Predicting food requirements of overwintering shorebird populations on the Solway Firth.

A report to Scottish Natural Heritage and Marine Scotland.

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1. Summary

In this report we use a recently-developed spreadsheet model to predict the overwinter food requirements of two shorebird species, oystercatcher (*Haematopus ostralegus*) and red knot (*Calidris canutus*), within the Solway Firth. The model is based on the energy requirements of the birds together with the energy value of their shellfish food. The model predicts the quantity of shellfish required to maintain high survival rates, and hence avoid significant mortality events within the oystercatcher and knot populations.

Knot were assumed to consume 5-14mm cockles (*Cerastoderma edule* L.), 5-24mm mussels (*Mytilus edulis* L.) and 8-16 mm tellin (*Macoma balthica* L.). Oystercatcher were assumed to consume >15mm cockles, 30-60mm mussels and >12mm tellin. The biomasses of invertebrate prey were derived from intertidal surveys of the site. The population sizes of the bird species were derived from Wetland Bird Survey (WeBS) core counts. Predictions were for the winter of 2013-2014. Shellfishing was assumed to exploit >28mm cockles.

The food requirements of oystercatcher and knot were predicted for different combinations of food supply. All scenarios assumed that the birds could consume cockles, mussels and tellin. Alternative scenarios assumed that knot and oystercatcher could consume other food from upshore areas, or that oystercatcher could consume food from terrestrial habitats. Cockle and tellin biomasses were estimated within Solway Firth, and at Wigtown Bay, a site outside the area in which bird population sizes were estimated. Further scenarios therefore assumed that birds either could, or could not, consume food from Wigtown Bay.

In each scenario the model initially predicted the amount of shellfish biomass not required by the birds. This was then converted into the biomass potentially available for fishing, accounting for the fact that the size range exploited by fishing did not overlap completely with that consumed by the birds. In the case of knot there was no overlap, and so the amount available to fishing was only calculated from the biomass of shellfish not required by oystercatcher.

The model predicted that approximately 700 tonnes of >28mm cockles could potentially be exploited by shellfishing during the winter of 2013-2014, after taking into

account the food requirements of the birds, excluding cockle and tellin biomass in Wigtown Bay, and assuming that oystercatcher consumed cockles, mussels, tellin and prey from upshore areas and terrestrial habitats. This was considered to be the most realistic scenario given that oystercatcher can potentially feed on terrestrial and upshore habitats, and given the distance between Wigtown and the area in which oystercatcher population size was estimated. The cockle, mussel and tellin surveys did not cover the entire extent of the Solway Firth, not recording cockles or tellin in English waters or mussels or the Scottish side, and so it is likely that a higher biomass of shellfish food is available to the birds in reality. However, without a more extensive survey it is not possible to quantify this.

The spreadsheet model's predictions for the winter of 2007-2008 were also compared with those of a more complex individual-based model that was developed for oystercatcher and knot in the Solway Firth based on shellfish biomass during 2005 to 2007. The individual-based model predicted that knot survival was 100% in all simulations for the winter of 2007-2008, consistent with the prediction of the spreadsheet model that 18038 tonnes of shellfish were not required by the birds during this winter. The spreadsheet model predicted that the oystercatcher population required all of the shellfish food available during the winter of 2007-2008. Similarly, the individual-based model predicted that oystercatcher were relatively sensitive to the amount of biomass removed by fishing during this winter. With a shellfishing Total Allowable Catch (TAC) set at 1000 tonnes there was a predicted reduction in survival and TACs set at 500, 750 and 1000 tonnes were predicted to reduce body mass. The spreadsheet model predicted that birds required all of the food during 2007-2008 and hence that any TAC would reduce survival. This demonstrates that the spreadsheet model is capable of producing broadly similar predictions to the more complex individual model, although the latter is more sensitive when stock levels are more critical.

2. Introduction

Temperate estuaries within northern Europe are important sites for populations of shellfish, which support commercial shellfisheries. Commercial shellfish harvesting is estimated to be worth £250 million per annum to the UK economy, providing both food and employment (DEFRA, 2013). These shellfish are also the principal overwintering food resource for a range of species of migratory wading birds, hereafter referred to as 'shorebirds'. Shorebird species are key components of UK coastal biodiversity and are protected under the European Union Wild Birds Directive (2009/147/EEC), which legally obligates the UK government to maintain healthy shorebird populations. The shared shellfish resources within estuarine areas have led to conflicts between economic and conservation interests across estuaries in northwest Europe (Tinker, 1974; Ens, 2006; Laursen *et al*., 2010; Stillman & Wood, accepted). Enough shellfish must be left unharvested to allow the birds to meet their food requirements. The responses of shorebird 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). Therefore, a 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 to survive through winter (*e.g.* Stillman, 2008a; 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 abundance 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.

A recent contract between Bournemouth University and the Welsh Government has started to develop such a model (Stillman & Wood, 2013a). The purpose of the model is to calculate the food requirements of a shorebird population consuming shellfish within a site. Data on the number of shorebirds of each species feeding on shellfish, the time for which the populations must be supported and the initial stocks of each shellfish species are entered into the model. The model then calculates the amount of food required in the environment to maintain high survival within the bird population. This is calculated using the results of empirical and individual-based modelling studies of invertivorous shorebirds in shellfisheries throughout the UK. The quantity of shellfish remaining after the bird requirements have been removed can then be used to set the TAC for shellfish harvesting. This allows managers to set TACs which enhances the economic potential of the shellfishery without threatening the conservation of shorebirds.

The Solway Firth (54°45'N, 03°40'W) is a large coastal area consisting of estuaries, intertidal sediments and saltmarshes, fed by nine major freshwater inputs. In terms of the shellfish assemblage, the key species of interest to fishermen are cockles (*Cerastoderma edule* L.), whilst shorebirds consume cockles, mussels (*Mytilus edulis* L.) and Baltic tellin (*Macoma balthica* L.) (Howell *et al*., 2007). The area is of high importance for shorebird conservation, supporting internationally significant populations of many species. As a consequence of its importance for shorebird conservation, the Solway Firth has been designated as a Special Protection Area (SPA), Site of Special Scientific Interest (SSSI) and Ramsar site. The Solway estuary is recognised as a site of international importance for both Eurasian oystercatcher (*Haematopus ostralegus* L.) and red knot (*Calidris canutus* L.), supporting the second and tenth largest populations respectively, within the UK (Holt et al., 2012).

An individual-based model of oystercatcher and knot feeding on shellfish in the Solway Firth was previously developed by Stillman (2008b). Predictions were based on 2007 surveys of cockles and tellin on the Scottish shore and 2005 to 2006 surveys of mussels on the English shore. The abundance of potential knot food was approximately 52.6 greater than the amount of food required by the knot population. The abundance of potential oystercatcher food was approximately 3.6 greater than the amount of food required by the oystercatcher population. As expected from the large amount of potential knot food available, and the facts that knot consume cockles smaller than those harvested and are not influenced greatly by interference competition when disturbance forces birds to feed at higher competitor densities, the model simulations predicted that shellfishing did not reduce knot survival. In contrast, the survival of oystercatcher was predicted to be reduced by shellfishing in some scenarios. In simulations without upshore supplementary feeding, the model predicted that TACs of 500, 750 and 1000 tonnes reduced oystercatcher survival. In simulations with upshore feeding, a TAC of 1000 tonnes reduced oystercatcher survival. The effect of shellfishing was less when upshore areas were present. The model did not incorporate terrestrial fields in which birds can feed over high tide to supplement feeding over low tide. Such high tide feeding does occur on the Solway, acting in a similar way to upshore feeding to buffer the oystercatcher population against any reduction in shellfish bed quality.

