# Nuclear power and coastal birds: predicting the ecological consequences of warm-water outflows

Clement Garcia[a]*, Richard A. Stillman[b], Rodney M. Forster[a, c], Tiago Silva[a] and Julie Bremner[a.]

[a] Centre for Environment, Fisheries & Aquaculture Science (Cefas), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, United Kingdom.

[b] Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset, BH12 5BB, United Kingdom.

[c] Institute of Estuarine & Coastal Studies (IECS), University of Hull, Hull, HU6 7RX, United Kingdom

*Corresponding author at: Centre for Environment, Fisheries & Aquaculture Science (Cefas), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, United Kingdom

E-mail: clement.garcia@cefas.co.uk

Telephone: +44 (0) 1502 521363

ABSTRACT

Local alteration of species abundance in natural communities due to anthropogenic impacts may have secondary, cascading effects on species at higher trophic levels. Such effects are typically hard to single out due to their ubiquitous nature and, therefore, may render impact assessment exercises difficult to undertake. Here we describe how we used empirical knowledge together with modelling tools to predict the indirect trophic effects of a future warm-water outflow on populations of shorebirds and wildfowl. Of the main potential benthic prey used by the birds in this instance, the clam *Macoma balthica* was the only species suspected to be adversely affected by a future increase of temperature. Various scenarios of decreases in prey energy content, simulating various degrees of temperature increase, were tested using an individual-based model, MORPH, in order to assess the effects on birds. The survival and body condition of eight of the 10 bird species modelled, dunlin, ringed plover, turnstone, redshank, grey plover, black-tailed godwit, oystercatcher and shelduck were shown to be not influenced even by the most conservative prey reduction scenarios. Most of these species are known to feed primarily on polychaete worms. For the few bivalve-feeding species, the larger size-classes of polychaete worms were predicted to be a sufficient alternative food. Only knot was predicted to have a lower survival under the two worst case scenario of decreased *M. balthica* energy content. We believe that this is the first time such predicted cascade effects from a future warm-water outflow have been shown.

*Keywords:* Thermal pollution; Individual-based model; Shorebirds; Benthic invertebrates; Temperature sensitivity; Cascade effects

## 1.INTRODUCTION

Guaranteeing energy security whilst ensuring the transition to a low carbon economy will be a key challenge for all the nations in the 21st century. The world's economies need to change the way energy is produced so that a greater proportion of it comes from low-carbon sources (IPCC, 2014). As a consequence, nuclear energy is on the policy agenda of many countries with projections for new build exceeding those in the early years of nuclear power, to the point that the term "*nuclear renaissance*" has been used to refer to the potential increase of the nuclear industry (World Nuclear Association, 2015).

Coastal sites are the preferred location for new nuclear build (NNB), as a reliable supply of water for cooling is often a prerequisite for operations. The cooling systems for nuclear power stations can produce considerable volumes (>100$m^3$ $s^{-1}$) of heated seawater (>10°C above ambient). The potential increase of nuclear power operations makes it pressing to assess the impact of such heated seawater discharge on the marine environment (Crema and Bonvicini Pagliai, 1980). The region of elevated temperature may extend for up to 10km (Suh, 2014), with bathymetry, tides and winds determining the rate of dispersion.

All species have a preferred temperature range and a local change can potentially lead to changes at population, species and community-levels. Benthic species, with a fixed location on the seabed and limited possibilities for avoidance, are exposed to more prolonged thermal effects than any other ecological compartments (Blake et al., 1976; Cowie, 2007; Robinson, 2010; Schiel et al., 2004). At any given location, benthic communities are likely to include some species that are close to either their minimum or maximimum thermal limits of distribution. It would then be expected that local temperature increase due to thermal effluent would potentially benefit the former and adversely affect the latter (Bamber, 1995). This could lead to a structural reorganisation of the community following local species depletion or loss and subsequent consequences through bottom-up cascading (or secondary) effects (Pimm, 1980) *via* compensation among competitors and interactions among trophic level. A recent review of empirical studies shows that cascading extinctions that result from loss of a focal species tend to be more likely if the species is highly connected in the food network as well as more severely affecting species at higher trophic levels when the loss is at low trophic levels (Duffy et al., 2009).

The aim of the investigations described by this paper is to explore the ecological consequences of a large thermal discharge on wading birds, including shorebirds and wildfowl. Using high spatial and temporal resolution benthic data and the output from a separately validated numerical hydrodynamic model, these investigations explore how to predict which low-trophic level species (i.e. benthic invertebrate) are most likely to be affected by a direct local thermal discharge over an intertidal mudflat  and how best to estimate the cascading, secondary consequences for their main avian predators further up the food chain. We answer these questions in two steps: first, by using an empirical understanding of benthic invertebrate physiology and ecology coupled with the outputs of a validated hydrodynamic model to assess the potential consequences of a local temperature increase on the benthic community; second, by using an understanding of bird physiology and behaviour in individual-based model to predict the knock-on consequences for the birds of changes in their invertebrate prey.

## 2 METHOD

### 2.1 Study site and context

The Severn Estuary (UK) is one of the largest estuaries in Europe and has the third largest tidal range in the world. It encompasses several sites supporting bird populations that are of national or international importance. Although the estuary is thought of as species-poor, prey items are found at very high densities across wide areas of intertidal mudflats and sandbanks (Boyden and Little, 1973; Mettam et al., 1994; Warwick and Somerfield, 2010; Warwick et al., 1991) which support considerable numbers of wading birds during the winter (Burton et al., 2010). The largest of these areas is Bridgwater Bay, which is composed of two main intertidal mudflats, Stert and Berrow flats respectively on the south and the north side of the River Parret (**Figure 1).** Adjacent to the bay, Hinkley Point (HP) is the location of two existing nuclear power stations (HPA – no longer operating and HPB – operational) and permission has recently been granted for a third (HPC), the operation of which could have impacts on the local marine fauna and flora, including the wading bird and their preys.

