermans et al. (2003) for a detailed description of the development of cockle stocks in recent years.)

METHODS

Data Collection

Integral bird counts in the Dutch Wadden Sea have been organized annually since 1972, and have in recent years been coordinated by SOVON Vogelonderzoek Nederland (Koffijberg et al. 2000, Leopold et al. 2004). The Wadden Sea is divided into 35 sub-areas, which were assigned to either the protected or the unprotected area. The counting areas were not designed to study the MPAs, and a few counting areas were assigned to an "intermediate" category. We ignored these in the analysis. Counts were done in different months in different years, and we restricted the analysis to January counts, because these were done in all recent years. Counts of areas were not always complete, and incomplete counts were interpolated using UINDEX (Underhill and Prys-Jones 1994).

We captured 520 oystercatchers at seven sites around the Dutch Wadden Sea (protected: n = 9, 149, 72, 169; unprotected: n = 36, 64, 20) with cannon nets or mist

nets (first site only). Time between first and last capture date was 34 days, and capture date did not differ systematically between protected (25 January, 1 February, 6 February, and 1 March, 2001) and unprotected sites (30 January, 16 February, and 27 February, 2001). All captures were in the vicinity of a site where a cockle bank had been present according to recent surveys (Craeymeersch et al. 2000).

Biometric parameters were measured following standard techniques (Le V.dit Durell et al. 1993). Bill tip shape was classified (Hulscher 1985), and birds were sexed on the basis of bill morphology (Zwarts et al. 1996a), a method that yields 87% correct sex. Birds were aged on the basis of plumage, bill, and leg characteristics. Age is expressed either as minimum age in calendar years (birds born in 2000 and captured in 2001 were in their 2nd calendar year), or in a yearling/older dichotomy when the analysis indicated that age effects were only found between yearlings and older birds. Age classes can be recognized up to the 4th calendar year, older birds are scored as >4th calendar year. All birds were color ringed.

Blood samples (one heparinized capillary, approximately 65 μL) were taken from the brachial vein, and centrifuged 10 min at 12477 g. Buffy coat and hematocrit were measured by Simon Verhulst using sliding callipers and a magnifying glass. Repeatabilities were high: hematocrit: r (s.e.) = 0.98 (0.007), buffy coat: r = 0.94 (0.02), n = 30 duplicate samples, both $F_{1,29} > 34.6$, $P < 0.0001$.

Calculations and Statistical Analysis

Statistical comparison of parameters between protected and unprotected areas was done using a randomization test (Adams and Anthony 1996). In brief, two grand means were calculated from the means per capture. The difference between these two means ($D = x_{unprotected} - x_{protected}$) was taken as test-statistic. The distribution expected under the null hypothesis $D = 0$ was generated by randomly distributing all values over the captures >10 000 times. The two-tailed P-value is the proportion of runs with more extreme (absolute) values of D than the observed (absolute) D. Thus, the tests are two tailed.

As input for the randomization tests, we used the residuals of multiple regression analysis to correct for confounding variables, because this was not possible within the context of the principal component analysis or the randomization test. Hematocrit and buffy coat are proportions and were arcsine square root transformed before analysis. Multiple regression models were selected using backward deletion of least significant terms until only significant terms remained. For the condition parameters, the following regression models were selected (with s.e. and P-value in parentheses): Mass = 16.0 (73.6, 0.82) + 68.4 (47.2, 0.14) * Ht – 170.1 (63.3, 0.007) * Ht^2 – 17.7 (3.9, 0.001) * sex + 17.1 (1.5, 0.001) * age + 2.2 (1.0, 0.01) * head + 4.0 (0.7, 0.001) * tato, R^2 = 0.33, n = 515, where Ht is the holding time between capture and measuring, in proportion of 24 h; sex is a dummy variable (females = 0, males = 1); head (in mm); tato (in mm) is length of tarsus plus middle toe up to the nail. Wing length was not entered, because it depends on state and behavior: high flight activity results in shorter wings. Hematocrit = 0.478 (0.004, 0.001) + 0.039 (0.016, 0.017) * Ht; R^2 = 0.02, n = 330. In the analysis of mass and hematocrit, there were no significant interactions of capture with holding time, sex or age. Buffy coat = 0.0065 (0.00009, 0.001) + 0.0013 (0.0002, 0.001) * yearling, R^2 = 0.11, n = 330, where yearling = 1 for birds in their 2nd calendar year, and yearling = 0 for older birds.