The purpose of the current project is to use a simplified model (Stillman & Wood 2013a) to predict the amount of shellfish food required by the overwintering oystercatcher and knot populations in the Solway Firth. Data on the abundance of shellfish and birds at the beginning of the overwinter period are used to calculate the amount of shellfish that need to be reserved for the birds to ensure that they can survive through the winter. The maximum TAC for shellfishing can then be calculated from the total amount of cockles minus the amount required by the birds.

3. A spreadsheet model for estimating shorebird food requirements

In order to estimate the oystercatcher and knot food requirements in the Solway Firth, we used the spreadsheet model developed by Stillman & Wood (2013a). This model has recently begun to be used to predict shorebird food requirements in UK estuarine sites (*e.g.* Stillman & Wood, 2013b). The purpose of the spreadsheet model is to calculate the ecological requirement of a shorebird population consuming shellfish within a site. Data on the number of oystercatcher and knot feeding on shellfish, the time for which the population must be supported and the initial stocks of shellfish are entered into the model. The ecological food requirements of the birds (the amount of food required in the environment to maintain high survival) is calculated from the physiological requirements of the oystercatcher and knot populations (the amount actually eaten) and an ecological multiplier (measuring how much greater the ecological requirements are than the physiological requirements). More food needs to be reserved in the environment than the amount actually eaten because birds cannot find all of the food, some birds can be excluded from the food through competition and food is lost due to factors other than the birds (Goss-Custard *et al.*, 2004). The quantity of shellfish remaining after the bird requirements have been removed can then be used to set the Total Allowable Catch for shellfish harvesting.

3.1. Site-specific data

In order to parameterise our model, we required data on the number of shorebirds of each species supported by shellfish in the site (N_{Bird}) and the time period over which shorebirds are supported (T). The number of shorebirds supported by shellfish can either be assumed to be the entire population, as these shellfish form the main prey of oystercatcher and knot, or can be estimated from counts of the number of oystercatcher and knot 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 shellfish. The time for which the bird population needs to be supported should be the time for which the majority of the oystercatcher and knot populations occupies the site – for example, a typical wintering period would be from 1st September until 31st March. The proportion of the oystercatcher and knot populations 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.

To calculate knot food requirements, the models requires the fresh mass of cockles and mussels within the following size ranges consumed by knot (Goss-Custard et al. 2006) to be calculated: cockles – 5mm to 14mm (B_{C5-14}); mussels – 5mm to 24mm (B_{M5-24}). The model accounts for uncertainty in the minimum size of cockles and mussels consumed by oystercatcher. 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. 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 (Stillman & Wood, 2013). To calculate oystercatcher food requirements, the model requires the fresh mass of cockles and mussels within the following size ranges to be calculated: cockles – 10mm to maximum ($B_{C10-max}$) and 15mm to maximum ($B_{C15-max}$); mussels – 20mm to 60mm (B_{M20-60}) and 30mm to 60mm (B_{M30-60}).

3.2. 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 (B_{Bird}; g) of oystercatcher is set to 540g and knot to 140g (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*. 1996). The efficiency with which mussels and cockles are assimilated (p_{assim}) is set to 0.85 for oystercatcher (Kersten & Visser 1996) and 0.75 for knot (Stillman *et al.* 2005). Assimilation efficiency is higher for oystercatcher as this species removes the prey flesh from the shell, whereas knot consume the prey whole. 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) (Stillman & Wood, 2013). In the absence of equivalent data for knot, the model assumes that the ecological multiplier for knot is the same as that for oystercatcher (i.e. M_{CM} = 3.3; M_M = 7.1).

3.3. The model

The model has up to two alternative ways of calculating the daily energy requirements of each bird 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).

$$E_{Bird} = 10.5\left(B_{Bird}\right)^{0.681} \qquad \text{Equation 1}$$

where E_{Bird} = daily energy requirements of each bird (KJ) and B_{Bird} = body mass (g). For oystercatcher, 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).

$$E_{Bird} = \left(1 - p_{therm}\right)673.2 + p_{therm}\left(673.2 + 31.8\left(10 - t_{therm}\right)\right) \qquad \text{Equation 2}$$

where p_{therm} = proportion of time for which temperature is below that at which oystercatcher need to thermoregulate (i.e. 10 ^{o}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^{o}c (Zwarts *et al*. 1996c) the daily energy requirements of each bird are increased by 31.8 KJ (Zwarts *et al*. 1996c). At the time of writing, the daily energy requirements of knot are just calculated using the all bird equation of Nagy (1987).

The total ash-free dry mass (AFDM) (g) consumed by each bird 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.

$$C_{Bird} = \frac{T \cdot E_{Bird}}{p_{Assim} \cdot E_{CM}} \qquad \text{Equation 3}$$

Where C_{Bird} = 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 bird population is calculated from the mean number of birds present.

$$C_{BirdPop} = N_{Bird} C_{Bird} \qquad \text{Equation 4}$$

where $C_{BirdPop}$ = total AFDM consumed by the bird population (g AFDM) and N_{Bird} = 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.

$$R_{Phys} = \frac{C_{BirdPop}}{1000000 \cdot p_{DryFresh}} \qquad \text{Equation 5}$$

where R_{Phys} = Physiological food requirement of the bird 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 birds, is calculated from the proportion of birds feeding on mussels and cockles.

$$M = \begin{cases} M_{CM} & \text{if } p_{Mussel} < 1 \\ M_{M} & \text{if } p_{Mussel} = 1 \end{cases} \qquad \text{Equation 6}$$

where M_{CM} = ecological multiplier for birds feeding on cockles alone or a mixture of cockles and mussels, M_M = ecological multiplier for birds feeding on mussels alone and p_{Mussel} = proportion of birds feeding on mussels. Stillman & Wood (2013a), based on a review of modelling and empirical studies, estimated M_{CM} as 3.3 and M_M as 7.1 for oystercatcher. At the time of writing, the same values are used for knot. The ecological requirement is then found by multiplying the physiological requirement by the combined ecological multiplier.

$$R_{Ecol} = M \cdot R_{Phys} \qquad \text{Equation 7}$$

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 8

$$R_{EcolM} = p_{Mussel} \cdot R_{Ecol}$$ Equation 9

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

$$X_{C10-max} = B_{C10-max} - R_{EcolC}$$ Equation 10

$$X_{C15-max} = B_{C15-max} - R_{EcolC}$$ Equation 11

$$X_{M20-60} = B_{M20-60} - R_{EcolM}$$ Equation 12

$$X_{M30-60} = B_{M30-60} - R_{EcolM}$$ Equation 13

For knot, calculations are based on the range of cockle and mussel sizes consumed, 5-14mm ($X_{C5\text{-}14}$) and 5-24mm ($X_{M5\text{-}24}$) respectively. The biomass not required by the birds is found by subtracting their requirements from the initial biomass of cockles and mussels within these size ranges.

$$X_{C5-14} = B_{C5-14} - R_{EcolC}$$ Equation 14

$$X_{M5-24} = B_{M5-24} - R_{EcolM}$$ Equation 15

Stillman & Wood (2013a) explains the graphical output of the spreadsheet model and describes some example results. Furthermore, Stillman & Wood (2013b) reports the use of this model to predict the food requirements of the overwintering oystercatcher population on the Dee Estuary.

4. Parameterising the spreadsheet model for the Solway Firth

The main site-specific parameters required by the model are the time over which the shorebird population needs to be supported (i.e. duration of overwintering period), the size of the overwintering shorebird populations feeding on shellfish, the start of winter biomass of shellfish within the size range consumed by shorebirds and the proportion of energy obtained from shellfish. The following sections describe how each of these parameters was derived.