### 2.2 Identification of the potential thermal impact on benthic invertebrate species

The benthic invertebrate species *Corophium volutator*, *Hediste diversicolor*, *Macoma balthica* and *Peringia (Hydrobia) ulvae* are among the key biological features of the intertidal mudflats (Boyden and Little, 1973; Warwick et al., 1991). These species are known to form a component of shorebird diets (Goss-Custard et al., 2006; Langston et al., 2007) and the birds have been observed to actively utilise the mudflats to obtain the majority of their diet from the mudflat infauna (Burton et al., 2010; Clark and Prys-Jones, 1994). The trophic link between the birds and their infaunal prey means that any NNB activities potentially affecting the mudflat habitat may have direct implications for the benthic prey and knock-on secondary consequences for the bird populations at higher trophic levels.

### 2.2.1 Assessment of the sensitivity to elevated temperature for the main benthic taxa

The putative effect of a temperature increase on benthic taxa was first assessed by a literature review. Two elements were specifically sought: (i) the area of distribution where the species has been recorded and (ii) any specific physiological features tested *via* (e.g.) field or lab experiment or monitoring studies **(Table 1)**. Only *M. balthica* showed evidence of temperature sensitivity. The clam is a cold-water species with a latitituṇal distribution along the eastern Atlantic ranging from the Arctic Pechora Sea to the Gironde estuary (Hummel et al., 1997) and various laboratory experiments, long-term monitoring and correlative studies have provided evidence to suggest that *M. balthica* might be sensitive to increasing seawater temperature (e.g. Honkoop and Van Der Meer, 1998; Honkoop et al., 1998; Philippart et al., 2003). The species is also thought to currently be experiencing a range contraction in western Europe primarily due to warming temperature in the southern limit of its distribution (Bachelet et al., 1990; Beukema et al., 2009; Jansen et al., 2007).

### 2.2.2 Thermal sensitivity of *M. balthica*

Growth of *M. balthica* is thought to cease at 15°C (de Wilde, 1975), in the Wadden sea its main growth period has been observed to be between the time of first spawning in early spring and the time at which mean seawater temperatures reaches the 15°C threshold. At other places however, populations have shown dual growing seasons during both spring and autumn, when food availability is sufficient to support a second growth in the latter part of the year (Beukema and Desprez, 1986). Nevertheless, the single annual growing season in spring and early summer appears to be the rule in western Europe, while the dual growing season exceptions are thought to be restricted to the southern limit of distribution (south of ~50°N) (Beukema and Desprez, 1986). With the assumption that the Severn Estuary populations follow the single growing season rule, future thermal effluents in the study area are expected to bring forward the 15°C threshold, with an overall shortening of *M. balthica*'s only annual growth period and retarding biomass gain. As *M. balthica* is assumed to exhibit a linear growth (Beukema and De Bruin, 1977; Beukema and Desprez, 1986), an estimate of thermally-induced reduction of the growth period can therefore be used to predict resulting effects on biomass accrual using linear modelling (**Figure 2**).

## 2.3 The individual-based model

### 2.3.1 Rationale

The selection of an appropriate model for investigating the trophic interactions between the birds and their infaunal preys requires consideration of aspects of the birds' ecology. Mortality and reproductive rate of the birds are the two most important demographic factors to assess (Stillman and Goss-Custard, 2010). Individual-based models (IBM) are considered to be appropriate tools for such tasks since they consider important aspects of species interaction such as interference and competition and incorporation of individual variations (Stillman and Goss-Custard, 2010).

MORPH is a flexible IBM platform designed to be used with a wide range of species and environmental issues (freely available at: http://individualecology.bournemouth.ac.uk/index.html). The tool is described in detail in Stillman (2008). Briefly, the basic principles of MORPH are as follows: Time progresses in discrete, fixed duration time-steps, the birds arrive on site on their species-specific arrival day, they remain at the same location during a time-step, either on a feeding patch or travelling between patches but cannot move between time-steps. They alter their location and the food they consume in order to maximise their perceive fitness and finally leave the site on their species-specific departure day. During the model period, each day, each model bird aims to meet its temperature-related energy demand by selecting feeding locations, times of the day and tidal zones where the intake rate is highest. Survival is then determined by the balance between daily consumption rate and energy demands.

### 2.3.2 The model global environment

The model simulations were run over a generic period from 1st September to 31st March, encompassing the major overwintering period of most shorebirds in the UK. The time step was set to one hour and environmental conditions assumed to remain constant during each time step.

### 2.3.3 The model patches

Ten profiles covering the full tidal range were defined over Bridgwater Bay (A to K, from south to north), using site-specific information on the resources available over the modelled area (Bolam et al., 2011; Musk et al., 2011a, 2011b, 2010a, 2010b). Each of these zones was divided into three areas according to their tidal elevation (low, mid or high tide). A low-lying sandbar in the mouth of the Parrett River was also defined as a patch, as was a supratidal roosting area (where the birds can go when the tide covers the entire feeding area). The modelled area of Bridgwater Bay was thus divided into 31 feeding and 1 roosting patches **(Figure 1** and **Appendix A)**.

### 2.3.4 Patch resources

*Benthic data source*

A seasonal survey of the intertidal benthic community was conducted in 2010/2011 with one visit per season (April, July and November 2010 and January 2011). For each species ash-free dry weight was calculated either individually or at the species level. Additionally, shell length/total length in mm was measured for most polychaetes and mollusc taxa collected.

*Prey size class*

Common shorebird species forage mainly across a particular prey size range (Goss-Custard et al., 2006). In order to classify the potential dietary sources in an ecologically realistic manner, the invertebrate species were grouped by size. All taxa whose average length was less than 10mm were attributed to one of the resource categories with no size differences (**Appendix B**); the majority of species recorded from the mudflats belonged to this category. Species whose lengths exceeded 10mm – the bivalve *M. balthica* and the polychaetes *H. diversicolor*, *Eunereis longissima*, *Nephtys hombergii*, *Nephtys cirrosa* and *Eteone longa/flava* - were divided into resource-specific size-classes, based on published information on size range of prey handling by different bird species (Goss-Custard et al., 2006). Thus, bivalves were divided into two (<10mm and >10mm) and polychaetes into four (<10mm, 10-20mm, 20-50mm and >50mm) size classes (**Appendix B & C**).

