Towards a simplified approach for assessing bird food requirements on shellfisheries.

A report to the Welsh Government.

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1. Summary

In northwest Europe conflicts have routinely occurred between economic and conservation interests regarding shellfish such as cockles and mussels. The harvest of these species is economically important, but shellfish also constitute the main overwinter food supply of the oystercatcher *Haematopus ostralegus*. In this report we describe attempts to produced a simplified modelling approach to predict the quantities of shellfish which need to be left unharvested in order to ensure high overwinter survival of oystercatcher.

We review oystercatcher diet and prey selection in order to quantify the dependence of this species on shellfish, and determine the size ranges of shellfish which the birds consume. We also review the food requirements of oystercatchers, based on their energetic needs and the nutritional quality of shellfish. In general the data agree well with those used in previous oystercatcher modelling studies. However, there is a possibility that the daily energy requirements, calculated from an all bird allometric equation, may yield an underestimate of oystercatcher food requirements. A comparison of the physiological food requirements, *i.e.* the quantity directly consumed, and the ecological food requirements, *i.e.* the quantity required to avoid high mortality, indicated that the ecological food requirement was between 2.0 and 7.8 times greater, with the value depending on the proportion of cockles *Cerastoderma edule* and mussels *Mytilus edulis* in a site. These ratios are calculated from empirical data on oystercatcher survival and the predictions of individual-based models predicting the relationship between mortality rate and the abundance of the food supply. Data from the Burry Inlet indicated that the mean ecological food requirement was 3.3 times greater at this site.

We describe a simplified spreadsheet model, which we used to predict the food requirements of the oystercatcher population of the Burry Inlet, and thus the quantity of shellfish which must be left unharvested in order to maintain low mortality rate. The model is based on parameter values derived from the literature reviews in this study, including the energy requirements of the birds, the energy content of shellfish, the minimum size of cockles and mussels consumed, and the ratio of the ecological and physiological requirements. We describe the assumptions and limitations of the model,

and compare the model with more detailed individual-based models that can be used to predict the mortality rate of shorebirds in relation to the amount of food available.

2. Introduction

Welsh estuaries are important sites for shellfish, such as mussels (*Mytilus edulis* L.) and cockles (*Cerastoderma edule* L.), which support commercial shellfisheries. These shellfish are also the principal overwintering food resource for migratory wading birds, including the Eurasian oystercatcher (*Haematopus ostralegus* L.). These shared shellfish resources have led to conflicts between economic and conservation interests across estuaries in northwest Europe (Tinker, 1974; Ens, 2006; Laursen *et al.*, 2010). Enough shellfish must be left unharvested to allow the birds to meet their food requirements. The responses of oystercatchers and other wading bird species to insufficient food supplies during the overwinter period, which include reduced individual body condition, increased mortality and reduced population sizes, have been well-documented in the scientific literature (Camphuysen *et al.*, 1996; Verhulst *et al.*, 2004; Atkinson *et al.*, 2003; Atkinson *et al.*, 2005; Atkinson *et al.*, 2010). The latest Wetland Bird Survey (WeBS) counts reveal the continued importance of Welsh estuaries for Oystercatcher populations (Table 1).

Table 1. The five most important sites for Overwintering Oystercatchers in Wales, based on the 2010/11 WeBS counts. The mean UK population was estimated at 153,120 (Holt et al., 2012). Locations with over 3000 individuals are designated as 'Sites of National Importance in Great Britain', whilst sites with over 8000 individuals are designated as 'Sites of International Importance'.

Location	Mean no. individuals	Percentage of UK population
Dee Estuary	23,486	15.3 %
Burry Inlet	13,654	8.9 %
Carmathan Bay	11,442	7.5 %
Lavan Sands, Conway Bay	6,606	2.3 %
Swansea Bay	3,565	4.3 %

Therefore, the central question facing statutory authorities of estuaries is: how much food should be left unharvested for the bird population? Detailed individual-based models (IBMs) can predict the amount of food required by populations of shellfish-feeding birds (including oystercatchers) to survive through winter (*e.g.* Stillman, 2008; Stillman & Goss-Custard, 2010). These models have been developed for a number of shellfisheries, most recently the Burry Inlet in Wales (Stillman *et al.*, 2010). By predicting the amount of food required by the birds, these models can be used in the process of setting shellfishing Total Allowable Catch. However, specialist knowledge is required to run the models, and they have typically been applied on a site by site basis. Despite recent attempts to make IBMs more user-friendly (*e.g.* West *et al.*, 2011), model complexity is still perceived as a barrier to the successful use of IBMs. It would be preferable if a simplified approach could be used to set such Total Allowable Catches and if the approach could be used in a consistent way across a range of sites. The simplified approach could synthesis the predictions of the more detailed models. An ideal would be a piece of software into which data on the number of birds and density and species of shellfish are entered, which then predicts using simple steps, the amount of food required by the birds. The predictions should be accompanied by appropriate caveats, the assumptions used to calculated them, and confidence limits. The simplified approach could potentially be used in combination with individual-based models, highlighting priority systems in which more detailed modelling and data collection could occur.

The purpose of this project is to trial the development of such an approach for predicting the food requirements of oystercatchers. The starting point is Goss-Custard *et al.* (2004), a paper which used detailed individual-based models to predict the food requirements of oystercatchers on a range of sites. The amount of food per bird required in a site to maintain high overwinter survival was predicted (termed the *ecological food requirement*). This amount was then compared to the amount of food actually consumed by each bird (termed the *physiological food requirement*). A value termed the *ecological multiplier* describes how many times greater the ecological food requirement is relative to the physiological food requirement; the ecological requirement was predicted to be two to eight times higher than the physiological requirement. Thus more food needed to be present within a site than the quantity

actually eaten by the birds because they were not able to find all the food, because some birds could exclude others from part of the food supply (through interference competition) and because some food was lost due to factors other than the birds themselves. The difference between the ecological and physiological requirements was smaller on sites dominated by cockles than on sites dominated by mussels (Goss-Custard *et al*. 2004). This is because more birds can be excluded through interference competition from highly aggregated mussel beds than from more dispersed cockle beds. The approach of comparing ecological and physiological requirements provides a relatively simple way of predicting the amount of food that birds require to survive through winter, and also synthesises the predictions of detailed individual-based models.

3. A review of oystercatcher diet and prey selection

In this section we review the current knowledge of oystercatcher diet, prey selectivity and energetic quality. Oystercatchers have been observed to be highly selective in their choices of prey items, showing strong preferences between and within species (Sutherland & Ens, 1987). Oystercatchers are similarly selective in their feeding habitats, with the consequence that intertidal habitats support the majority of overwintering individuals, despite comprising only a small proportion of the total available landscape. For example, in the Ythan estuary (Scotland) Heppleston (1971) reported that at low tide the mussel beds (12 ha or 2.8 % of total), mud flats (173 ha or 40.4 %) and grass fields (243 ha or 56.5 %) accounted for 62.7 %, 25.6 % and 11.6 % of oystercatchers respectively. Such findings demonstrate that intertidal areas are disproportionately important to overwintering populations. In contrast, marginal habitats such as grasslands comprise large areas but support a relatively small proportion of the total population. However, these habitats themselves can be critical for bird survival at times when the birds are unable to obtain all of their daily energy requirements from intertidal habitats (e.g. Stillman *et al*. 2000).