4.1. Duration of overwintering period

The time for which both the oystercatcher and knot populations need to be supported by the Solway Firth was set to 196 days, from 1 September until 15 March, which reflects the period of usage by these shorebirds (Holt *et al*., 2012).

4.2. Sizes of overwintering shorebird populations

The model only considers the shellfish food of the birds and does not consider changes in shorebird population size through the winter. The sizes of the overwintering oystercatcher and knot populations on the Solway Firth were based on the numbers observed during the Wetland Bird Survey (WeBS) counts (Holt *et al*., 2012) (**Figures 1 and 2**). Between 2008 and 2013 the mean (± 95% confidence intervals) sizes of the oystercatcher and knot populations were 45099 (± 8898) and 17275 (± 3670) individuals respectively. For the September 2013 survey, 30315 oystercatcher and 12252 knot were reported. The model was parameterised with the mean overwintering oystercatcher and knot populations between 2008 and 2012 either in the Solway as a whole, or for the Scottish and English shores (**Table 1**). The model required as a parameter the proportion of birds feeding on mussels. This was calculated as the proportion of birds on the English shore, as the food supply used in the model was derived from cockle and tellin surveyed in Scotland, and mussel surveyed in England.

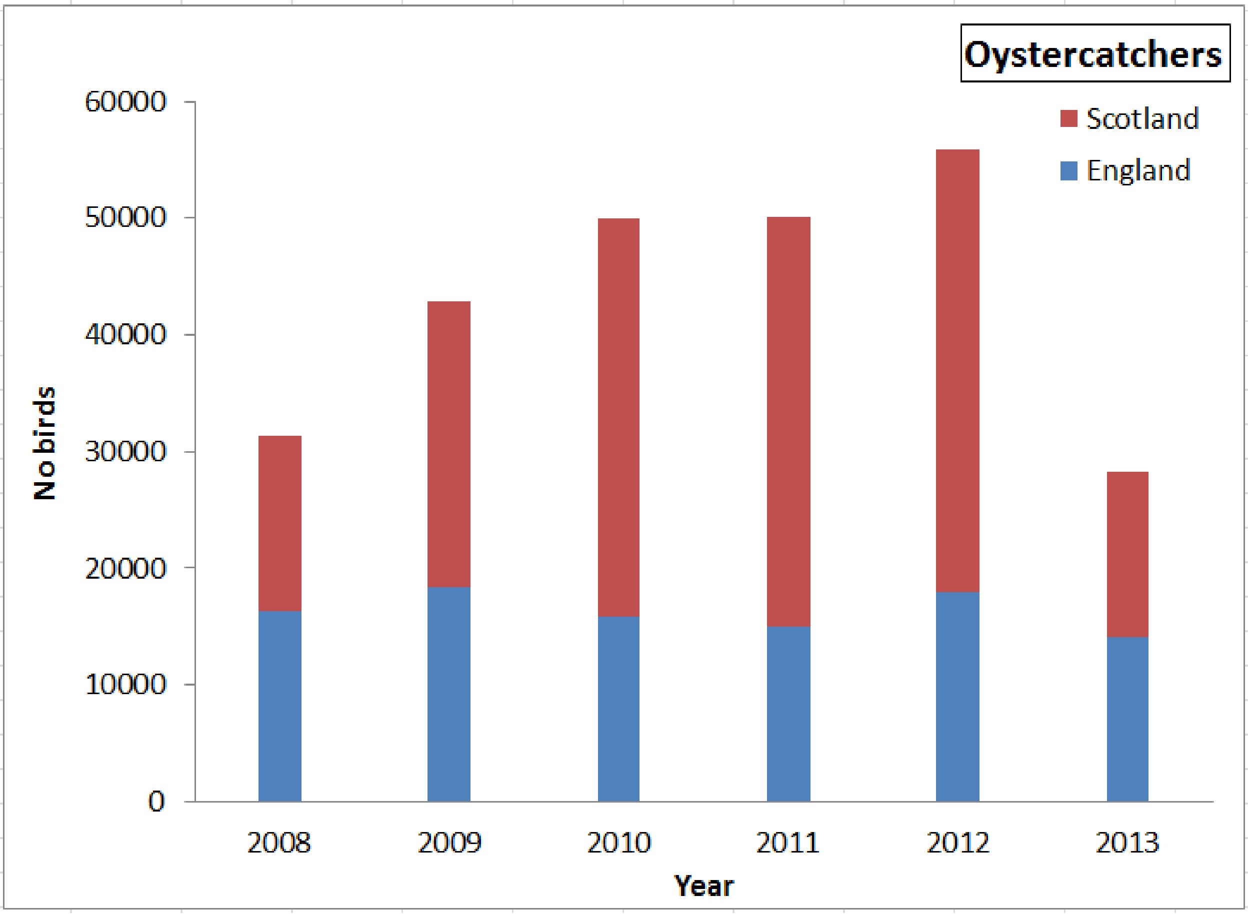


Figure 1: The peak overwinter oystercatcher counts for the Solway Firth, recorded during the Wetland Bird Survey (WeBS) counts. The 2013 data are for September only.