*Resource identity and density at the start of the model period*

The birds' prey-specific intake rates are not fully defined with respect to all macro-invertebrate species present in the mudflat. Fortunately, they were still available for the most abundant species (Goss-Custard et al., 2006). We however chose not to ignore the potential extra sources of energy from the other, rarer species but, in so doing, had to simplify the prey-species input in MORPH by arranging all species into functional resource groups, referred to as 'resource group' hereafter. Apart from the bivalve group which exclusively contains *M. balthica,* the resource groups were based on the most abundant taxa on site: *P. ulvae*, *Pygospio elegans*, *C. volutator*, *H. diversicolor* and the oligochaete family Enchytraeidae and the remaining species were grouped with one of the closest abundant taxa according to shape, size and life form (**Appendix B**). Their respective initial density was then calculated using the July 2010 abundance data (**Appendix C)**. These resource groups[1] were named and defined as follow:

- "PolErr" (Polychaeta Errantia or motile worms, e.g. *Hediste* spp, *Nephtys* spp): 4 size-classes (<10mm – PolErr0to10, 10-20 – PolErr10to20, 20-50 – PolErr20to50 and >50mm – PolErr50plus)

---

[1] The resource groups do not follow taxonomical convention since they are composite groups that may include different taxa or/and specific size-classes. In order to avoid any confusions, the resource groups names are underlined hereafter, e.g. <u>PolErr0to10 resource group</u>.

- “PolSed” (Polychaeta Sedentaria or sessile or discretely motile worms, e.g. *P. elegans*): 1 size-class
- “Interstitial” (Interstitial worms and small motile worms, e.g. Nematoda): 1 size-class
- “Crustacea” (small crustaceans, e.g. *C. volutator*, *Diastylis* spp): 1 size-class
- “Macoma” (*M. balthica only*): 2 size-classes (<10mm – Macoma0to10 and >10mm – Macoma10plus)
- “Gastropoda" (gastropod, e.g. *P. ulvae*): 1 size-class

*Prey energy content at the start of the model period*

- Benthic invertebrates

Ash-free dry weight (AFDW) was used as the proxy for the prey individual energy content. As with the calculation of faunal density, for all resource groups AFDW was calculated using the July 2010 data. Average AFDW per individual of each resource group was calculated for each feeding patch.

- Microphytobenthos

The microphytobenthic (MPB) biofilm is also known to be used as a food source for some bird species (e.g. Kuwae et al., 2012, 2008; Mathot et al., 2010). Inspection of multispectral Landsat images from the period 1999-2010 has shown that the mid to upper shore of Bridgwater Bay has a region of enhanced infra-red reflectance indicative of dense MPB cover (van der Wal et al., 2010). Unfortunately, no representative MPB samples were available for the site, so an indirect estimation based on sediment grain size was utilised. Muddy sediments are known to always support a higher MPB biomass than sandy sediments and dense surface biofilms only occur when the silt content is high (Paterson, 1989).

The grain size of the sediment where infauna samples were collected was therefore used as an indicator of the biofilm food resource, with an assumed inversely proportional relationship between chlorophyll and increasing grain size converted to an algal equivalent AFDW per m$^2$, assuming the following relations:

- 1mg chl *a*=50x1mgC (de Jonge, 1980)
- 1mg AFDW=0.4x1mgC (Finlay and Uhlig, 1981).

However, the way the ingestion rate of birds changes with MPB density (i.e. functional response see **section 2.3.6**) is unknown which prevents direct inclusion of MPB as an independent resource group in MORPH. Therefore, MPB was linked to the benthic resource groups, assuming that invertebrate prey physically covered with MPB would display a higher energy value than would the same type of prey not covered by MPB. Larger individuals are able to burrow deeper in the sediment, but MPB biofilms are mainly found in the upper 2mm of sediment. With this in mind, only the small group resources were considered to benefit from this supplementary energetic value. The average MPB AFDW/m$^2$ was apportioned between the six smallest resource groups presented above (i.e. PolErr0to10 resource group, Gastropoda resource group, Interstitial resource group, PolSed resource group, Macoma0to10 resource group and Crustacea resource group) (see **Appendix C)**.

*Resource dynamics*

- Densities

It was difficult to determine the shape of the relationship between resource groups abundance and time with measurement at four intervals through the year; we chose to assume a constant proportional loss of prey per day that followed an exponential model decrease. A second problem was related to the extent to which the non-predation mortality (i.e., mortality not caused by birds) affects the resource groups. We used a conservative estimate by considering the difference in density between July 2010 and the average of January 2011 and April 2010 (**Figure 3a**) to be only due to non-predation mortality. In summary, the resource group densities were considered to decrease throughout the winter by the resource group-specific proportions shown in **Table 2**.

- Average Ash-free dry weight per individual

Similarly to the density dynamic, the exact nature of the individual weight change was difficult to characterise. Zwarts and Wanink (1993) made a seasonal study of body weight of *M. balthica*, *Scrobicularia plana*, *Cerastoderma edule* and *Mya arenaria* and found a linear decrease of 28% between May/June and November to March. We assumed that all of the resource groups followed a similar linear decrease; the difference in average individual AFDW content between the average of the month of January and April data (end point) and the July data (starting point) were used to set the extent of the decrease (**Table 2** and **Figure 3b**). No seasonal data were available for the MPB, therefore only the energy content that relates to the benthic species was considered.