3.1 Contributions of shellfish to oystercatcher diets

We examined the proportions of shellfish and other prey species in the diet of overwintering oystercatchers reported in the published literature (Table 2). A large body of evidence indicates the importance of cockles and mussels in the diet of

oystercatchers (*e.g.* Goss-Custard *et al.*, 1977; Ens *et al.*, 1996a; Goss-Custard *et al.*, 2006). Smaller proportions of other species may be consumed, in particular during the breeding season. These include other shellfish species such as peppery furrow shell (*Scrobicularia plana* Da Costa, 1778) and Baltic macoma (*Macoma balthica* L.), as well as non-shellfish species such as ragworm (*Nereis diversicolor* Müller, 1776) (Boates & Goss-Custard, 1989; Bunskoeke *et al.*, 1996; Ens *et al.*, 1996b). Terrestrial invertebrates such as earthworms (*Lumbricus terrestris* L.) and leatherjackets (*Tipula* spp.) may also be eaten by birds feeding in grass fields (Heppleston, 1971). However, overwintering oystercatchers are largely reliant on cockles and mussels in intertidal habitats (Heppleston, 1971; Goss-Custard *et al.*, 1977).

Table 2. The percentages of mussels, cockles and other prey items to the diet of oystercatchers, based on biomass.

Location	Date	Mussels (%)	Cockles (%)	Other (%)	Reference
Wadden Sea (Netherlands)	October 1983	25	74	1	Ens *et al.* (2006a)
Wadden Sea (Netherlands)	February 1984	32	60	8	Ens *et al.* (2006a)
Wadden Sea (Netherlands)	March 1984	27	70	3	Ens *et al.* (2006a)
Wadden Sea (Netherlands)	-	80		20	Atkinson *et al.* (2010)
Wadden Sea (Netherlands)	-	60		40	Van de Pol *et al.* (2010)
Exe Estuary (England)	Winters 1986-1991	93	7	0	Durell *et al.* (1993)
Exe Estuary (England)	Winters 1986-1991	94	5	1	Durell *et al.* (1993)

3.2 Minimum prey sizes

We found a mixture of field and model evidence regarding the sizes of shellfish which are consumed by oystercatchers. Sutherland & Ens (1987) reported that whilst oystercatchers showed preferences for mussels with shell lengths between 25-50 mm,

mussels in the 20-25 mm size class, the smallest available during the experiments, were also consumed. No mussels greater than 60 mm were consumed (Sutherland & Ens, 1987). In a set of prey choice experiments, birds offered mussels between 15 and 55 mm consistently preferred 25-35 mm mussels (Leopold *et al.*, 1989). Additionally, there is some evidence that size preferences vary seasonally with availability and profitability; Cayford & Goss-Custard (1990) observed that the mean size of mussel consumed by oystercatchers in the Exe estuary varied between 48 mm in February and 28 mm in May. In arguably the most authoritative study on oystercatcher prey selection, Goss-Custard *et al.* (2006), based on a review of published and unpublished studies, reported that mussels between 30 – 59 mm were consumed. These values have been used in previous oystercatcher models (*e.g.* Stillman, 2009; Stillman *et al.*, 2010).

Norris & Johnstone (1998) found that cockles as small as those in the 7-15 mm size class were consumed in the Burry Inlet, but that birds consumed greater proportions of larger cockles as winter progressed, possibly due to declining prey quality. Furthermore, Norris (1999) used a prey size selection model to predict that oystercatchers would consume only cockles > 15 mm in November, and > 22 mm in January, indicating some seasonal variability in minimum size selection. Above these threshold minima, prey choice experiments offering cockles in the range 20-45 mm have typically reported no significant differences between the sizes offered and the sizes consumed (Leopold *et al.*, 1989). Furthermore, Leopold *et al.* (1989) found no differences in the sizes of cockles eaten during daylight and night. Goss-Custard *et al.* (2006), based on a review of published and unpublished studies, reported that cockles between 15 – 40+ mm were consumed, which suggested that there is no maximum size for cockle prey. These values have been used in previous oystercatcher models (*e.g.* Stillman, 2009; Stillman *et al.*, 2010).

However, there are problems associated with relating the short-term prey choice experiments on captive birds to oystercatcher minimum prey size selection in the wild. Firstly, such studies typically do not offer the full range of sizes available in the wild; it is generally the smallest size classes which are omitted. Secondly, whilst captive birds may consume some very small or very large shellfish, it does not logically follow that a bird could survive a winter solely consuming these size classes. Therefore, using such data to

inform size selection in the model could underestimate the minimum size class and thus risk mortality events due to starvation.

3.3 Predicting optimal prey size selection

In view of the problems of estimating minimum prey size detailed above, using prey size-selection models (e.g. as used by Norris & Johnstone (1998)) to estimate the most profitable size classes could possibly be a more reliable approach. This section describes how these models are developed and the data required to parameterise them. The models determine which prey size classes an animal should include within its diet to maximise the rate at which it consumes energy. Whether or not prey size classes are included in the diet depends on the amount of energy (or biomass) within a prey item within each size class, the time taken to consume a prey item within each size class and the rate at which prey size classes are encountered by the animal. Most frequently size selection models have been derived from Holling's disc equation (Holling 1959) which relates the rate at which an animal can feed to the density of prey in the environment.

$$\frac{N}{T} = \frac{\lambda}{1 + \lambda h} \qquad \text{Equation 1}$$

Where N = number of prey consumed, T = time that animal is foraging for, h = handling time of prey (= time take to consume one prey item) and λ = encounter rate with prey (= number of prey encountered (e.g. seen, touched) per unit time). Prey encounter rate is related to prey density and so increases as prey density increases. This model assumes that the animal consumes each prey item that it encounters and that all prey are identical. The model predicts that the number of prey consumed per unit time (termed intake rate) is zero when encounter rate (prey density) is zero but increases to approach a maximum value as prey encounter rate (prey density) increases. One unrealistic assumption of this model is that all prey are identical. Charnov (1976) developed a multi-prey version of the disc equation that could predict the range of prey types (called size classes below) that should be included in the diet.

$$\frac{E}{T} = \frac{\sum E_i \lambda_i Q_i}{1 + \sum \lambda_i h_i Q_i} \qquad \text{Equation 2}$$

where E_i = energy content of prey size class i, h_i = handling time of prey size class i, λ_i = encounter rate with prey size class i and Q_i = probability that animal will consume prey size class i after it is encountered. Charnov (1976) showed that to maximise energy intake, Q_i = 1 if $E/T < E_i/h_i$ and Q_i = 0 if $E/T > E_i/h_i$ (note that there is a typing error in Norris & Johnstone (1998) and the "<" and ">" symbols are reversed). So the animal should consume an individual of prey size class i if its profitability (E_i/h_i; = the rate of consuming energy from the size class once it has been encountered) is above the overall energy intake rate (E/T; = the overall rate of consuming energy from a range of size classes including the time taken to encounter prey). This model makes a number of assumptions that are applicable to oystercatchers feeding on bivalves (Meire & Ervynck 1986), with the exception that prey are assumed to be identified instantaneously without error. In contrast to this assumption, oystercatchers do waste time inspecting prey that are subsequently not consumed. Meire & Ervynck (1986) therefore developed an extension to the Charnov (1976) model to account for this extra time cost.

$$\frac{E}{T} = \frac{\sum E_i \lambda_i P_i Q_i}{1 + \sum \lambda_i \left(P_i h_i + (1 - P_i) w_i \right) Q_i} \qquad \text{Equation 3}$$

where w_i = time wasted handling an item of prey size class i which is subsequently not consumed and P_i = probability that an item of prey size class i attacked by the animal will be consumed. To maximise energy intake, Q_i = 1 if $E/T < E_i P_i/(P_i h_i + (1-P_i)w_i)$ and Q_i = 0 if $E/T > E_i P_i/(P_i h_i + (1-P_i)w_i)$. So the animal should consume an individual of prey size class i if its profitability including waste handling time ($E_i P_i/(P_i h_i + (1-P_i)w_i)$; = the rate of consuming energy from the size class once it has been encountered, including the time spent handling prey that are subsequently not consumed) is above the overall energy intake rate (E/T; = the overall rate of consuming energy from a range of size classes including the time taken to encounter prey).