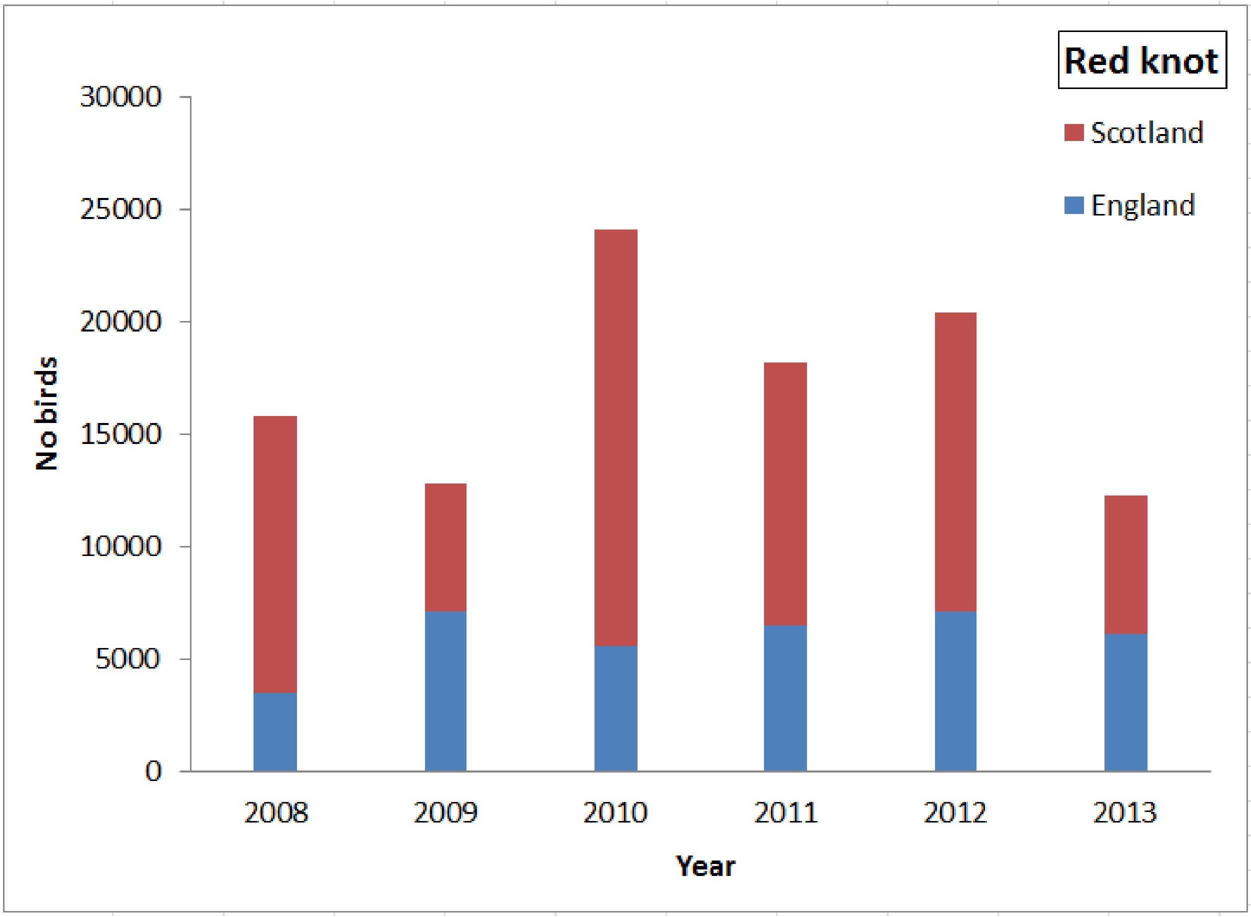


Figure 2: The peak overwinter knot counts for the Solway Firth, recorded during the Wetland Bird Survey (WeBS) counts. The 2013 data are for September only.

Table 1: Oystercatcher and Knot population sizes used in the model. *Peak* values are 2008 to 2012 peak count averages from Wetland Bird Survey (WeBS) counts. Mean values are peak values adjusted by the ratio of mean to peak numbers on the Solway during September to March from 2000 to 2005 (=0.78 for oystercatcher and 0.72 for knot). The proportion of birds feeding on mussels is the proportion of birds on the English shore, as the food supply used in the model was derived from cockle and tellin surveyed in Scotland, and mussel surveyed in England.

	Oystercatcher	Knot
Peak		
Solway total	46046	18279
Scottish shore total	29378	12350
English shore total	16667	5929
Mean		
Solway total	35916	13161
Scottish shore total	22915	8892
English shore total	13000	4269
Proportion feeding on mussels	0.36	0.32

4.3. Biomass of shellfish at start of winter

Estimates of shellfish biomass were provided by Scottish Natural Heritage. Biomass of cockles and tellins on the Scottish shore were based on intertidal surveys conducted during 2013 by Marine Ecological Solutions Ltd. The survey divided the area into 9 discrete areas: Auchencairn; Barnhourie; North Bank; Carsethorn; Orchardton; Glenisle; Rough Island; Fleet Bay; and Wigtown. Each area was surveyed on a grid comprised of a number of square strata. The survey estimated the total biomass (fresh mass including shell) of cockles and tellin within 1mm size classes within each strata. These were summed to obtain the total biomass of 1mm size classes within each area, and for the Scottish shore as a whole. For the entire surveyed area, 13541.4 tonnes of cockles and 11023.3 tonnes of tellins were recorded (**Figure 3**). Individual sizes ranged from 5 – 41 mm for cockles and 5 – 25 mm for tellins (**Figure 4**). **Table 2** shows the cockle and tellin biomasses used in the model. Model scenarios were run either including or excluding the biomass of cockles and tellin surveyed at Wigtown Bay, as this is distant from the Inner Solway and hence unlikely to provide feeding grounds for birds from the Inner Solway.

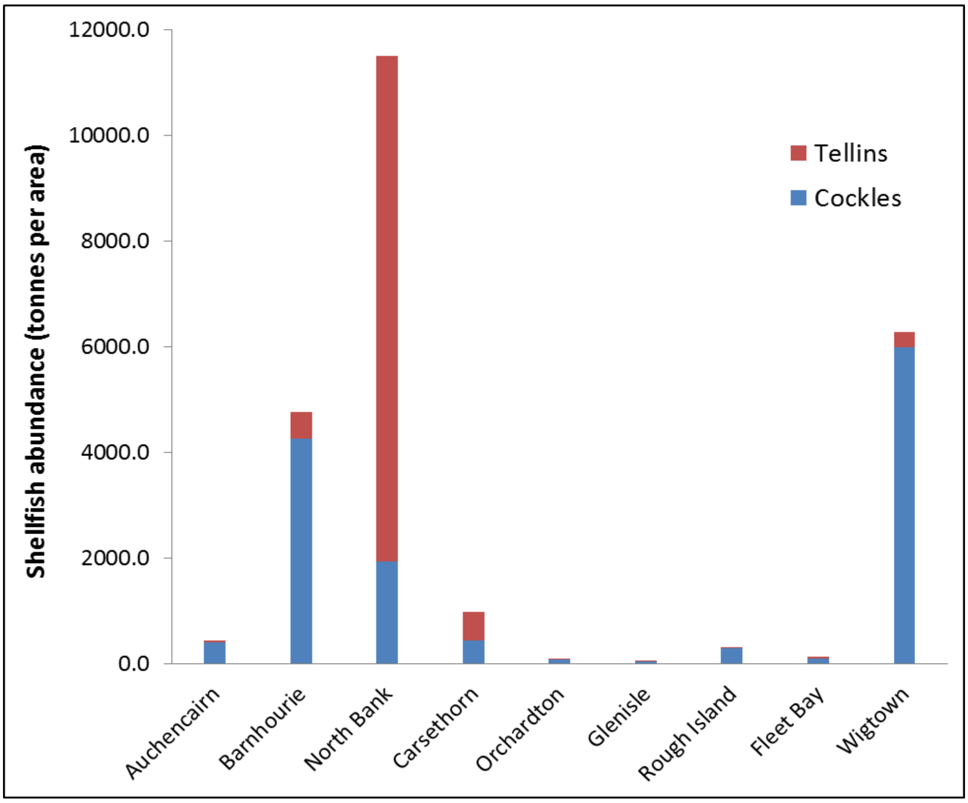


Figure 3: Shellfish abundance, measured as tonnes of cockles and tellins (including shells) in each area surveyed in 2013 within the Solway Firth.

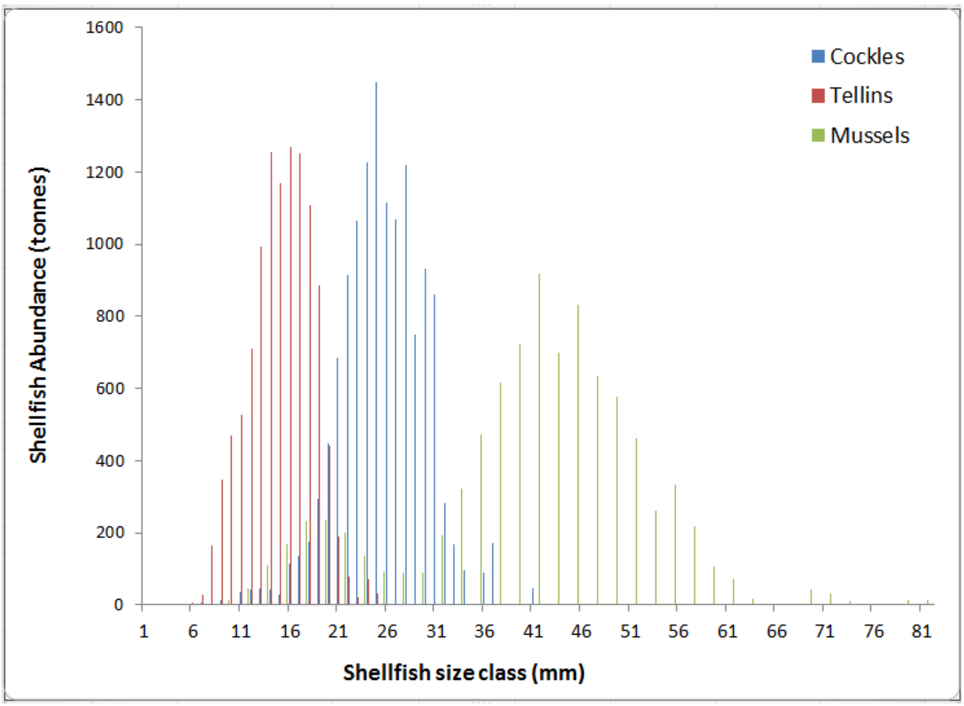


Figure 4: The distribution of the 2013 total Solway Firth shellfish stocks between different size classes.