### 2.3.5 The bird assemblage

The bird assemblage data needed to parameterise MORPH are overall mean monthly count, arrival day and departure day for each forager species. Data used for the present MORPH model were obtained from the Wetland Bird Survey (WeBS) Core Counts scheme (http://www.bto.org/volunteer-surveys/webs/taking-part/core-counts, data obtained in August 2012). In Bridgwater Bay bird data were available from four areas (Berrow flats, Berrow, Burnhamon-Sea and Bridgwater Bay). These areas have been surveyed for several consecutive years and have been summarised in order to build a generic September to March period.

The WeBS dataset provided the bird counts as a monthly average per species per area. Ten species of birds were considered to be the most important species in terms of overwintering in Bridgwater Bay (Burton et al., 2010) and feeding off the intertidal zone (Goss-Custard et al., 2006): dunlin (*Calidris alpina*), ringed plover (*Charadrius hiaticula*), turnstone (*Arenaria interpres*), knot (*Calidris canuta*), redshank (*Tringa totanus*), grey plover (*Pluvialis squatarola*), black-tailed godwit (*Limosa limosa*), oystercatcher (*Haematopus ostralegus*), curlew (*Numenius arquata*) and shelduck (*Tadorna tadorna*) (**Table 3**). Relevant bird data were extracted from the database and, for each species, the monthly averages were summed across the four areas to give monthly averages for the whole of the Bridgwater Bay (**Table 3** and **Figure 4**). MORPH does not allow for the temporal variation of bird number, only an arrival, a departure date and a mean of monthly counts. Between the arrival and the departure, no bird individual can be added to the site and any removal only occurs by death of the individuals if they cannot meet their energy requirements. Therefore, in order to capture some of the temporal variation in bird population changes, any monthly count below 10% of the winter maximum was ignored and average bird numbers were calculated from the remaining months of data. Similarly, a bird species was considered absent if the 10% threshold was not reached. In this way, it was possible to estimate the arrival and departure dates parameters for each species (**Table 3** and **Figure 4**).

### 2.3.6 Forager feeding ecology

The following sections describe the derivation of forager feeding parameter values specific to the present MORPH version. The other, more generic, parameter values are given in **Appendix D**.

#### *Diet*

There is an abundant literature on feeding of coastal birds (see e.g. Anders et al., 2009; Evans, 1987; Goss-Custard et al., 2006; Quaintenne et al., 2010; Scheiffarth and Nehls, 1997; Zwarts and Wanink, 1993). This information was used to characterise a bird-specific diet for all the forager species selected in the model based on a specific selection of the resource groups, in other words, a bird diet group[2] was defined as a combination of one or more resource groups (**Table 4a and b**).

---

[2] The bird diet groups do not follow taxonomical convention since they are composite groups that includes one or more resource groups which in turn may include one or more taxa and or specific size-classes. The diet groups names are underlined hereafter, e.g. <u>PolErr20plus diet group</u>

### *Day and night variation in foraging efficiency*

Many species of waders forage extensively at night, but there is little information on the relevance of this behaviour for the energy budget of waders wintering in estuarine wetlands. In the present model the relative rates at which waders could feed during the day and night were derived from Lourenço et al. (2008) and Sitters (2000) (**Appendix E**). In their paper, Lourenço et al. (2008) calculated night-time efficiency as the proportion of day time energy consumption obtained during the night for four species: ringed plover (49%), redshank (95%), grey plover (100%) and black-tailed godwit (87%). It is unclear whether grey plover obtains more energy at night (Kalejta, 1992) or during the day (Turpie and Hockey, 1993); as a consequence, a value of 100% was used for this species. For oystercatchers, night-time efficiency has been calculated at 100% of daytime for individuals opening prey using the stabbing feeding method and 62% of daytime for individuals opening prey using the hammering feeding method (Sitters, 2000); as we do not know the specific mechanism used by oystercatchers in this instance, we used the average of these two values (81%). No other estimation of night-time efficiency was available to our knowledge, so the average of the values given above was used (82%) for the remainder of the species.

### *Bird functional response*

The functional response parameter utilised within MORPH is a mathematical formulation describing the way a species ingestion rate varies with respect to food density. In theory, a functional response is species-specific but in practice species with similar feeding behaviour and prey items can share similarities in their functional response. As such the shorebird species included in MORPH (i.e. dunlin, ringed plover, turnstone, knot, redshank, grey plover, black-tailed godwit, oystercatcher and curlew) share a common formulation of the functional response while shelduck, being a wildfowl, is expected to be different.

- Shorebirds

The functional responses utilised in the model are based on body mass, using the equation of Goss-Custard et al. (2006):

$$IFIR = f\,\frac{IFIR_{max}\,B}{B_{50} + B}$$

Where $IFIR$= Interference-free intake rate (mg.s$^{-1}$), $f$= foraging efficiency of the focal individual, $B$= patch biomass density of prey within the size range consumed (mg.m$^{-2}$), $IFIR_{max}$= maximum intake rate when prey are superabundant and $B_{50}$= prey biomass density at which intake rate is 50% of its maximum. Values of $f$, $B$ and $B_{50}$ were taken from Goss-Custard et al. (2006) and $IFIR_{max}$ was related to shorebird body mass and prey mass with the following equation:

$$\ln(IFIR_{max}) = -2.802 + 0.245 \ln M_{bird} + 0.365 \ln rM_{prey}$$

Where $M_{bird}$ = average body mass (g) of the bird species at the start of the model period, $M_{prey}$ = mean ash-free dry weigh (mg) of prey within the size consumed and $r$=1.05 (assumed ratio of size of prey consumed to size in patch) (Goss-Custard et al., 2006)