To avoid multiple testing of the same null hypothesis when comparing condition, we used principal component analysis to summarize our data (Hair et al. 1998). The first component explained 37% of the variation, and loading was approximately equal for each of the three parameters (mass: 0.53; hematocrit: 0.61; buffy coat: -0.58). Thus, high mass, high hematocrit, and low buffy coat resulted in a high value of the first principal component. In the remainder of this paper we refer to the first principal component as "condition."

Mortality estimates were based on birds reported dead by the public (n = 14). One capture site (Mokbaai on Texel) is a permanent study site where observation intensity is very high (>7 observations per individual per winter). Four out of 70 birds released at this site were not seen the next winter (2001–2002), and we assume that these four birds had also died (n = 18 dead birds total). The correlation between condition and the probability of death was investigated using logistic regression; P-values were calculated using F-tests. Capture site was included as factor to accommodate spatial variation in recovery probability and, therefore, only sites from which at least one bird was presumed dead were included (n = 458 birds, n = 5 sites).

RESULTS

Numbers and Distribution

In 1987 and 1997, numbers in January were very low because of temporary frost migration (Ens 2003) and we omitted these years from the analysis. The total number of oystercatchers wintering in the Dutch Wadden Sea has decreased from 250 000 to 150 000 in recent years (Fig. 1; $F_{1,12} = 22.0$, $P < 0.001$, using log-transformed numbers). However, there is no indication that the oystercatchers have redistributed themselves with respect to the cockle food supply, because oystercatchers have not become relatively more numerous in the protected areas (Fig. 1; interaction period * regime: $F_{1,24} = 2.17$, $P = 0.2$). Thus, the data do not support the assumption made in the food reservation policy that birds will redistribute themselves in response to a change in distribution of their main food source. Note that, when viewed on a much longer time scale (since the 1970s), the proportion of oystercatchers wintering in the protected areas has actually declined (Leopold et al. 2004), but our analysis indicates that this trend did not continue after 1986.

Fig. 1. Numbers of oystercatchers declined in recent years, but relative numbers in protected and unprotected areas did not change. Numbers counted in January in protected (before □, and after ■ protection became effective) and unprotected areas (○), and the total counted in the Dutch Wadden Sea (●). The dashed vertical line indicates the year that protection became effective.
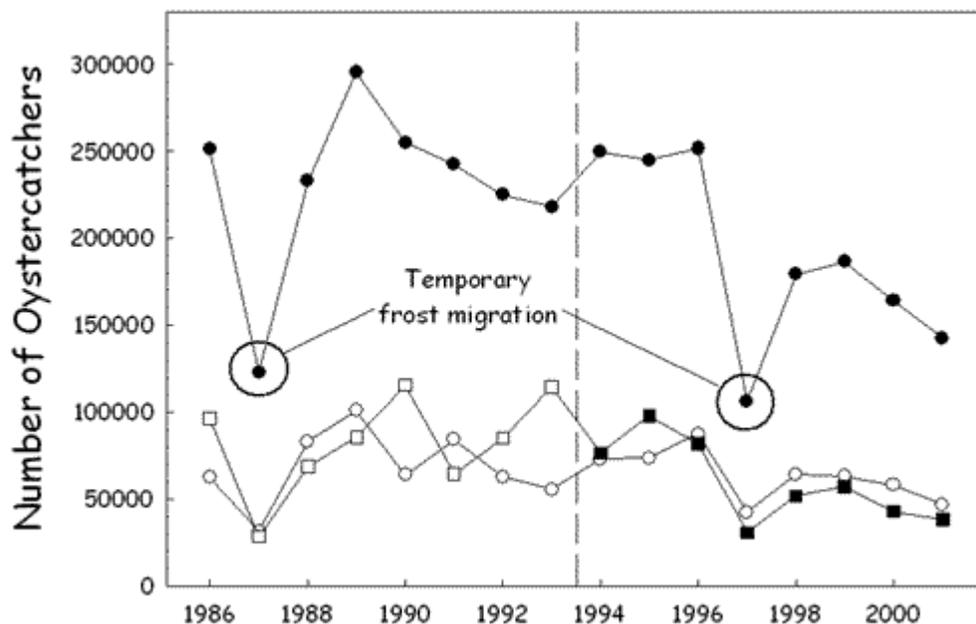