Biomass of mussels was based on intertidal surveys undertaken in 2009 (Lancaster & Newman, 2009); due to historically low mussel stocks and resulting lack of commercial interest, no mussel surveys have been undertaken since 2009. Mussel survey sites were on the English shore and so did not overlap with survey sites for cockles and tellins. For 2009 the total mussel stock was estimated at 7341 tonnes (**Figure 5**). Based on the annual surveys undertaken between 1999 and 2009 the mean (± 95 % confidence interval) total mussel stock was estimated at 10623 ± 2846 tonnes. In order to calculate the biomass of each size class, we first converted the numbers of mussels of each size class into biomass using the equation:

$$\log_{10} W = -1.946 + 2.919 * \log_{10} L \qquad \text{Equation 14}$$

where W was AFDM (mg) and L was shell length (mm) (Goss-Custard *et al.*, 1993). AFDM was transformed to wet weight (including shell), assuming that AFDM = 4.6 % wet weight (Ricciardi & Bourget, 1998). Observed size classes during the 2009 survey ranged from the 1-2 mm class up to the 81-82 mm class (**Figure 4**). Size class data for the 1999 – 2008 surveys were not available. **Table 2** shows the mussel biomasses used in the model.

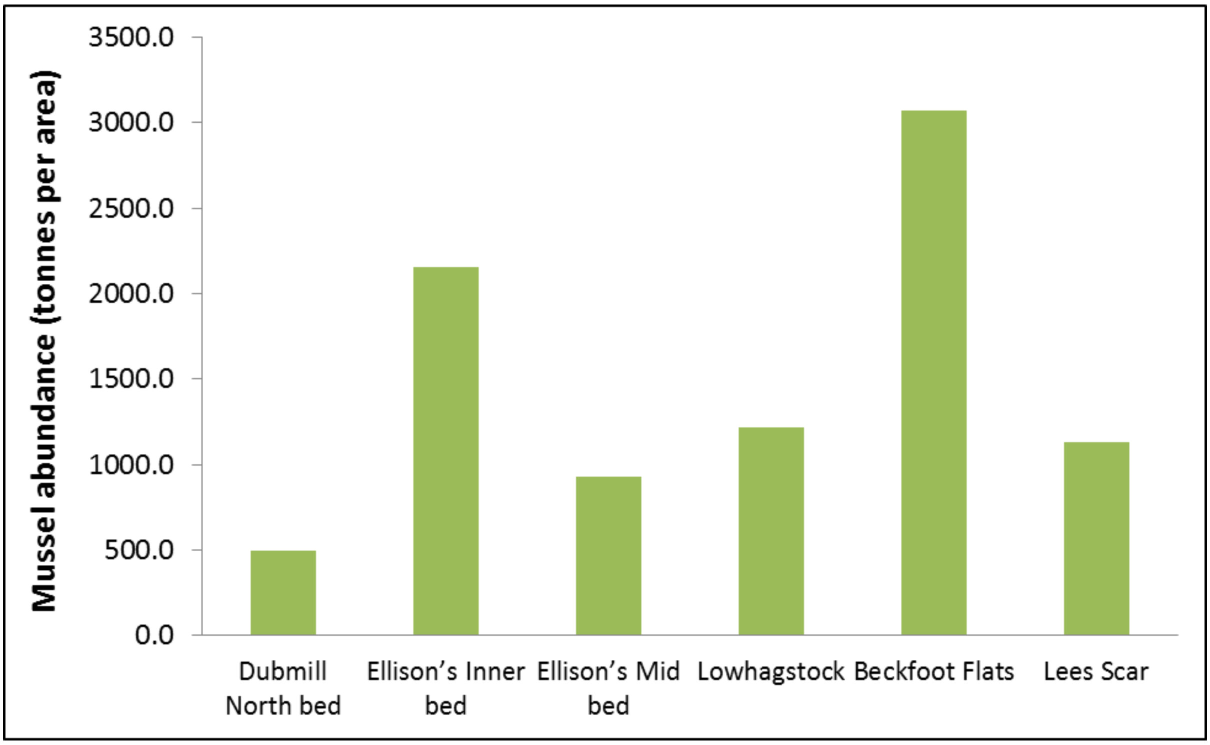


Figure 5: Mussel abundance (including shells), found in each area surveyed in 2009 within the Solway Firth. No more recent mussel surveys have been undertaken.

Table 2: Cockle, mussel and tellin biomasses used in the model. The top values are the range of size classes assumed to be consumed by knot and oystercatcher, and exploited by shellfishing in different scenarios. Values below size ranges are the biomass of shellfish within the size range (tonnes fresh mass); the value in brackets excludes the biomass of cockles and tellin in Wigtown Bay. Size ranges are those typically consumed by oystercatcher and knot.

	Cockle	Mussel	Tellin
Knot	5-14 214 (189)	5-24 1148	8-16 6911 (6660)
Oystercatcher	15-max 13327 (7369)	30-60 7460	12-max 9473 (9235)
Shellfishing	28-max 4613 (2812)		

4.4 Proportion of shellfish within the size range harvested

Oystercatcher were assumed to consume cockles >15mm whereas shellfishing harvests cockles >28mm. Therefore, the proportion of cockles >28mm in September was calculated in order to determine the biomass of cockles that could potentially be harvested. Knot were assumed to consume cockles <14mm and so the size classes consumed by this species did not overlap with those taken by shellfishing.

4.5. Proportion of energy obtained from shellfish

The simulations run by Stillman (2008b) incorporated upshore food resources that could be consumed by birds when the cockle beds were covered by the tide. The upshore resources were assumed to be available for two hours longer than the cockle and mussel beds, which themselves were assumed to be available for 6 hours. Birds were assumed to consume food at 0.67 mg s^{-1} while feeding on the upshore areas. Goss-Custard et al. (2006) showed that cockle- and mussel-feeding oystercatcher consume approximately 2 mg s^{-1}. Alternative sets of predictions were produced from the spreadsheet model, assuming either that the birds obtained all of their energy requirements from shellfish, or assuming that a proportion was obtained from upshore food. The proportion of energy obtained from shellfish (p_{Energy}) in the second case was calculated as

$$p_{Energy} = \frac{6\ \text{hr} \cdot 2\ \text{mg s}^{-1}}{\left(2\ \text{hr} \cdot 0.67\ \text{mg s}^{-1}\right) + \left(6\ \text{hr} \cdot 2\ \text{mg s}^{-1}\right)} = 0.90 \qquad \text{Equation 15}$$

This assumed that birds fed on shellfish for 6 hrs with an intake rate of 2 mg s^{-1} and on the upshore areas for 2 hrs with in intake rate of 0.67 mg s^{-1}. To account for the energy obtained from upshore food the daily energy requirements of the birds in the spreadsheet model was multiplied by 0.90. It was assumed that the proportion of energy knot obtained from upshore areas was the same as for oystercatcher.