- Shelduck

Using the shorebird functional response equation “as it is” for shelduck was inappropriate because it was developed for shorebirds but shelduck is a wildfowl and this would result in an underestimation of its intake rate calculation. However, since no functional response value existed for shelduck, we adapted the shorebird equation to account for the different way of feeding. The classic shorebirds functional response follows the general forms of the ‘disc equation’, which is a theoretical model of a decelerating rate of intake (see e.g., Goss-Custard et al., 2006, Hiddink, 2003 and Smart and Gill, 2003) where the maximum (or asymptotic) intake rate is determined by how long it takes the forager to capture and swallow prey items, the ‘handling time’. At the asymptote of the functional response, the prey items are so abundant that the forager finds another prey immediately after it swallows the preceding, the intake rate being only limited by the rate at which the gut can process food. However, instead of probing or pecking for individual prey items as shorebirds do, shelduck sweeps the surface of the mud in broad arcs (‘scything’) which results in an omnivorous diet (Ferns and Reed, 2009) that may include MPB (Meininger and Snoek, 1992), *P. ulvae*, young *M. balthica*, young mussels, young cockles and many kind of worms (including *H. diversicolor*) (Anders et al., 2009; Ferns and Reed, 2009; Leopold et al., 2004a, 2004b). Additionally, shelduck is the largest species of all the birds considered in the present study and feeds on rather small prey sizes with respect to its own body mass. This is a very wildfowl-specific characteristic since amongst the shorebirds, the larger the bird species, the larger the prey size (Goss-Custard et al., 2006; Johnson, 1985). The long-term trend of shelduck winter counts suggests a slightly increasing overwintering population in Bridgwater Bay (Burton et al., 2010); this means that the current observed survival for the species in the area must be high. Consequently, the shorebird equation, which underestimates shelduck intake rate (and overestimate its mortality), was corrected by progressively increasing to the value of the $IFIR$ until the resulting modelled survival reached values very close to 100% - this happened after a 50% increase of the $IFIR$ coefficient for shelduck.

2.4 Simulation procedures

Each simulation was run for one autumn-winter period. The simulation predictions vary each time it is run, due to the particular characteristics of the individuals in each run. Five simulations for each combination of parameter values were therefore run.

Site carrying capacity was measured by assessing bird survival against prey biomass densities (gAFDW.m$^{-2}$) variation from 0 to 250% of the current condition.

The only intertidal invertebrate species in Bridgwater Bay considered to be potentially adversely sensitive to increasing seawater temperature is *M. balthica*. A temperature rise due to thermal effluents can be expected to shorten the growth period and retard biomass gain (**Figure 2**). Thus, we modelled the effect of reductions in the growth period of the species on its bird predators.

The length of the growing season was estimated using bottom water temperature values from a run of an existing validated and calibrated numerical hydrodynamic model utilising the General Estuarine Transport Model (GETM, the model was obtained from https://www.getm.eu) (Stips et al., 2004). This model was run in 3D with 100m resolution and 15 depth intervals, providing simulated temperature outputs for the intertidal areas covering periods of both immersion and emersion. The 3D domain included the Severn Estuary and the inner Bristol Channel up to the line between Minehead and Cowbridge. The elevation and current boundary conditions were supplied from a larger 2D GETM run and the meteorological forcing from ECMWF (European Centre for Medium-Range Weather Forecasts: http://www.ecmwf.int/en/research/climate-reanalysis/era-interim) ERA interim reanalysis data. The GETM model was run at 1.5 second internal time steps for one full year and includes the cooling water discharge from HPB power station, which has a flow of 33m.s$^{-1}$ and a temperature increase at the outfall of 11°C. The GETM model was successfully validated against measurements from tidal gauges in the Severn and Acoustic Droppler Current Profilers (ADCP) data and temperature sensors previously deployed in the Bridgwater Bay area. For more details of this model and its corroboration see Fernand et al. (2011).

The GETM model output allowed for a determination of the the extent of the spring growth period as the number of Julian days between mid-March, the estimated start of the growth period (Beukema et al., 1985) - Julian day number 80 - and the point at which 15°C was achieved for two or more consecutive days. The baseline length of the growth period was based on the current situation (**Table 5**). The GETM model was used to calculate the potential reduction in the length of the growing season in *M. balthica* exposed to the thermal plume.

The reduction in biomass accrued over a single growing season was translated into MORPH by decreasing the average AFDW content of individual *M. balthica* and therefore the temperature effect concerns only the two model resource groups including this species (Macoma0to10 resource group and Macoma10plus resource group). Three scenarios of biomass reduction were simulated (B, C and D in **Table 5**) and compared against the reference conditions (A in **Table 5**).

# 3.RESULTS

## 3.1 Corroboration of the MORPH model

The principle of a model corroboration, as defined by Grimm et al. (2014), is to compare model predictions against data recorded in a separate independently collected data set not utilised in the development of that model. Here we compared model estimates and actual observations of (1) the overall proportion of time foraging by the birds and (2) the distribution of wading birds around Bridgwater Bay.

The field observation data came from EDF/NNB Genco Entec Ltd dataset (described in EDF/NNB Genco Entec UK Ltd, 2009). These data classify observed activities into a number of different types. After removing the "activity unclear", five main activities remained: "Commuting", "Flushed", "Foraging", "Loafing" and "Roosting". MORPH does not provide such detailed outputs of bird behaviour since "Foraging" and "Roosting" are the only possible activities of modelled birds. Observed bird activities were thus rearranged into "Foraging" and "Not Foraging" (the latter including "Commuting", "Flushed", "Loafing" and "Roosting"). An "observed" average proportion value of birds "Foraging" and "Not Foraging" was then compared to the "predicted" value emerging from MORPH along with their respective 95% confidence interval (**Figure 5**).

For eight (8) of the bird species, the predicted foraging time was within the 95% confidence interval of the mean of those observed. The two bird species for which modelled and observed foraging times were different, oystercatcher and curlew, are predicted to spend more time feeding than observed.

For testing the spatial predictions of the model, field observations were taken from WeBS low tide counts (http://www.bto.org/volunteer-surveys/webs/taking-part/low-tide-counts data obtained in August 2012).