The optimal size selection is calculated by setting the values Q_i to 0 and 1 for different prey size classes to determine the size selection that maximises energy intake rate. The prey size classes are ordered by their profitabilities, usually with the result that larger size classes are more profitable than smaller size classes. This happens because energy content usually increases more rapidly with increasing prey size than does the time costs of handling the prey. An initial model is built that just includes the most profitable

prey size class (Q_i = 1 for this size class and Q_i = 0 for all others). A second model is then built that includes the most and second most profitable prey size classes. A check is made to determine whether the profitability of the second most profitable prey size class is greater than energy intake rate. If this is true the process is repeated by building a model that also includes the third most profitable prey size class. This process is repeated until the profitability of the nth most profitable prey size class is lower than energy intake rate. At this point the final model excludes the nth most profitable prey size class but includes all those previously added. The set of prey size classes included in this model comprise the size selection that maximises energy intake rate. As profitability usually increases with prey size, the size classes are usually added in order of decreasing size and so this approach can be used to predict the minimum size class included in the diet.

Although optimal size selection models can predict the minimum size of prey included in the diet, they require detailed foraging and energetics data that will typically not be available for most systems. The required parameters are the energy content of each prey size class (E_i), the handling time of each prey size class (h_i), the time wasted handling an item of prey size class which is subsequently not consumed (w_i) and the probability that an item of each prey size class attacked by the animal will be consumed (P_i). The encounter rate with prey is usually calculated from a combination of the density of each prey size class and the area of habitat searched per unit time.

$$\lambda_i = aD_i \qquad\qquad\qquad \text{Equation 4}$$

where a = area of habitat searched per unit time (also called area of discovery) and D_i = density of prey size class i. For example, Norris and Johnstone (1998) calculated encounter rate from the rate at which the birds explored the habitat by touch. a can potentially depend on the size class, for example if large prey items can be detected over greater distances. Further studies are required to apply size selection models to a wider range of sites to find for generalities in optimal size selection.

In the absence of generalities in optimal size selection, and given that the data required will be absent for the majority of sites, it was decided to subsequently derive size selection from the literature review in Section 3.2.

3.4 Prey quality

To assess the nutritional quality of shellfish and non-shellfish prey items for oystercatchers, we examined published values of the energy content of each species (Table 3). Based on these values, the mean (± SD) energy content is 22.6 ± 1.1 kJ g^{-1} for mussels, and 21.5 ± 0.8 kJ g^{-1} for cockles. These are close to the mean values used in previous oystercatcher models; Stillman (2009) used values of 22.0 kJ g^{-1} for bivalves (i.e. cockles and mussels) based on the data presented in Zwarts *et al.* (1996a).

Table 3. Energy content values for shellfish and non-shellfish prey of oystercatchers across temperate estuaries. AFDW energy content values can be converted to Total Wet Weight (including shell) using the formula: AFDW = 0.055 · TWW (Munch-Petersen & Kristensen, 2001).

Prey type	Prey species	Location	Energy content (kJ g^{-1} AFDW)	Reference
Shellfish: bivalves	*Mytilus edulis*	-	22.0	McLusky (1989)
	Mytilus edulis	Wadden Sea (Germany)	20.8	Hilgerloh (1997)
	Mytilus edulis	Wadden Sea (Netherlands)	23.3	Zwart & Wanink (1993)
	Mytilus edulis	Ythan Estuary (Scotland)	22.2	Chambers & Milne (1979)
	Mytilus edulis	Conway Estuary (Wales)	23.3	Dare & Edwards (1975)
	Mytilus edulis	Plymouth (England)	24.0	Bayne & Worral (1980)
	Mytilus edulis	Ythan Estuary (Scotland)	22.6	Heppleston (1971)
	Cerastoderma edule	Wadden Sea (Netherlands)	22.2	Zwart & Wanink (1993)
	Cerastoderma edule	Ythan estuary (Scotland)	20.6	Chambers & Milne (1979)
	Cerastoderma edule	Conway Estuary (Wales)	21.7	Hughes (1970)
	Macoma balthica	Wadden Sea (Netherlands)	22.0	Zwart & Wanink (1993)
	Macoma balthica	-	21.8	De Wilde & Berghuis (1978)
	Macoma balthica	Ythan estuary (Scotland)	20.0	Chambers & Milne (1979)
	Macoma balthica	Wadden Sea (Netherlands)	22.9	Beukema & De Bruin (1979)

Table 3 (continued). Energy content values for shellfish and non-shellfish prey of oystercatchers across temperate estuaries. AFDW energy content values can be converted to Total Wet Weight (including shell) using the formula: AFDW = 0.055 · TWW (Munch-Petersen & Kristensen, 2001).

Prey type	*Prey species*	Location	Energy content (kJ g^{-1} AFDW)	Reference
	Scrobicularia plana	Wadden Sea (Netherlands)	21.8	Zwart & Wanink (1993)
	Scrobicularia plana	Conway Estuary (Wales)	21.4	Hughes (1970)
	Mya arenaria	Wadden Sea (Netherlands)	21.6	Zwart & Wanink (1993)
	Mya arenaria	Massachussetts (USA)	20.8	Edwards & Huebner (1977)
	Mya arenaria	Oslofjord (Norway)	21.7	Winther & Gray (1985)
Shellfish: non-bivalves	*Crangon crangon*	Wadden Sea (Netherlands)	21.7	Zwart & Wanink (1993)
	Carcinus maenas	Wadden Sea (Netherlands)	20.7	Zwart & Wanink (1993)
	Carcinus maenas	Wadden Sea (Netherlands)	23.0	Klein Breteler (1975)
	Corophium volutator	Ythan estuary (Scotland)	19.9	Chambers & Milne (1979)
	Corophium volutator	Nova Scotia (Canada)	20.2	Boates & Smith (1979)
Non-shellfish	*Nereis diversicolor*	Wadden Sea (Netherlands)	22.2	Zwart & Wanink (1993)
	Nereis diversicolor	Ythan estuary (Scotland)	21.8	Chambers & Milne (1979)
	Arenicola marina	Wadden Sea (Netherlands)	22.1	Zwart & Wanink (1993)
	Nephtys hombergii	Wadden Sea (Netherlands)	22.8	Zwart & Wanink (1993)

The energy gain per gram of food is not only determined by the prey energy quality, but also by the digestive efficiency, i.e. the proportion of energy within the food that can be extract by the bird. Oystercatcher digestive efficiency for mussels has been estimated at 85.4 % (Kersten & Visser, 1996a). Furthermore, the oystercatcher digestive system has been reported to process energy at a constant rate of 0.233 g min^{-1}, independent of the quantity of food consumed (Kersten & Visser, 1996a).

4. A review of oystercatcher food requirements

In this section we review the food requirements of oystercatchers, based on their energetic requirements, digestive performance, and the energetic quality of shellfish.