Although not incorporated by Stillman (2008b), oystercatcher can also supplement their intertidal feeding by feeding on terrestrial fields when intertidal habitats are covered by the tide. Following the approach used by Stillman & Wood (2013b) for the Dee Estuary, terrestrial food resources were assumed to be available while the upshore areas and shellfish beds were covered by the tide for 6 hours, but only to be exploited by the birds during daylight. Birds were assumed to consume food at 0.34 mg s^{-1} while feeding terrestrially. A further set of predictions were produced for oystercatcher assuming that a proportion of energy was obtained from upshore and terrestrial food. The proportion of energy obtained from shellfish (p_{Energy}) fo these predictions was calculated as

$$p_{Energy} = \frac{6 \text{ hr} \cdot 2 \text{ mg s}^{-1}}{\left(2.4 \text{ hr} \cdot 0.34 \text{ mg s}^{-1}\right) + \left(2 \text{ hr} \cdot 0.67 \text{ mg s}^{-1}\right) + \left(6 \text{ hr} \cdot 2 \text{ mg s}^{-1}\right)} = 0.85 \qquad \text{Equation 16}$$

This assumed that birds fed on cockles for 6 hrs with an intake rate of 2 mg s^{-1}, on the upshore areas for 2 hrs with in intake rate of 0.67 mg s^{-1} and on the fields for 2.4 hrs (assuming that 40% of the 6 hrs of high tide was in daylight) with an intake rate of 0.34 mg s^{-1}. To account for the energy obtained from upshore and terrestrial food the daily energy requirements of oystercatcher in the spreadsheet model was multiplied by 0.85. Although terrestrial habitats provide a potential food source, high tide surveys in the Solway Firth show that most oystercatchers roost rather than feed over high tide (Information provided by Chris Miles (Scottish Natural Heritage)).

5. Predicted shorebird food requirements

The food requirements of oystercatcher and knot were predicted for different combinations of food supply (**Table 3** and **Figures 6-8** show these predictions). The values given below are from **Table 3** and assume that the typical size range of cockles and mussels is consumed (i.e. over 15mm and 30-60mm respectively for oystercatcher, and 5-14mm and 5-24mm for knot). All scenarios were run either including or excluding the biomass of cockles and tellin surveyed at Wigtown, as this is likely to be too distant from the area in which bird population sizes were estimated and shown to be regularly used by these birds. A greater biomass of cockle and tellin was required by the birds if the biomass of these prey within Wigtown were excluded from calculations (as can be seen by comparing **Table 3a** with **Table 3b**). The difference was approximately 6000 tonnes for oystercatcher and 200 tonnes for knot, due to the biomass of cockles and tellin with in the size ranges consumed by the birds at Wigtown. Sections 5.1, 5.2 and 5.3 discuss predictions excluding the biomass of cockles and tellin at Wigtown as these are the most precautionary predictions.

5.1. Cockle, mussel and tellin scenario

In this scenario birds were assumed to consume cockles, mussels and tellin, but not upshore or terrestrial prey. The model predicted that oystercatcher did not require 1826 tonnes of cockle / tellin, but required all of the surveyed mussel biomass (**Table 3b**; **Figure 6**). The model predicted that knot did not require 4248 tonnes of cockle / tellin, but required all of the surveyed mussel biomass (**Table 3b**; **Figure 6**).

5.2. Cockle, mussel, tellin and upshore prey scenario

This scenario also incorporated feeding in upshore areas by reducing the energy requirements of the birds to account for the energy obtained from other sources. The model predicted that oystercatcher did not require 3305 tonnes of cockle / tellin, but required all of the surveyed mussels (**Table 3b**; **Figure 7**). The model predicted that knot did not require 4508 tonnes of cockle / tellin, and 47 tonnes of mussels (**Table 3b**; **Figure 7**).

5.3. Oystercatcher plus terrestrial prey scenario

The previous oystercatcher scenario assumed that this species did not feed on terrestrial prey, whereas this can occur in the real system. Therefore, a scenario was modelled in which oystercatcher were assumed to also feed on terrestrial prey. This was incorporated by reducing the energy requirements of the birds to account for the energy obtained from terrestrial sources. When assuming that oystercatcher consumed cockle, mussel, tellin, upshore and terrestrial prey, the model predicted that oystercatcher did not require 4044 tonnes of cockle / tellin, and 395 tonnes of mussels (**Table 3b**; **Figure 8**).

5.4 Biomass of cockles available to fishing

The size range of cockles exploited by fishing does not overlap those consumed by knot (**Table 2**) and so the following predictions were for oystercatcher alone. The biomass of cockles and tellin not required by oystercatcher (**Table 3**) refers to the biomass of >15mm cockles and >12mm tellin whereas the cockles exploited by fishing are larger (≥28mm). Furthermore, cockle and tellin biomasses were combined in the model, but only cockles are exploited by fishing. The biomass of >15mm cockles and >12mm tellin not required by the birds was multiplied by the proportion of cockles >28mm (**Table 2;** 0.20 when including Wigtown Bay; 0.17 when excluding Wigtown Bay) to predict the biomass of cockles potentially available to shellfishing. **Table 4** presents the biomass of cockles >28mm not required by the birds for each of the scenarios described above.

When Wigtown Bay cockle and tellin biomass was included the model predicted that between 1604 (excluding upshore and terrestrial feeding) and 2048 (including upshore and terrestrial feeding) tonnes of >28mm cockles were potentially available to fishing (**Table 4a**). When Wigtown Bay cockle and tellin biomass was excluded the model predicted that between 310 and 687 tonnes of >28mm cockles were potentially available to fishing (**Table 4b**).

5.5 Comparison with individual-based model for 2007-2008

The individual-based model of oystercatcher and knot in the Solway Firth (Stillman 2008b) was based on 2007 surveys of cockles and tellin on the Scottish shore and 2005 to 2006 surveys of mussels on the English shore. The model incorporated cockles, mussels and tellin as potential shellfish food, as well as upshore feeding areas. The model did not include terrestrial habitats. The spreadsheet model was parameterised for the winter of 2007-2008 using the bird numbers and shellfish biomass used by Stillman (2008b), and assuming that birds did not feed in terrestrial habitats and that the proportion of birds feeding on mussels was the same as in the 2013 model. **Table 5** summarises the parameters and predictions of the spreadsheet model when parameterised using these data. The spreadsheet model predicted that 18038 tonnes of shellfish were not required knot during 2007-2008. Similarly, Stillman (2008b) noted that the abundance of potential knot food was approximately 52.6 greater than the amount of food required by the knot population. The individual-based model predicted that knot survival was 100% in all simulations, consistent with the prediction of the spreadsheet model that 18038 tonnes of shellfish were not required by the birds. The spreadsheet model predicted that the oystercatcher population required all of the shellfish food during 2007-2008. Similarly, Stillman (2008b) noted that the abundance of potential oystercatcher food was approximately 3.6 greater than the amount of food required by the oystercatcher population, close to the ecological multiplier of 3.3. The individual-based model predicted that a shellfishing Total Allowable Catch (TAC) of 1000 tonnes reduced oystercatcher survival and TACs of 500, 750 and 1000 tonnes reduced body mass. The spreadsheet model predicted that birds required all of the food and hence that any TAC would reduce survival during 2007-2008.