The primary purpose of the WeBS scheme is to investigate relative distributions averaged over several dates, which makes it an ideal dataset for validating spatial prediction. The observed winter low tide counts (November 2009 to February 2010) were compared against predicted bird distribution on the patches (i.e., A, B-C, D-E, F, G, H, I, J, K) (**Figure 6)**. Most modelled bird species show the same pattern of distribution spending most of their time on the same two main patches, a primary and a secondary one. Overall, MORPH runs predicted the bird distribution among patches with a high degree of accuracy especially for the primary feeding patches. The two main discrepancies concern: (i) knot, for which the model predicted foraging on Berrow flats (i.e. I and K) whilst observations showed that the actual preference was for Stert flats (i.e. A, B-C and D-E) and (ii) oystercatcher for which the primary feeding ground was predicted to be Stert flats whilst observations showed a preference for Berrow flats (i.e. from patch G to K). Additionally, the observed secondary feeding patches on Berrow flats by curlew (~10%) and shelduck (~20%) were not well predicted by the model.

For all species except knot, Stert flats (B-C and D-E) was observed to be the predominant foraging habitat which is in accordance with MORPH predictions.

## 3.2 Model simulations outputs

### 3.2.1 Bird survival and prey selection

Food availability, as average biomass density (i.e. mean biomass multiplied by the density), mainly controls the survival and body condition (respectively expressed as the percentage of the number of birds alive / total and the final average bird mass / target mass – the average mass of a healthy bird) of the birds on site. These bird-specific values recorded at the end of the winter season are two of the major outputs of MORPH (**Table 6).** With an average of 14.49 gAFDW/m$^2$ of benthic invertebrates and MPB prey supply, Bridgwater Bay is predicted to sustain in excess of 97% of the overall overwintering bird population under reference (i.e. current) conditions. Of the 10 bird species selected, 7 had a survival rate of over 99% and body condition over 98%. Of the 3 remaining species, MORPH predicted shelduck, oystercatcher and curlew body condition to be 91, 90 and 73.3% and survival rates to be 100, 91.6 and 64.7% respectively.

Half of the bird species were predicted from MORPH outputs to feed on only one type of resource while the other half were expected to have a more diverse diet (**Figure 7**). The PolErr resource groups (mix of size-classes) were predicted to sustain the majority of the bird species, exclusively for grey plover and black-tailed godwit (PolErr20plus diet group), oystercatcher and curlew (PolErr50plus diet group) and in majority for turnstone and redshank (PolErr20plus diet group) and shelduck (PolErr50plus diet group). Dunlin and ringed plover were predicted to mainly use the Crustacea diet group and knot were predicted to feed on the large Macoma10plus diet group. Resources composing the Gastropoda diet group and Worms0to10 diet group are not expected to be major dietary items for the birds.

### 3.2.2 Effects of changes in prey biomass across all patches

In order to test how sustainable Bridgwater Bay is for the bird feeding on the mudflats, prey biomass densities, encompassing all resource groups, were varied between 0 and 250% of the current (2010) mean (in gAFDW/m$^2$) to determine the threshold below which survival would be adversely affected (**Figure 8**). As a result, dunlin, turnstone, knot, redshank, grey plover and black-tailed godwit were predicted to show a survival rate >94% until the food supply was reduced to 25%. Ringed plover remained at 100% survival when food supply was reduced to 75%. Shelduck survival was shown to decrease immediately after the food supply was reduced (83% survival rate at 75% AFDW). Finally, survival for oystercatcher and curlew within Bridgwater Bay was predicted to be lower than 100% with the current food supply (100%). Oystercatcher reaches 100% survival with an extra 25% food supply but even with up to 250% of the reference biomass condition curlew survival only reaches 97%. Thus, for all species except oystercatcher and curlew, the available data suggest that the current observed food supply within Bridgwater Bay is sufficient or more than sufficient to support the observed number of birds. Shelduck and ringed plover are predicted to be the most sensitive species to reductions in food supply.

### 3.2.3 Effects of changes in prey biomass due to warm-water outflow

The body condition and survival of dunlin, ringed plover, turnstone, redshank, grey plover, black-tailed godwit, oystercatcher, curlew and shelduck are not predicted to be adversely impacted by reductions in *M. balthica* average AFDW brought on by any of the four tested scenarios (**Figures 9 & 10**). Knot, on the other hand, is predicted to be slightly affected by scenario B (1.2% reduction in survival), C (1.5% reduction in survival) and D (3% reduction in survival).

Resources consumed by the birds are predicted to remain similar under all three scenarios considered. This is not surprising as, according to the model (**Figure 10**), dunlin and knot are the only two predators using *M. balthica* as a resource. Scenario C is predicted to be sufficient to trigger a switch in dunlin foraging activity from <u>Macoma0to10 diet group</u> to the <u>PolErr10to50 diet group</u>. Knot on the other hand, is predicted to feed on <u>Macoma10plus diet group</u> under every scenario.

## 4.DISCUSSION

### 4.1 Predicting the ecological consequences of a warm-water outflow

In this paper, we used empirical evidence coupled with two models, a previously validated hydrodynamic model and an IBM – MORPH – to predict the secondary consequences of a future heated effluent on bird populations. Efforts were made to incorporate observational data on all of the main bird species overwintering on our study site, Bridgwater bay; this includes shorebirds and wildfowl. Additionally, the model was implemented using high spatial and temporal resolution benthic data and a microphytobenthic component was included in order to build the most accurate estimation of prey stock and change through time for MORPH use. Model outputs for a reference case were also corroborated against independantly sourced field data not utilised in model development. To our knowledge, this is the first time that this has been done. We first endeavoured to qualitatively identify potential temperature sensitivity among the prey species living on the mudflat (i.e. benthic invertebrate). Then, an existing validated and calibrated numerical hydrodynamic model (GETM) was used to assess the quantitative extent of the thermal and seasonal sensitivity and its inherent consequences on the populations of the clam *M. balthica*, the only species suspected to be adversely affected by a warm-water outflow. The biological link between benthic prey species and their avian predators was formalised by implementing a Bridgwater Bay-specific version of MORPH. GETM outputs which described *M. balthica* growth period shortening were then fed into MORPH and different prey decrease scenarios were thus simulated. MORPH predicted that a local temperature increase due to the the proposed power station development (HPC) would cause little difference for worm-feeding birds and that even primarily bivalve-feeding species would have the ability to shift to a more worm-based diet if necessary.