4.1 Body mass

A range of field studies have reported that adult oystercatcher body mass is approximately 500-550 g (Kersten, 1996; Kersten & Visser, 1996b; Zwarts *et al.*, 1996b), although these values vary between locations and seasons. In a field study in the Wadden Sea (Netherlands), Zwarts *et al.* (1996b) reported that typical winter body masses for adults (≥ 4 years old) were 550-640 g, for subadults (2-4 years old) were 560-650 g, and for juveniles (< 2 years old) were 520-610 g. Similarly, a field study in the Exe estuary (England), Durell *et al.* (1993) reported that mean body mass values over the entire year for adults were 524 g, for subadults were 573 g, and for juveniles were 542 g. The British Trust for Ornithology Bird Facts website (www.bto.org/about-birds/birdfacts) based on a review of studies estimates the body mass of male and female oystercatchers as 540 g.

4.2 Starvation

Each individual oystercatcher must forage to gain sufficient energy and nutrients to meet its requirements. If energy intake is lower than energy expenditure, an individual oystercatcher can compensate by converting body tissues to energy and as a consequence their body mass decreases (Goede, 1993). However, this can only be a short term strategy as an oystercatcher will die if their body mass decreases below a threshold value, termed the starvation mass. Hulscher (1989) calculated expected survival during a severe winter period in which the birds could not feed; the first birds were predicted to starve after 3 days, and almost all individuals were predicted to

starve within 10 days. Previous oystercatcher models have assumed starvation mass values of 300 g for juvenile oystercatchers, 340 g for 2-4 year old subadult oystercatchers, and 350 g for > 4 year old adult oystercatchers (Stillman *et al.*, 1996). These values are consistent with the minimum starved winter mass values reported for each oystercatcher age class by Zwarts *et al.* (1996b).

4.3 Energy requirements

Previous models of oystercatcher foraging have typically estimated individual energy requirements based on allometric scaling relationships between daily energy expenditure and body mass across avian species, due to the lack of robust field measurements (*e.g.* Stillman, 2009). For example, the Nagy (1987) all bird equation estimates daily energy requirement as: Daily energy requirement (kJ d^{-1}) = $10.5 \cdot M^{0.681}$, where M is body mass (g). Therefore the daily energy requirement of an individual oystercatcher, based on the equation of Nagy (1987), would be within the range 723 – 772 kJ d^{-1} for an individual of body mass 500 – 550 g. However, the work of Kersten & Piersma (1987) has suggested that the metabolic rates and energy expenditure of wading birds are typically greater than all bird equations indicate. Therefore, calculating food requirements for oystercatchers based on all bird equations could lead to an underestimation of the quantity of food required.

No accurate measurements of energy expenditure in wild (*i.e.* free living) oystercatchers during winter have been reported, although some data from summer exist. Kersten & Piersma (1987) calculated an energy requirement of 602 kJ d^{-1} for caged individuals at 10°C; this value is lower than that derived from the all bird equation because the caged birds could not fly, which is an energetically expensive activity which oystercatchers on intertidal habitat typically spend up to 9 % of time engaged in (Kersten, 1996; Shamoun-Baranes *et al.*, 2012). Free-living birds are known to have higher energy expenditure than reported for studies of caged birds (Pimm, 1976). Therefore it would not be valid to use values for caged individuals in a model of free living birds.

Some field data on free-living oystercatcher energy requirements have been reported for a small number of sites. Based on field measurements of oystercatchers during summer using an electronic nest balance, Kersten & Visser (1996b) calculated that daily energy expenditure values of male and female adult oystercatchers were 535 kJ d^{-1} and

565 kJ d^{-1} respectively. Similarly, Kersten (1996) measured energy expenditure in the summer breeding season, which ranged between 511 and 687 kJ d^{-1} (mean = 605 kJ d^{-1}). These values are slightly lower than the 723 – 772 kJ d^{-1} currently used in the models. However, it would not be correct to directly use these summer values in the overwintering models due to strong seasonal differences in the costs associated with thermoregulation. Due to the higher thermoregulatory costs incurred during cold temperatures, the energy requirements of wading birds are greatest in winter and lowest in summer (Evans, 1976; Kersten & Piersma, 1987). Thus the use of summer energy expenditure values in a model of overwintering birds would lead to a substantial underestimation of food requirements and should be avoided. Indeed, Zwart *et al*. (1996c) estimated that oystercatcher daily energy requirements increase by 31.8 kJ for every 1 °C below 10 °C due to additional thermoregulatory costs. Based on these calculations, the model in Stillman *et al*. (2000) estimated energy expenditure as 673.2 kJ d^{-1} plus an additional 31.8 kJ for every 1 °C below 10 °C.

There is some evidence that the energy requirement values are currently too low and thus likely to underestimate food requirements. Firstly, a number of studies have found that the metabolic rates and energy expenditure of wading birds are typically greater than predicted by all bird equations (e.g. Speakman, 1984; Castro, 1987; Kersten & Piersma, 1987). Secondly, because of the greater energy costs of thermoregulation during winter, several studies have reported greater energy consumption and expenditure during winter to values which exceed the current model parameter range of 723 – 772 kJ d^{-1}. For example, Kersten (1996) estimated that oystercatcher energy expenditure increases from 600 kJ d^{-1} between May and September to 875 kJ d^{-1} in January. Goede (1993) reported that daily energy intake in captive oystercatchers rose to > 1000 kJ d^{-1} in winter.

4.4 Comparison of physiological and ecological food requirements

A number of empirical and modelling studies have estimated both the physiological and ecological food requirements for overwintering oystercatchers (Table 4). These 13 studies indicate that the quantity of food required to prevent overwinter mortality can be between 2.0 and 7.8 times greater than the quantity predicted from the physiological requirement of the birds alone. This value is termed the 'ecological multiplier'. This range is similar to the range reported by Goss-Custard *et al*. (2004) for 5 studies, 2.5 -

7.8. For the Burry Inlet, for which most data has been reported (n = 7), the range was 2.0 – 5.7, with a mean (± SD) ecological multiplier of 3.3. The average ecological multiplier for mussel dominated sites was 7.1 and the average for cockle dominated or mixed cockle / mussel sites was 3.3. Using the mean value for the Burry Inlet instead of all 7 values still gave a mean ecological multiplier of 3.3 for cockle dominated or mixed cockle / mussel sites. In mixed cockle / mussel estuaries it would be difficult to avoid using an intermediate ecological multiplier value without knowing the proportions of cockle-feeding and mussel-feeding oystercatchers in the population. If this information was known it could be possible to estimate the TACs for cockles and mussels separately, perhaps even at fine spatial scales (*i.e.* individual beds). In practice, however, this information is unlikely to be available for most estuaries.