Table 3: Predicted shellfish biomass not required by oystercatcher and knot in the Solway Firth for the winter of 2013-2014. Predictions are for alternative scenarios differing in the range of prey species consumed by the birds (see text for details). Values are the biomass of prey species (tonnes fresh mass including shell) not required by the birds. Predictions assume that the typical size range of cockles and mussels is consumed (i.e. over 15mm and 30-60mm respectively for oystercatcher, and 5-14mm and 5-24mm for knot). Predictions were not produced for knot consuming terrestrial prey, as this species does not feed on these prey.

(a) Including Wigtown Bay cockle and tellin biomass

	Oystercatcher		Knot	
Scenario	Cockle / Tellin	Mussel	Cockle / Tellin	Mussel
Cockle, mussel and tellin	8022	0	4524	0
Cockle, mussel, tellin and upshore prey	9501	0	4784	47
Cockle, mussel, tellin, upshore and terrestrial prey	10240	395	-	-

(b) Excluding Wigtown Bay cockle and tellin biomass

	Oystercatcher		Knot	
Scenario	Cockle / Tellin	Mussel	Cockle / Tellin	Mussel
Cockle, mussel and tellin	1826	0	4248	0
Cockle, mussel, tellin and upshore prey	3305	0	4508	47
Cockle, mussel, tellin, upshore and terrestrial prey	4044	395	-	-

Table 4: Cockle biomass potentially available to shellfishing in the Solway Firth for the winter of 2013-2014 after accounting for the food requirements of oystercatcher. Predictions are for alternative scenarios differing in the range of prey species consumed by the birds (see text for details). The first data columns are repeated from Table 3 to show the biomass for cockles and tellin combined. Values in remaining columns are the biomass of cockles >28mm (tonnes fresh mass including shell) not required by the birds. Predictions assume that the typical size range of cockles and mussels is consumed (i.e. over 15mm and 30-60mm respectively for oystercatcher).

(a) Including Wigtown Bay cockle and tellin biomass

Scenario	Cockle > 15mm Tellin > 14mm	Cockle >28mm
Cockle, mussel and tellin	8022	1604
Cockle, mussel, tellin and upshore prey	9501	1900
Cockle, mussel, tellin, upshore and terrestrial prey	10240	2048

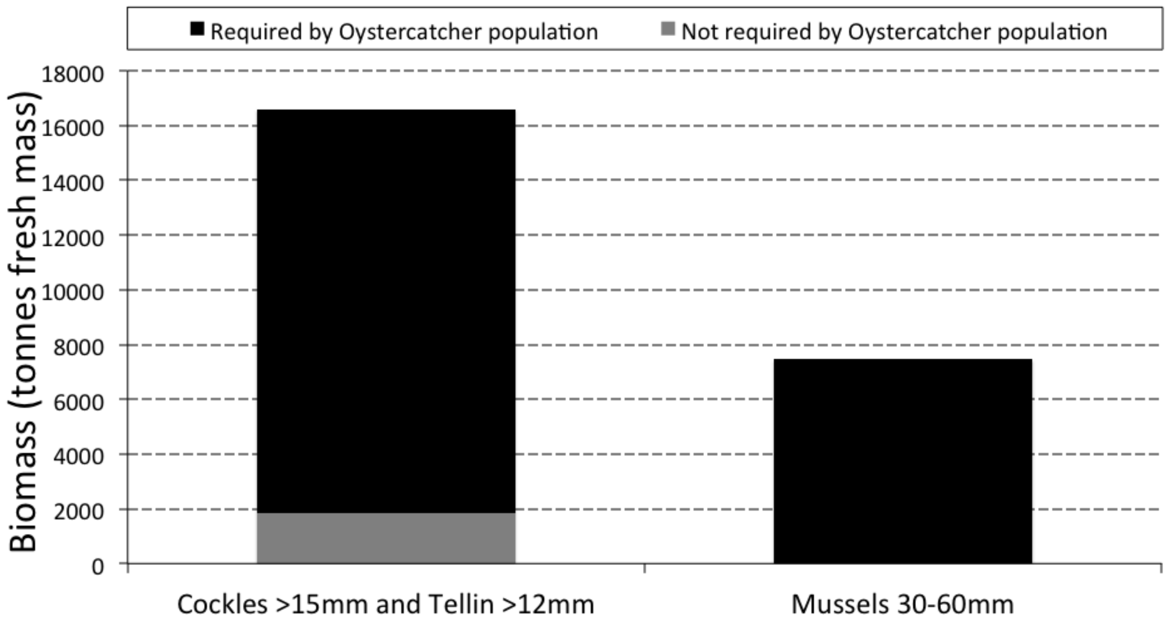
(b) Excluding Wigtown Bay cockle and tellin biomass

Scenario	Cockle > 15mm Tellin > 14mm	Cockle >28mm
Cockle, mussel and tellin	1826	310
Cockle, mussel, tellin and upshore prey	3305	562
Cockle, mussel, tellin, upshore and terrestrial prey	4044	687

Table5: Predictions of the spreadsheet model for the winter of 2007-2008 when paramterised to mimic as closely as possible the individual-based model developed by Stillman (2008b). The model assumed that the birds could feed on cockles, tellin, mussels and upshore areas. The proportion of birds feeding on mussels (as opposed to cockles and tellin) was the same as in the 2013 model. The predictions are for the standard size range of cockles and mussels consumed by oystercatcher (i.e. >15mm for cockles and 30-60mm for mussels).

Scenario	Oystercatcher	Knot
Cockle biomass (tonnes fresh mass)	4047	3483
Tellin biomass (tonnes fresh mass)	2891	9525
Mussel biomass (tonnes fresh mass)	5622	6366
Number of birds	30060	4641
Predicted shellfish biomass not required by the birds (tonnes fresh mass)	0	18038

(a) Oystercatcher



(b) Knot

Figure 6: *Cockle, mussel and tellin scenario*: predicted food requirements of oystercatcher and knot in the Solway Firth for the winter of 2013-2014 assuming that just cockles, mussels and tellin are consumed. Predictions exclude cockle and tellin biomass in Wigtown Bay.