## 4.2 Understanding the effects of thermal impact on benthic invertebrates

Depending upon the precise disposition of the discharge and the local tidal regime, warm-water discharges from coastal power stations can be expected to have an effect that extends to local intertidal areas. Infaunal communities living between the low and the high water marks will already experience daily variations in environmental stress (e.g. wave-induced sediment remobilisation, temperature, salinity, dessication) (Raffaelli and Hawkins, 1996) and this can be even more pronounced if the area is also located in or close to an estuary due to the presence of and variance in freshwater discharge (Little, 2000) or where the tidal range is extreme leading to higher levels of superficial sediment disturbance (Raffaelli and Hawkins, 1996). Consequently, most benthic species living on the intertidal mudflats are ecologically adapted to such varying environments. Understandably, all dominant benthic species in Bridgwater Bay are euryhaline and eurythermic and present some form of resistance to most stresses caused by their intertidal and estuarine medium (Little, 2000). As a result these species are not expected to be readily sensitive to thermal stress unless they are already close to their warmer limit of geographic distribution and are already undergoing some sort of stress (temperature or otherwise), whereby an extra thermal pressure during a critical period of the year could “push them over the edge”. In first considering possible thermal effects of a new power station development on the intertidal area of Bridgwater Bay, through published evidence from field and laboratory studies and due to its reported southern limit of distribution (see **section 2.2.1**), we identified the cold-water clam *M. balthica* as potentially temperature sensitive. The study that has been reported here suggests, however, that this will not be of great concern because the direct thermal impact on the *M. balthica* population will be somewhat local (mostly on Stert flat) and the indirect effect on its bird predators attenuated by the availability of alternative choices of prey. Beside, competitive realease means that this local loss may lead to a structural reorganisation of the community *via* compensatory mechanisms (Duffy et al., 2009; Ernest and Brown, 2001); the outcome of which cannot be known for certain until it occurs but scenarios of benthic succession along various environmental gradient, together with the knowledge of the other locally dominant species suggest that a shift to polychaetes-dominated community might happen (Rosenberg, 2001). This, in turn, could potentially account for the extra predatory pressure forecast by the model on these taxa. In Bridgwater Bay *M. balthica* is not predicted to be the main prey for the birds normally present, hence the negligible cascade effects on bird predators. It cannot, however, be assumed that this will consistently remain the case since prey/predator linkages are known to differ between sites. For example, a study in the Wash, England, showed that a similar local depression of two clams the cockle *Cerastoderma edule* and the mussel *Mytily edulis* (due to fishery activity) progressively changed the population of birds from a bivalve-diet species to a worm-based species thus qualitatively changing the bird populations (Atkinson et al., 2010).

### 4.3 Model corroboration

IBMs like MORPH are relatively complicated, but they still represent a considerable simplification of real ecosystems. In considering potential impacts on a localised area such as Bridgwater Bay it is important that they consider the main drivers of the processes at stake in order to make accurate and usable simulations. They must represent the best compromise between simplification and accuracy of the processes modelled. IBMs have been shown to accurately predict or postdict survival rate in shorebirds at a range of sites (e.g., Stillman et al., 2007), and both survival (Goss-Custard et al., 2004) and behaviour (Stillman et al., 2010) have been accurately postdicted in a site nearby, the Burry Inlet. MORPH has also been used and validated in a variety of estuarine and coastal systems where applications emcompassed site-quality monitoring and scenario testing in relation to habitat loss or creation, tidal barrages, human disturbance, shell-fishing or climate change (e.g. the Humber estuary, Stillman et al., 2005; Pool Harbour, Dit Durell et al., 2006; the Bay of Somme, Dit Durell et al., 2008 or the Bay of Seine, Dit Durell et al., 2005).

In Bridgwater Bay, predictions were corroborated with field data from different sources than those used in developing the model itself. Overall, MORPH accurately predicted the present-day distribution of dunlin, ringed plover, turnstone, redshank and black-tailed godwit between the two main mudflats. However, knot, oystercatcher and, to a lesser extent, shelduck and curlew distributions were less well predicted. Modelled knot were predicted to feed entirely in high shore Berrow flats due to a high density of the Macoma10plus diet group in these areas. Observations, however, show that knot primarily fed on Stert flats which would have corresponded to a preferential use of the PolErr10to50 diet group and/or Gastropoda diet group. High-density patches of bivalves may have been missed despite our high spatial resolution surveys since *M. balthica* density has been observed to vary widely over a rather short spatial scale in other intertidal locations (Azouzi et al., 2002) and the medium-large *M. balthica* standing-stock of Stert flats could have been underestimated. Oystercatcher, curlew and shelduck's main feeding patches were correctly predicted but some of the secondary ones much less so. Realistically, not all parameters included in MORPH can be site-specific and some had to be derived from generic relationships defined with data from other areas (see **section 2.3.6** and **Appendix D**) (Stillman and Goss-Custard, 2010). These relationships, combined with the uncertainties of food abundance records, can explain some of the differences between predictions and observations. This is consistent with previously published applications, where MORPH sometimes failed to predict spatial occupation of some species, curlew and oystercatcher in Poole Harbour (Dit Durell et al., 2006) and dunlin and curlew in the Humber estuary (Stillman et al., 2005). These shortcomings have not prevented these models to make useful predictions.