Ecological multipliers were calculated from a combination of field and modelling data on two sites, the Wash and Exe Estuary. The mortality rates predicted by an individual-based model in these sites were relatively close to those observed (Stillman *et al*. 2000, 2003; Stillman & Goss-Custard 2010). The model also predicted the absence of mortality in the Burry Inlet during 2000/01 when shellfish stocks were abundant and the real birds fed for only a small proportion of each day, implying that they were able to meet their energy requirements with relative ease (West *et al*. 2003). Individual-based models have also predicted the amount of time oystercatchers spend feeding relatively accurately (Stillman *et al*. 2010) in these and other sites, implying the both the model and real birds in the tested sites were having similar difficulty surviving through winter. Burton *et al.* (2010) used long term ringing data to estimate the *apparent* annual mortality of oystercatcher in the Burry Inlet between 1989/90 and 2007/08. Apparent annual mortality does not separate emigration from *true* mortality, nor measure overwinter mortality as predicted by individual-based models, and so is likely to be greater than true overwinter mortality. The best fitting model predicted that annual apparent mortality was 9% in all years except 2004/05 (the year in which cockle stocks first declined in the site) in which it was predicted to be 74% (Burton *et al.* 2010). In contrast, individual-based models, when parameterised using observed oystercatcher population size, predicted overwinter mortality to be 100% in 2000/01 (West *et al*. 2003) and 2004/05 to 2007/08 (Stillman 2009). Individual-based models did not predict the observed decline in apparent survival during 2004/05, suggesting either

that the apparent mortality was due to emigration or non-winter mortality rather than true overwinter mortality or that the individual-based model was under-predicting mortality. In the second case, the individual-based model would be predicting that the amount of food available was sufficient to support the birds when in fact it was not, implying that the model would have underpredicted the size of the ecological multiplier in this year. Given the current paucity of empirical data, there is a need for detailed field studies which measure oystercatcher overwinter starvation in relation to food abundance, and compare these observations with model predictions.

Table 4. A comparison of the physiological and ecological food requirements reported in the literature. Following the method of Ens (2006) the kg AFDM estimates of Goss-Custard *et al.* (2004) and Stillman *et al.* (2010) were transformed to kg wet flesh, assuming that 1 kg wet flesh corresponded to 0.041 g AFDM (Ricciardi & Bourget 1998).

Location of study	Type of study	Dominant prey species	Physiological requirement (kg bird^{-1} winter^{-1})	Ecological requirement (kg bird^{-1} winter^{-1})	Ecological multiplier	Reference
Baie de Somme (France)	Modelling	Cockle	85	424	5.0	Goss-Custard *et al.* (2004)
Oosterschelde (Netherlands)	Empirical	Cockle	146	366	2.5	Rappoldt *et al.* (2003a)
The Wash (England)	Empirical and modelling	Cockle	102	256	2.5	Goss-Custard *et al.* (2004); Stillman et al (2003)
Wadden Sea (Netherlands)	Empirical	Cockle	159	488	3.1	Rappoldt *et al.* (2003b)
Burry Inlet (Wales)	Modelling	Cockle & mussel	100	566	5.7	Goss-Custard *et al.* (2004)
Burry Inlet 2004 (Wales)	Modelling	Cockle & Mussel	54	134	2.5	Stillman *et al.* (2010)
Burry Inlet 2005 (Wales)	Modelling	Cockle & Mussel	54	122	2.3	Stillman *et al.* (2010)
Burry Inlet 2006 (Wales)	Modelling	Cockle & Mussel	54	232	4.3	Stillman *et al.* (2010)
Burry Inlet 2007 (Wales)	Modelling	Cockle & Mussel	54	232	4.3	Stillman *et al.* (2010)
Burry Inlet 2008 (Wales)	Modelling	Cockle & Mussel	54	122	2.3	Stillman *et al.* (2010)
Burry Inlet 2009 (Wales)	Modelling	Cockle & Mussel	54	110	2.0	Stillman *et al.* (2010)
Bangor Flats (Wales)	Modelling	Mussel	100	641	6.4	Goss-Custard *et al.* (2004)
Exe Estuary (England)	Empirical and modelling	Mussel	100	783	7.8	Goss-Custard *et al.* (2004)

5. A spreadsheet model for estimating oystercatcher food requirements

The purpose of the spreadsheet model is to calculate the ecological requirements of an oystercatcher population consuming mussels and cockles within a site. Data on the number of oystercatchers feeding on mussels and cockles, the time for which the population must be supported and the initial stocks of mussels and cockles are entered into the model. The food ecological requirements of the birds is calculated from the physiological requirements of the oystercatcher population and the ecological multiplier. The amount of mussel and cockle stocks remaining after the bird requirements have been removed can then be used to set the Total Allowable Catch for shellfishing. The spreadsheet model is intended to test whether this approach to calculating oystercatcher requirements can be applied quickly and reliably to a range of sites. If successful, the next step would be to create a piece of software that automated data entry and the generation of predictions. Figure 1 shows a screenshot of the Model worksheet of the spreadsheet model. The test data used in the model are from the Burry Inlet during the winter of 2009/10 (Stillman *et al.* 2010).

5.1. Site-specific data

The model requires data on the number of oystercatchers supported by mussels and cockles in the site (N_{Oyc}) and the time period over which oystercatchers are supported (T). The number of oystercatchers supported by cockles and mussels can either be assumed to be the entire population, as these shellfish form the main prey of oystercatchers, or can be estimated from counts of the number of oystercatchers feeding on these prey. For example, birds feeding on other prey within the site, or feeding on prey outside of the site could potentially be excluded from calculations. The number of birds used in the model should either be the mean number counted within the site or the mean number counted feeding on mussels and cockles. The time for which the oystercatcher population needs to be supported should be the time for which the majority of the oystercatcher population occupies the site – for example, a typical wintering period would be from 1st September until 31st March. The proportion of the oystercatcher population feeding on mussels (p_{Mussel}), as opposed to cockles, should also be estimated. This is used to calculate the amount of cockle and mussel biomass that

needs to be reserved for the birds, and also to calculate the size of the ecological multiplier.

The model accounts for uncertainty in the minimum size of cockles and mussels consumed by oystercatchers. Calculations are either based on the typical minimum size of cockles and mussels consumed, 15mm and 30mm respectively, or lower minimum sizes that may be consumed when larger prey are absent, 10mm and 20mm respectively (see Section 3.2). It is assumed that there is no maximum size of cockle that can be consumed by oystercatcher but that mussels greater than 60mm in length cannot be consumed (see Section 3.2). The model requires the fresh mass of cockles and mussels within the following size ranges to be calculated: cockles – 10mm to maximum ($B_{C10\text{-}max}$) and 15mm to maximum ($B_{C15\text{-}max}$); mussels – 20mm to 60mm ($B_{M20\text{-}60}$) and 30mm to 60mm ($B_{M30\text{-}60}$).

The model can potentially account for temperature-dependent thermoregulatory costs of the birds. To do this it needs site-specific data on (i) the proportion of time for which temperature is below the temperature at which oystercatchers need to thermoregulate (i.e. 10°c), and (ii) the mean temperature during this time.

5.2. Default parameters

A number of default parameters are used in calculations which are assumed to be the same in all sites. The average body mass (g) of oystercatcher (B_{Oyc}) is set to 540g based on a review of body masses (www.bto.org/about-birds/birdfacts). The energy content of mussels and cockles (E_{CM}) is set to 22 KJg^{-1}, the average value for bivalves (Zwarts *et al*. 1996a). The efficiency with which mussels and cockles are assimilated (p_{assim}) is set to 0.854 (Kersten and Visser 1996). The ratio of AFDM to fresh mass ($p_{DryFresh}$) is set to 0.041, the average for mussels and cockles (Ricciardi & Bourget 1998). The ecological multiplier is set to 3.3 for oystercatcher populations consuming cockles or a mixture of cockles and mussels (M_{CM}), and to 7.1 for oystercatcher populations just consuming mussels (M_M) (see Section 4.4).