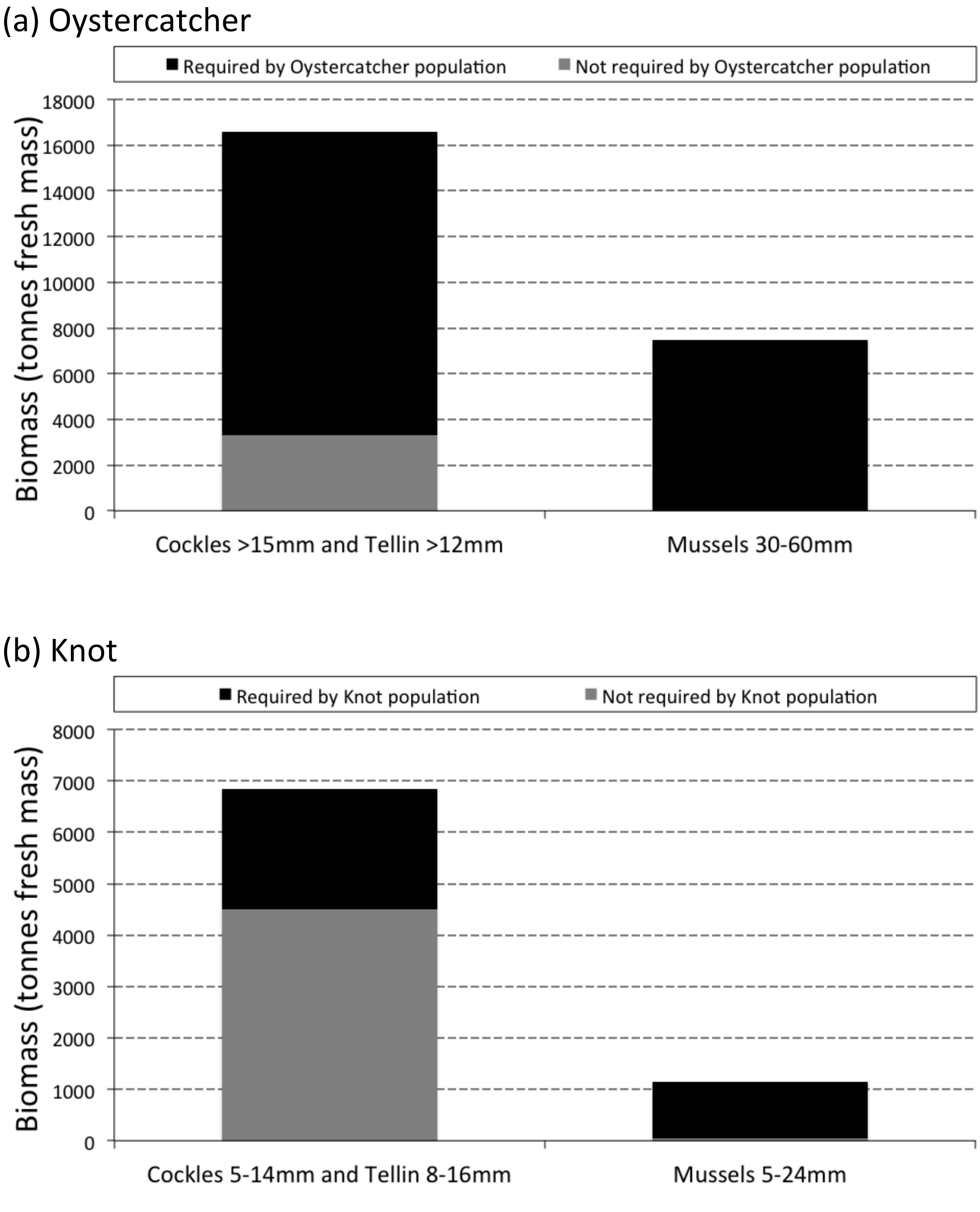


Figure 7: *Cockle, mussel, tellin and upshore scenario*: predicted food requirements of oystercatcher and knot in the Solway Firth for the winter of 2013-2014 assuming that cockles, mussels, tellin and upshore prey are consumed. Predictions exclude cockle and tellin biomass in Wigtown Bay.

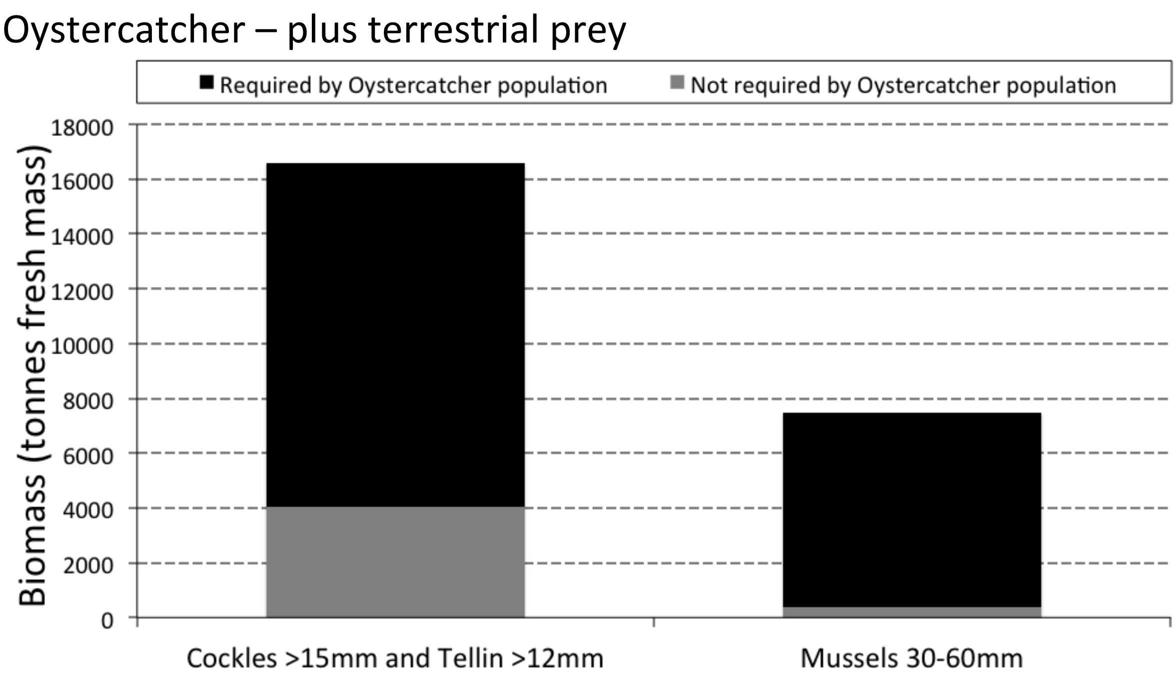


Figure 8: *Oystercatcher plus terrestrial prey scenario*: predicted food requirements of oystercatcher in the Solway Firth for the winter of 2013-2014 assuming that cockles, mussels, tellin, upshore and terrestrial prey are consumed by oystercatcher. Predictions exclude cockle and tellin biomass in Wigtown Bay.

6. Conclusions

The purpose of this report was to use the recently developed spreadsheet model of Stillman & Wood (2013a) to estimate the overwintering food requirements of the Solway Firth oystercatcher and knot populations. The model predicted that approximately 700 tonnes of >28mm cockles could potentially be exploited by shellfishing, after taking into account the food requirements of the birds excluding Wigtown cockle and tellin biomass, and assuming that the birds consumed cockles, mussels, tellin and prey from upshore areas and / or terrestrial habitats. This is considered to be the most realistic scenario given that oystercatcher can potentially feed on terrestrial habitats, and given the distance between Wigtown and the Inner Solway. The spreadsheet model is based on the food requirements of birds, as was a more detailed individual-based model previously developed for the Solway Firth (Stillman 2008b).

Both models have their advantages and disadvantages. The individual-based model can simulate the system in more detail, and predict, for example, how the daily quota or distribution of fishing between beds affects the birds. It also directly predicts how changes influence the survival rate and body condition of the birds. It is however relatively complicated which makes it more difficult to clearly explain how it works and the assumptions it makes. It must also be run by someone with modelling experience. The spreadsheet model is more simple and so its assumptions can be more clearly explained. It is also relatively straightforward to run, meaning that a person using the model does not need to have previous experience of modelling. It cannot however directly predict the survival of the birds or simulate important details of the real system in the way the individual-based model can, for example, between-bed differences in shellfish biomass or fishing effort.

Both models represented the alternative upshore and terrestrial food resources of oystercatcher in a relatively simple way as no data were available. If subsequent surveys showed that sufficient alternative food resources existed for the birds, more cockles could potentially be harvested without being predicted to adversely affect the birds. Detailed quantitative surveys of the Solway Firth benthic invertebrate community (in addition to cockles, mussels and tellin) would need to be undertaken. Therefore the availability of alternative prey has important implications for the setting of shellfishing quotas, and the current predictions can be considered as precautionary. For example, not all of the mussel and other shellfish stocks were included in the surveys. Incorporating these into the model would have meant that a greater biomass of cockles would have been predicted to have been potentially available for fishing.

The spreadsheet model described in this report does not replace the need for individual-based models but does have the advantage that it 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.

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