Captures

There was no difference in body size or age between oystercatchers in protected and unprotected areas (Fig.2A; randomization test, all $P > 0.5$). The absence of an age difference is important because, on a local scale, the young birds are concentrated on roosts where birds generally have lower phenotypic quality (Swennen 1984). This suggests that there is no accumulation of individuals of low "phenotypic quality" in unprotected areas.

Did oystercatchers in the protected areas eat more shellfish? In oystercatchers, individual differences in diet can be inferred from the abrasion of the bill tip: pure shellfish diets typically result in blunt tips (Sutherland et al. 1996). Bill tip shape is flexible, in the sense that it changes following a dietary switch (Hulscher 1985). The proportion of oystercatchers with "shellfish tips" was higher in the protected areas (40.3%, $n = 4$ sites, vs. 24.5%, $n = 3$; $P < 0.02$). This difference was similar in the two sexes but, at each site, pure shellfish eaters were more numerous among males (males: 55.6%; females: 14.5%; $n = 7$). Thus, males may be more vulnerable to low shellfish stocks than females.

Fig. 2. Body size, age, and condition of oystercatchers. Shown are differences between protected and unprotected areas, expressed as standard deviations (of overall mean) to facilitate comparison of different measures. A. Oystercatchers in protected and unprotected areas did not differ in age or body size. B. Condition and the three condition components (mass, hematocrit [Hct], and buffy coat) for the sexes, both combined and separately (indicated by C, F, and M, respectively, above bars). High buffy coat indicates low condition and, for the sake of simplicity, the sign was reversed in the graph. Sample sizes: $n = 330$ for condition and haematological parameters (177 females, 153 males), and $n = 515–520$ for mass, size, and age (284 females, 231 males). ** $P < 0.01$, + $P < 0.1$.
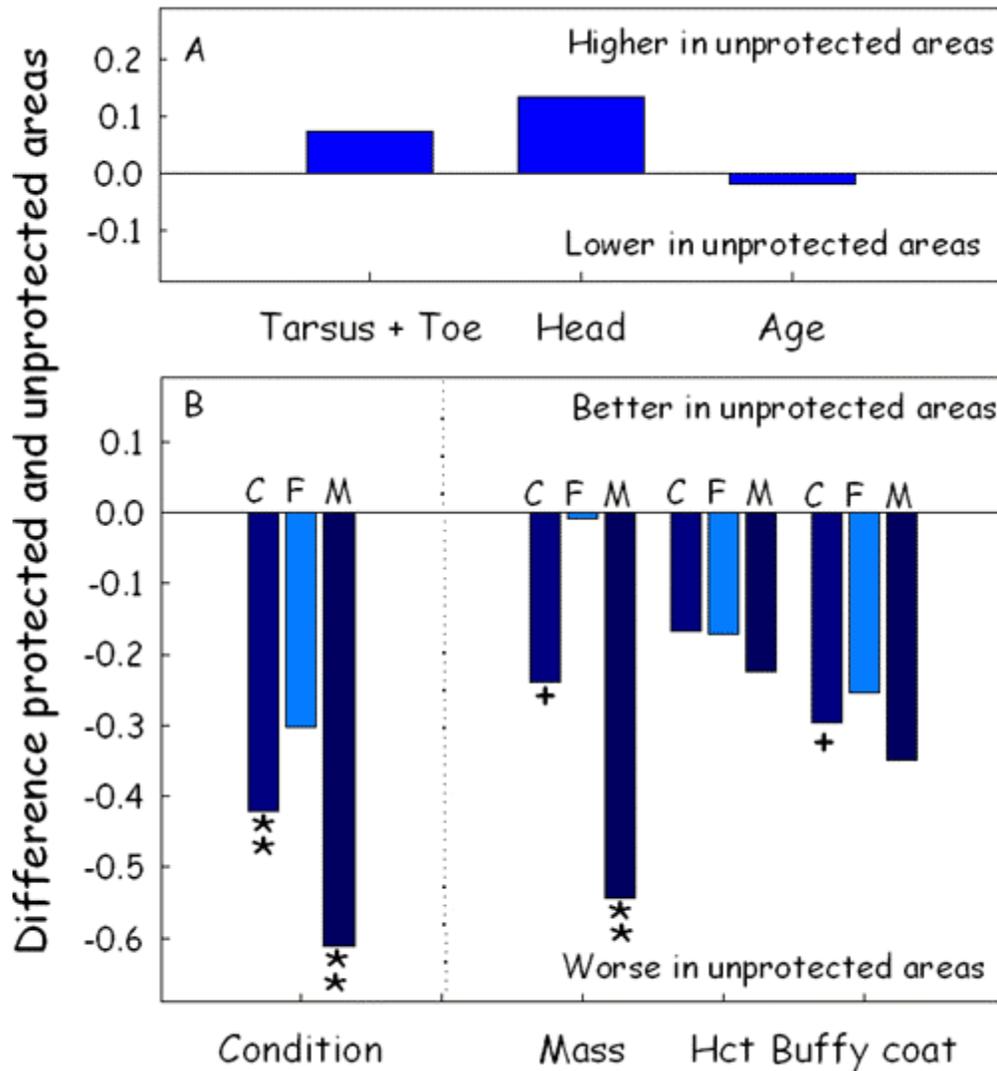
Condition was significantly lower in the unprotected areas for the sexes combined ($P < 0.01$) and in males ($P < 0.01$), but not in females ($P = 0.15$). When testing the condition components separately (sexes combined), trends were found for mass ($P < 0.09$) and buffy coat ($P < 0.06$), but not for hematocrit ($P = 0.3$). Note that these tests are two tailed and thus conservative, despite a clear predicted direction of effect. The difference in male mass was significant ($P < 0.01$), but the difference in female mass was negligible; for mass, the interaction between sex and area type was significant in a one-tailed test ($P = 0.04$). Differences in haematological parameters were of similar magnitude in the two sexes but, because of reduced sample size, P-values were higher than for the sexes combined (all $P > 0.1$).