5.3. The model

The model has two alternative ways of calculating the daily energy requirements of each oystercatcher in the population. If no data are available on overwinter temperature the model calculates daily energy requirements from body mass using the all bird equation of Nagy (1987).

$$E_{Oyc} = 10.5 \left(B_{Oyc} \right)^{0.681}$$

Equation 5

where E_{Oyc} = daily energy requirements of each oystercatcher (KJ) and B_{Oyc} = body mass (g). If suitable overwinter temperature data are available the model calculates daily energy requirements from energy expenditure in the absence of thermoregulation and the additional costs due to thermoregulation following Stillman *et al.* (2000) and Zwarts *et al* (1996c).

$$E_{Oyc} = (1 - p_{therm}) 673.2 + p_{therm} \left(673.2 + 31.8 (10 - t_{therm}) \right)$$

Equation 6

where p_{therm} = proportion of time for which temperature is below that at which oystercatchers need to thermoregulate (i.e. 10 °c) and t_{therm} = mean temperature during this time. In this equation the daily energy demands of each oystercatcher is 673.2 KJ in the absence of thermoregulation. For every degree below 10°c (Zwarts *et al.* 1996c) the daily energy requirements of each bird are increased by 31.8 KJ (Zwarts *et al.* 1996c).

The total ash-free dry mass (AFDM) (g) consumed by each oystercatcher is then calculated from the duration of the time period for which the birds need to be supported, the daily energy requirements of the bird, the energy content of cockles and mussels and the efficiency with which cockles and mussels are assimilated.

$$C_{Oyc} = \frac{T \cdot E_{Oyc}}{p_{Assim} \cdot E_{CM}}$$

Equation 7

Where C_{Oyc} = total AFDM consumed by each bird (g AFDM), T = time period for which birds need to be supported (days), p_{Assim} = efficiency of assimilating energy from cockles and mussels and E_{CM} = energy content of cockles and mussels (KJ g^{-1}). The total AFDM (g) consumed by the oystercatcher population is calculated from the mean number of birds present.

$$C_{OycPop} = N_{Oyc}C_{Oyc}$$

Equation 8

where C_{OycPop} = total AFDM consumed by oystercatcher population (g AFDM) and N_{Oyc} = mean number of birds present. The physiological food requirement of the population is found by converting AFDM to fresh mass and converting g to tonnes.

$$R_{Phys} = \frac{C_{OycPop}}{1000000 \cdot p_{DryFresh}}$$

Equation 9

where R_{Phys} = Physiological food requirement of oystercatcher population (tonnes fresh mass including shell) and $P_{DryFresh}$ = ratio of AFDM to fresh mass including shell in cockles and mussels. The combined ecological multiplier (M), which accounts for the proportion of cockles-and mussel-feeding oystercatchers, is calculated from the proportion of birds feeding on mussels and cockles.

$$M = \begin{cases} M_{CM} & \text{if } p_{Mussel} < 1 \\ M_M & \text{if } p_{Mussel} = 1 \end{cases}$$

Equation 10

where M_{CM} = ecological multiplier for oystercatchers feeding on cockles alone or a mixture of cockles and mussels, M_M = ecological multiplier for oystercatchers feeding on mussels alone and p_{Mussel} = proportion of birds feeding on mussels. The ecological requirement is then found by multiplying the physiological requirement by the combined ecological multiplier.

$$R_{Ecol} = M \cdot R_{Phys}$$

Equation 11

where R_{Ecol} = ecological requirement (tonnes fresh mass including shell). The ecological requirement obtained from cockles (R_{EcolC}) and mussels (R_{EcolM}) is then calculated from the proportion of birds feeding on mussels.

$$R_{EcolC} = (1 - p_{Mussel}) \cdot R_{Ecol}$$

Equation 12

$$R_{EcolM} = p_{Mussel} \cdot R_{Ecol}$$

Equation 13

The final step is to calculate the biomass of cockles and mussels that are not required by the oystercatcher population. Calculations are either based on the typical minimum size of cockles and mussels consumed, 15mm ($X_{C10-max}$) and 30mm ($X_{C15-max}$) respectively, or lower minimum sizes that may be consumed when larger prey are absent, 10mm (X_{M20-60}) and 20mm (X_{M30-60}) respectively. The biomass not required by the birds is found by subtracting their requirements from the initial biomass of cockles and mussels.

$$X_{C10-max} = B_{C10-max} - R_{EcolC} \qquad\qquad \text{Equation 14}$$

$$X_{C15-max} = B_{C15-max} - R_{EcolC} \qquad\qquad \text{Equation 15}$$

$$X_{M20-60} = B_{M20-60} - R_{EcolM} \qquad\qquad \text{Equation 16}$$

$$X_{M30-60} = B_{M30-60} - R_{EcolM} \qquad\qquad \text{Equation 17}$$

The spreadsheet model graphically represents the values calculated in Equations 12 to 17 in the Graph worksheet (Figure 2). The black bars show the amount of cockle (Equation 12) and mussel biomass (Equation 13) required by the birds. The amount required does not depend on the minimum sizes of cockles and mussels included in the diet. The division of requirements between cockles and mussels is calculated from the proportion of birds feeding on cockles (1 - p_{mussel}) and mussels (p_{mussel}). The grey bars show the amount of cockle (Equations 14 and 15) and mussel biomass (Equations 16 and 17) not required by the birds. This depends on the amount required by the birds and the minimum sizes of cockles and mussels consumed, as this determines the total stock of cockles and mussels available to the birds.

5.4 Example results

Figures 1 and 2 show example outputs of the Spreadsheet model based on oystercatcher and shellfish data from the Burry Inlet during the winter of 2009/2010 (Stillman *et al.* 2010). Site specific data are entered in rows 3 to 11 of the Model worksheet. In this example it is assumed that temperature data are available, with the proportion of the winter with temperatures below 10°c set to 0.75, and the mean temperature during this time set to 5°c. These are not actual measurements from the Burry Inlet, but just examples to demonstrate the model. These values are left blank in the model if no suitable data are available. Default model parameters are shown in rows 14 to 19. The

model calculates the daily energy requirements of the birds in two alternative ways on rows 22 and 23. Row 22 shows the calculation based on body mass derived from the Nagy (1987) all bird equation. If temperature data are entered in rows 10 and 11, row 23 shows the calculation of daily energy requirements incorporating thermoregulatory costs. The daily energy requirement used in the model (row 26), is based on the Nagy (1987) equation unless temperature data are entered in rows 10 and 11. Rows 27 and 28 convert the daily energy requirement of each oystercatcher into the biomass of shellfish consumed by the oystercatcher population over the course of winter. Rows 31 to 35 calculate the physiological and ecological food requirements of the oystercatcher population. The ecological multiplier (row 32) is set to that for mussels if only mussels are consumed, otherwise it is set to the value for birds consuming just cockles or a mixture of cockles and mussels. The amount of cockle and mussel biomass required is calculated from the proportion of birds feeding on mussels (row 9). Rows 38 to 41 show the amount of shellfish not required by oystercatchers based on differing assumptions of the minimum size of cockles and mussels consumed by oystercatchers. The references used to derive parameter values are shown at the bottom of the worksheet.

Figure 1. Screenshot of the Model worksheet of the spreadsheet model.