Fig. 3. Mortality in relation to condition and shellfish fishing. A. Birds reported dead had lower condition than birds not reported dead. Differences are expressed as standard deviations of the overall mean (*** $P < 0.001$, ** $P < 0.025$). Significance was tested using logistic regression, controlling for capture site (condition: $F_{1,281} = 23.5$, $P < 0.001$; mass: $F_{1,450} = 15.6$, $P < 0.001$; hematocrit: $F_{1,281} = 5.5$, $P < 0.025$; buffy coat: $F_{1,281} = 6.0$, $P < 0.025$). B. Mortality estimates were significantly higher in unprotected areas for the sexes combined (randomization test, $P < 0.02$), and for males ($P = 0.03$), but there was only a trend for females ($P < 0.1$).
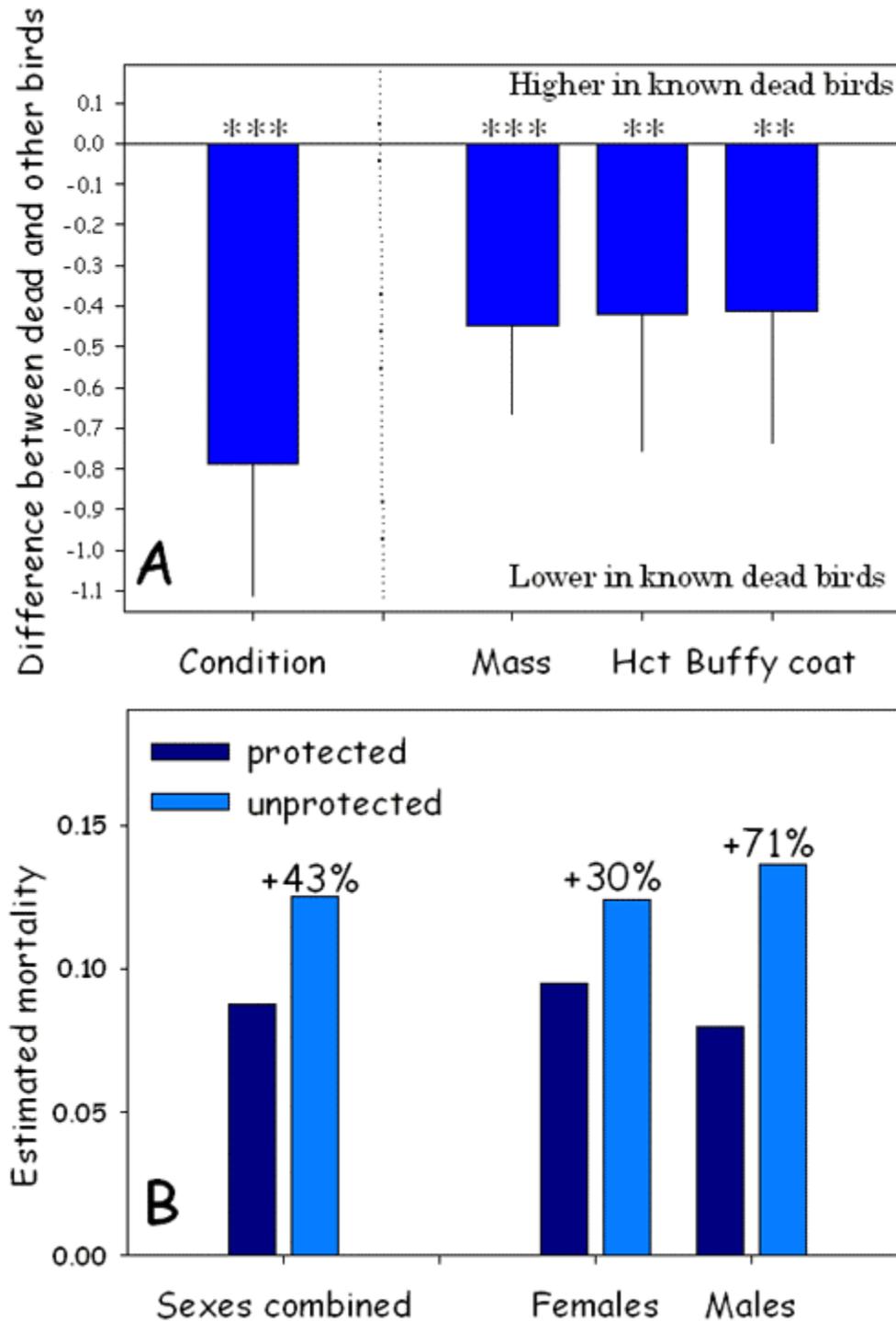
Mortality

Measures of condition are only relevant insofar as they predict variation in mortality and reproduction. Insufficient time has elapsed to estimate mortality on the basis of capture–recapture models, but birds found dead within a year scored lower for condition and its components (Fig.3A). Using the relationship between condition and the probability of being found dead, we estimated the mortality probability for the year after capture for all individuals. For birds for which there were no haematological data, we used residual mass only. Estimated probability of being found dead was corrected for the reporting probability of dead birds, which is 24% (Camphuysen et al. 1996). Mean mortality was in agreement with published mortality rates (around 10%), and the probability of death in the unprotected areas was 43% higher (Fig. 3B). In agreement with the sexual difference in diet, the mortality effect of shellfish fisheries was larger in males (Fig. 3B). There was indeed a difference in sex ratio between protected and unprotected areas (protected: 47.8% males, unprotected: 40.3%). Although this difference was not statistically significant ($P = 0.3$), overall sex ratio was significantly skewed toward females (44.6% males, $n = 518$, binomial test, $P < 0.01$).

DISCUSSION

Despite the large difference in cockle stocks between protected and unprotected areas there was no observable redistribution of oystercatchers (Fig.1). One potential explanation is that there was still sufficient food in the unprotected areas, in which case condition and mortality should be similar in MPAs and unprotected areas. However, birds in the unprotected areas had lower condition, and their estimated mortality was substantially higher. The effect on mortality, if permanent, halves the reproductive lifespan of oystercatchers in the unprotected areas. These data indicate that the shellfish fishery has caused at least part of the population decline (Fig.1). True effects of shellfish fishing on population dynamics may be even greater, when there are carryover effects of condition in winter on subsequent reproductive success. Reproductive success of Dutch oystercatchers has indeed declined in recent years (Heg 1999, Hulscher and Verhulst 2003), but a link between winter condition(s) and reproductive success remains to be established. The effect of the shellfish fishery on condition was greater in males, as predicted

from the sexual difference in diet. In agreement with these results, the sex ratio of the population was significantly female biased.

Condition was significantly correlated with mortality probability, which allowed us to use condition as an intermediary value to estimate mortality effects. This is in itself a useful result, because it shows that our measure of condition can be used as an "early warning system" to monitor environmental quality, at least for oystercatchers. A further advantage of this method is that the sample size required for a precise measurement of condition is much smaller than the sample size needed to estimate mortality on the basis of ringing data. All three condition components appeared to contribute equally to the association between mortality and condition and, for hematocrit and buffy coat, this is to our knowledge a new result. However, the combined condition measure was a better predictor of mortality than any of the components on its own (Fig. 3A), which illustrates the value of integrating different variables in one estimate of condition. Although more work is needed before more general conclusions can be drawn regarding the optimal measure of condition, our data indicate this is a research avenue worth exploring.

In the design of the MPAs and the food reservation policy, it was implicitly assumed that oystercatchers would distribute according to an "ideal free" pattern (Fretwell and Lucas 1970) but, despite large differences in cockle stocks, we found no redistribution over MPAs and unprotected areas (Fig.1). This is in agreement with data on the behavior of individual wintering oystercatchers, which show high site fidelity (Dare 1970, Goss-Custard et al. 1982, Verhulst et al. 2003). Because food intake rate decreases with increasing oystercatcher density (Ens and Cayford 1996, Triplet et al. 1999), the absence of redistribution was probably critical in generating the differences in condition and mortality. On a small scale, oystercatcher distribution has been successfully predicted assuming an ideal free distribution (Goss-Custard et al. 1996, Stillman et al. 2000) but, on a larger scale, oystercatchers apparently die rather than emigrate when faced with food shortage created by human intervention (Lambeck et al. 1996, Atkinson et al. 2000). This behavior is understandable because, under natural conditions, an oystercatcher that emigrates to avoid low cockle stocks is unlikely to encounter better feeding conditions elsewhere because cockle stocks tend to be low or high on a very large

scale (Strasser et al. 2003). More generally, the success of MPAs may depend critically on the extent to which the design is tailored to the distribution mechanisms of target species, thereby avoiding the creation of "ecological traps" (Schlaepfer et al. 2002).

SPECULATION

Wintering oystercatchers do not depend solely on cockles, but also eat other shellfish, in particular mussels (Ens 2003). When mussel beds were still common in the 1980s, the distribution of oystercatchers in the Wadden Sea was closely correlated with the area of mussel beds (Ens 1993) and it was estimated that more than half the wintering population depended on these mussel beds (Smit et al. 1998). Intertidal mussel beds had all but disappeared from the Dutch Wadden Sea by the early 1990s (Beukema 1993) and had still not recovered when we collected our data. Oystercatchers are particularly sensitive to low cockle stocks in years that mussel stocks are also low (Atkinson et al. 2003). Low mussel stocks have, therefore, probably contributed to the high mortality effect of cockle fishing. Thus, the sustainable exploitation of cockles in the future seems contingent on successful recovery of the intertidal mussel beds.

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