Site-specific data	Symbol	Value	Units	Explanation
Total number of oystercatcher feeding on mussels and cockles in site	N_{oyc}	6286	No. individuals	Excluding oystercatcher feeeding outside of site or feeding on other prey
Number of days for which oystercatcher population needs to be supported	T	212	days	1st September until 31st March
Biomass of cockles over 10mm in length	$B_{C10\text{-}max}$	4432	tonnes fresh mass	Total biomass of cockles over 10mm in length
Biomass of cockles over 15mm in length	$B_{C15\text{-}max}$	1695	tonnes fresh mass	Total biomass of cockles over 15mm in length
Biomass of mussels over 20mm in length	$B_{M20\text{-}60}$	3868	tonnes fresh mass	Total biomass of mussels over 20mm in length
Biomass of mussels over 30mm in length	$B_{M30\text{-}60}$	3490	tonnes fresh mass	Total biomass of mussels over 30mm in length
Proportion of birds feeding on mussels	p_{Mussel}	0.5	proportion	Average proportion of oystercatcher feeding on mussels
Propotion of time during which temperature is below 10°c (leave blank if no suitable data)	p_{therm}	0.75	proportion	Proportion of time for which oystercatcher need to thermoregulate
Mean temperature when temperature is below 10°c (leave blank if no suitable data)	t_{therm}	5	°c	Determines thermoregulatory costs of oystercatcher

Default parameters	Symbol	Value	Units	Explanation
Average body mass of oystercatchers	B_{Oyc}	540	g	From www.bto.org/about-birds/birdfacts based on a review of studies
Energy content of mussels and cockles	E_{CM}	22	KJ g^{-1}	Average for bivalves (Zwarts et al. 1996a)
Efficiency with which mussels and cockles are assimilated by oystercatchers	p_{Assim}	0.854	proportion	Kersten & Visser (1996)
Ratio of AFDM to fresh mass including shell	$p_{DryFresh}$	0.041	proportion	Average of value for mussels (0.046) and cockles (0.036) (Ricciardi & Edwin Bourget 1998)
Cockle and mixed cockle / mussel ecological multiplier	M_{CM}	3.3	number	See report
Mussel ecological multiplier	M_M	7.1	number	See report

Alternative calculations of daily energy requirements	Symbol	Value	Units	Explanation
Daily energy requirements of each oystercatcher from Nagy (1987)	E_{Oyc}	762	KJ	Calculated from body mass (g) using all bird equation of Nagy (1987)
Daily energy requirements of each oystercatcher incorporating thermoregulation	E_{Oyc}	792	KJ	Calculated following Stillman *et al*. (2000) and Zwarts *et al*. (1996b)

Energy and food requirements	Symbol	Value	Units	Explanation
Daily energy requirements of each oystercatcher	E_{Oyc}	792	KJ	Calculated from Nagy (1987) or following Stillman et al. (2000) and Zwarts et al. (1996b)
Total AFDM of mussels or cockles consumed by each oystercatcher	C_{Oyc}	8937	g	Calculated from energy requirements throughout season
Total AFDM of mussels or cockles consumed by oystercatcher population	C_{OycPop}	56177982	g	Calculated from energy requirements of each bird and number of birds

| Physiological and Ecological food requirements	Symbol	Value	Units	Explanation
Physiological requirement of oystercatcher population	R_{Phys}	1370	tonnes fresh mass	Calculated from ratio of AFDM to fresh mass
Combined ecological multiplier	M	3.3	number	This is the cockle and mixed cockle / mussel value unless birds only consume mussels
Ecological requirement of oystercatcher population	R_{Ecol}	4521	tonnes fresh mass	Physiological requirement multiplied by the combined ecological multiplier
Ecological requirement of oystercatcher population obtained from cockles	R_{EcolC}	2260.5	tonnes fresh mass	Calculated from proportion of birds consuming cockles
Ecological requirement of oystercatcher population obtained from mussels	R_{EcolM}	2260.5	tonnes fresh mass	Calculated from proportion of birds consuming mussels

Cockle and mussel stocks not required by oystercatcher population	Symbol	Value	Units	Explanation
Cockles over 10mm not required by oystercatcher population	$X_{C10\text{-}max}$	2171.5	tonnes fresh mass	Biomass of cockles over 10mm
Cockles over 15mm not required by oystercatcher population	$X_{C15\text{-}max}$	0	tonnes fresh mass	Biomass of cockles over 15mm
Mussels 20-60mm not required by oystercatcher population	$X_{M20\text{-}60}$	1607.5	tonnes fresh mass	Biomass of mussels 20-60mm
Mussels 30-60mm not required by oystercatcher population	$X_{M30\text{-}60}$	1229.5	tonnes fresh mass	Biomass of mussels 30-60mm

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Figure 2. Screenshot of the Graph worksheet of the spreadsheet model.
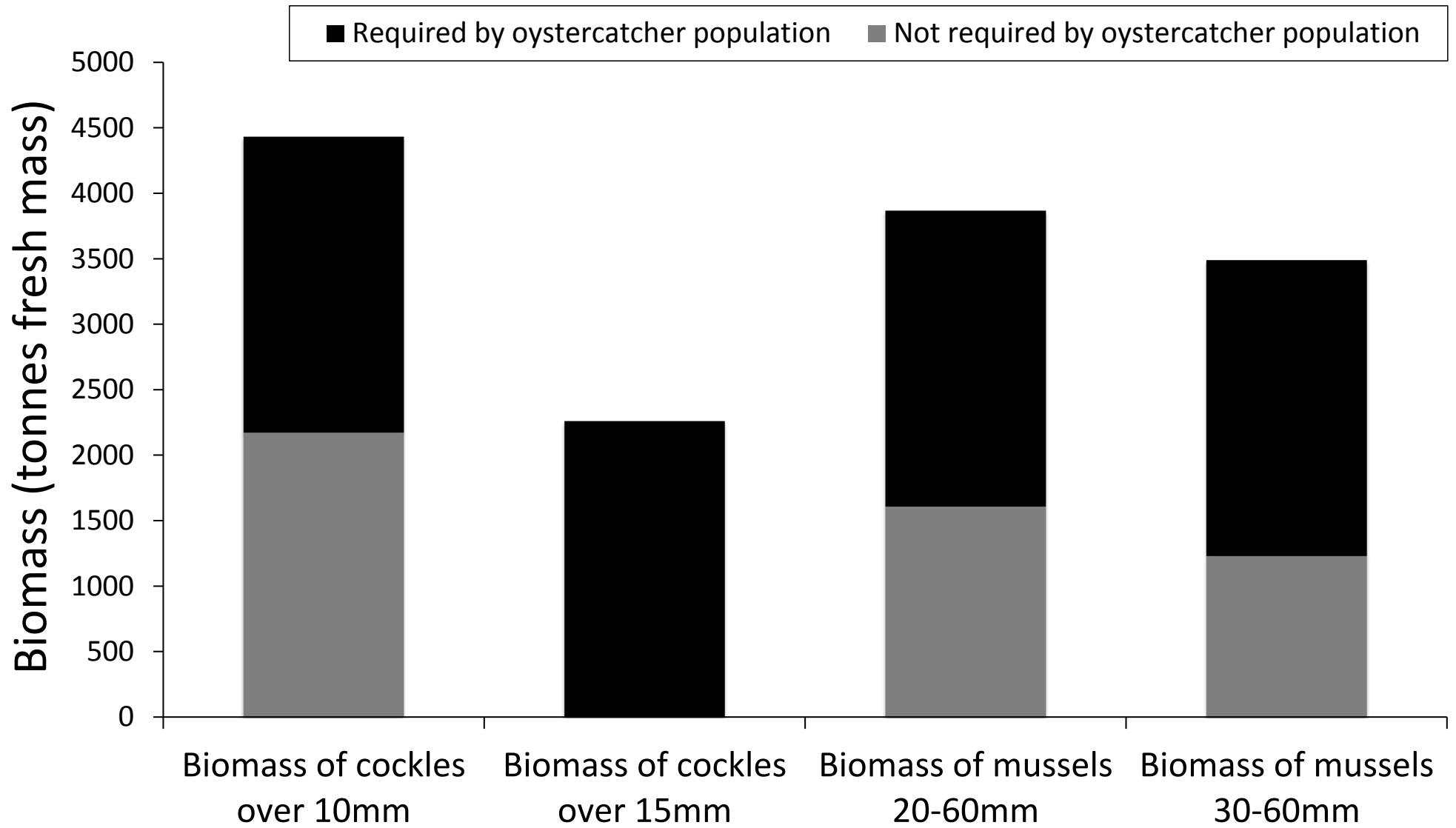
6. Conclusions

The purpose of this report is to explore how simple models could be used to inform the management of estuarine conflicts between wading bird conservation and shellfisheries. The spreadsheet model developed in this report is based on the same principles as the individual-based models previously used to model shorebirds (e.g. Stillman & Goss-Custard 2010; Stillman *et al.* 2010) but includes a number of simplifying assumptions. Individual-based models can produce more detailed predictions, but require more parameters and it is not always that straightforward to interpret the assumptions they make. The spreadsheet model is a less realistic representation of the real system but has fewer parameters and its assumptions can be expressed more clearly.

In both types of model the amount of food the birds need to consume each day depends on their energy requirements, the energy content of the prey and the efficiency with which energy within the prey can be assimilated. The spreadsheet model calculates the amount of food consumed by the bird population by multiplying the amount consumed by one bird during the overwintering season by the number of birds present. Individual-based models in addition also include the rate at which birds consume food, the tidal availability of the food and changes in the body mass of birds. They predict the proportion of time spent feeding, the distribution of birds throughout a site and the proportion of birds that survive to the end of winter. These predictions can be compared to observations in the real system to assess the accuracy of the models. The spreadsheet model does not consider the rate at which birds can feed, which is potentially a key limitation. Real birds die of starvation if they assimilate energy at a lower rate than they metabolise energy over a long enough period of time for their energy reserves to fall to zero, a process explicitly incorporated into individual-based models. Even if there is enough food to apparently meet the ecological requirements of the birds, they could still starve if food occurred at a very low density (and so could only be consumed at a very low rate), or if food was only available for a short time, for example, due to tidal availability or disturbance from human activities. By excluding the rate at which birds feed, the spreadsheet model could potentially, under the conditions described above, predict that there was enough food to support an oystercatcher

population, when in reality the birds could not consume food at a high enough rate to survive.

The contrast between the physiological and ecological requirements is a key component of the spreadsheet model. If food requirements were calculated on the basis of the physiological requirements, they would underestimate the amount of food required to support the bird populations. More food is required in the environment than the amount consumed by the birds because birds cannot find all of the food, interference competition between the birds can exclude some individuals from the food supply and some of the food will be lost due to factors other than the birds, such as disease and predation by marine fish and invertebrates (Möller & Rosenberg, 1983; Sanchez-Salazar *et al.*, 1987; Whitton *et al.*, 2012). A combination of empirical and modelling studies were reviewed to estimate the ecological multiplier which converts the physiological requirements to the ecological requirements. By collating published estimates of physiological and ecological food requirements for overwintering oystercatchers, we showed that the range of ecological multiplier values was 2.0 – 7.8. For the Burry Inlet, the site for which most data have been published, the mean ecological multiplier was 3.7 (range 2.0 - 5.6). The ecological multiplier was greatest (7.1) on two sites in which oystercatchers fed almost exclusively on mussels. It was lower (3.3) on sites in which oystercatcher fed either on cockles or on a mixture of cockles and mussels. The higher value for purely mussel-feeding birds can be explained as interference competition on highly aggregated mussel beds can exclude a higher proportion of the food than interference competition on dispersed cockle beds. Two values of the ecological multiplier were used in the spreadsheet model depending on whether oystercatchers feed solely on mussels (=7.1), or on cockles or a combination of mussels and cockles (=3.3). Ultimately, the amount of food that is predicted to be required by the birds is directly related to the size of the ecological multiplier. Further studies estimating the ecological multiplier across a range of sites would improve confidence in these values, and may allow its value to be more precisely related to the proportion of cockles and mussels on a site.

The literature review did not reveal any simple ways of calculating the minimum size of both cockles and mussels that are consumed by the birds. Norris & Johnstone (1998) present a model that predicts the size range of cockles consumed by oystercatchers

foraging by touch in relation to the size distribution of cockles present. However, this study is based on just one foraging technique (oystercatchers can forage by sight as well as by touch) and requires detailed data on the rate at which oystercatchers find and consume prey which are unlikely to be available for most sites. Similar, size selection models have been developed for mussel-feeding oystercatchers, but again rely on quite detailed foraging observation. The literature review showed that oystercatchers typically consume cockles and mussels over a threshold size, but that the minimum size can be smaller when very few large prey are available. The test data used in the spreadsheet model shows that the amount of food not required by the birds can be very sensitive to the assumed minimum size class of cockles and mussels (Figure 2). Currently, the spreadsheet model makes predictions based on both the typical minimum size of cockles and mussels consumed, 15mm and 30mm respectively, or lower minimum sizes that may be consumed when larger prey are absent, 10mm and 20mm respectively so that the sensitivity of predictions to these assumptions can be quantified.

The literature review suggested that the values for oystercatcher body mass, starvation mass, prey energy content and assimilation efficiency used in previous individual-based models of overwintering oystercatchers (*e.g.* Stillman *et al.*, 1996; Stillman, 2009; Stillman *et al.*, 2010) were appropriate. The review of daily energy requirements showed that estimates of this parameter varied widely between situations. The estimates derived from the Nagy (1999) all bird equation used in previous individual-based models and the spreadsheet model fall close to the centre of the observed range, but a number of estimates indicated that daily energy requirements of oystercatcher could on occasions exceed this value. The Nagy equation does not explicitly include an additional energetic cost due to thermoregulation, and so may underestimate daily energy requirements when thermoregulatory costs are high. To account for this uncertainty the spreadsheet model can also calculate energy requirements including thermoregulatory costs if suitable temperature data are available for a site. Detailed energy budgets of free-living oystercatchers during winter including thermoregulatory costs are currently lacking.

Although the spreadsheet model makes several simplifying assumptions, it still provides a straightforward way of quantifying the food requirements of the birds and

hence informing the setting of Total Allowable Catches. The next step would be to replace the spreadsheet model with a piece of simple, user-friendly software. The software would either read in site-specific data from a parameter file or allow a user to enter these on the screen. The calculations currently within the spreadsheet model (Equations 5 to 17 above) would then be performed within the software and the predictions presented numerically and as graphical output. The software would explain the steps and associated assumptions in the calculations, and the sources used to calculate parameter values. It would contain a user guide to explain the limitations of the approach, and explain the situations in which predictions may need to be treated with additional caution. The software could be updated through an online system to ensure that parameter values are based on the most up to date research.

The simple models described in this report do not replace the need for individual-based models – indeed the ecological multiplier parameter is largely based on the predictions of individual-based models – but do have the advantage that they can be used by people without specialist modelling experience and using the type of data typically available from shellfisheries. A potential strategy is to routinely use such models as a first step in assessing bird food requirements. Individual-based models and other approaches could then be used if there is some doubt as to the validity of predictions (e.g. in sites with a large amount of human disturbance) or if it is predicted that the bird food requirements are either not met or are only just met by the cockle and mussel stocks within the site.

7. References

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