The EDF/NNB Genco Entec UK Ltd (2009) data used to estimate the time spent foraging was derived from part of the model area only (Stert flats). Most of the bird species considered here primarily fed in this zone. As a consequence, the observed data, despite being partial, was considered to be a good proxy for the overall bird foraging effort across the whole area. Model outputs were in good agreement with observations. Though modelled birds seem to be foraging more than they do in nature, most of the predicted foraging is within the 95% confidence interval of the observed foraging, except for two species – oystercatcher and curlew. The observed time spent foraging for oystercatcher was less than that predicted by MORPH and this could potentially be explained by the discrepancy of coverage area between observations and model data. Modelled oystercatcher fed for only 50% of their time on Berrow flats and observations are lacking to explain a more complete account of the bird activities. The situation is similar for curlew as this species may also feed on other types of habitat besides intertidal mudflats, such as fields, saltmarsh, grasslands or freshwater areas at high tide (Del Hoyo et al., 1996). Such supplementary feeding grounds are not allowed for in MORPH, and this gap may explain why curlew was observed feeding more frequently than predicted. With only one main discrepancy for each test, we consider that MORPH provided a reasonable representation of the real system in this instance with perhaps a slight over-estimation of the energy needs when compared with what happens in nature.

## 4.4 Site quality

Inter-specific competition across bird species in MORPH only occurs through the depletion of shared resources (Stillman, 2008). More depletion will happen if many birds feed in the same area, i.e. if the area is perceived as attractive for maximising bird fitness. The predicted survival and body condition is a results from an indirect inter-specific competitions *via* shared food resources and direct intra-specific competition through variation in dominance and interference (Stillman et al., 2002, 2000; Triplet et al., 1999). Under the current conditions observed in Bridgwater Bay, curlew and oystercatcher had the lowest survival and body condition; all the other birds selected apart from shelduck were predicted to show a 100% survival rate and retain >98% of their body condition. Shelduck was predicted to have the same survival but at a slightly lower condition. Being a wildfowl, shelduck physiology might not be properly implemented in MORPH, the model having essentially been developed for shorebirds. However, shelduck survival and body condition predictions in this instance fell within the range of the other bird species considered and for which we have a higher modelling confidence. Moreover, no obvious higher mortality of shelduck was observed on the site since a consistently large population overwinters in Bridgwater Bay on an annual basis and, unlike curlew, shelduck is not known to forage on grounds other than mudflats (Bryant and Leng, 1975; Olney, 1965; Thompson, 1981). Additionally, the observed data on the overall proportion of time spent foraging and the distribution of shelduck within Bridgwater Bay confirmed the validity of the predictions. As a result we are confident that the shelduck-specific coefficient modification we applied to the shorebirds equation in this instance in order to account for its different feeding behaviour was a reasonable approximation of ecological reality. Even within the shorebirds group there are some species-specific differences in the observed functional responses (Goss-Custard et al., 2006) and yet case studies have shown that the functional equation considered in MORPH is powerful enough to account for these differences (e.g. Dit Durell et al., 2006; Stillman et al., 2005).

The low natural survival predictions for curlew in this instance were not unexpected: in a recent unpublished model of the Severn Estuary its predicted survival on the basis of mudflat use alone was around 50% (Stillman, Com. Pers). In reality curlew are also expected to feed on other grounds besides mudflats (Del Hoyo et al., 1996). A simulation of Poole Harbour (Dit Durell et al., 2006) confirmed that larger shorebirds require terrestrial feeding habitats. The curlew population observed within Bridgwater Bay could likely feed on such habitat at high tide in order to meet the energetic requirements which seem to be unsustainable by the mudflats alone, a behaviour that has indeed been observed within the Severn Estuary by Stillman (Com. Pers.).

In contrast, oystercatcher was predicted by MORPH to reach maximum survival and body condition with an additional 25% of food availability and should be able to survive with only the mudflat as a feeding ground. The predicted mortality with the current food conditions could be the natural mortality rate which is, indeed, expected to be in the range of 2-10% (Cramp and Simmons, 1983). Additionally, the night-time efficiency set for this bird – 81% - was derived from observations made in the Tejo Estuary in Portugal (Lourenço et al., 2008) and the efficiency could different in the Severn Estuary.

Overall the model predicted that there was more food available in Bridgwater Bay than that required by the birds; we are also confident that predictions for shorebirds and wildfowl have a similar level of accuracy. This implies that the bird community observed was not operating at the limit of the carrying capacity in Bridgwater Bay; this is consistent with the predictions of other MORPH applications (Stillman and Goss-Custard, 2010).

### 4.5 Effect of warm-water outflows on birds

The MORPH model simulated the effects of reduced *M. balthica* individual average AFDW due to a contraction of its growth period resulting from a warm-water discharge from a proposed new nuclear build within Bridgwater Bay. The exact effect of the future thermal impact on the clam's population dynamics cannot be confirmed until the station begins to operate. Some assumptions used in the present paper were not based on local field observations but instead on the authors' knowledge on the species' physiology, previously published temperature-related population dynamic studies and existing numerical hydrodynamic model outputs: one result was that we were obliged to use a wide range of potential AFDW decreases from that model to bracket the possible impact of the thermal influence on that particular parameter value. The simulation scenarios show that (i) eight of the 10 bird species included in the model did not differ in their survival and body condition under even the most conservative impact scenarios, most of these species being found to feed predominantly on worms and (ii) the progressive decrease of *M. balthica* attractiveness triggered a switch to the PolErr resource group (mix size-classes). The only bird species amongst those selected whose survival was predicted to be reduced by a *M. balthica* AFDW decrease was knot. Knot has been observed to feed on the worm *H. diversicolor*, but only on individuals ranging from 10 to 59mm (Goss-Custard et al., 2006); an older study even states that this species cannot feed on such prey larger than 30mm (Zwarts and Blomert, 1992). The model did not show knot turning to *H. diversicolor* to compensate for the loss of *M. balthica*. This could be because large *M. balthica* may be a better quality food source than small and medium size-classes of *H. diversicolor*. The drop in predicted survival was mild , at 3%, but is consistent with other studies documenting cases of bird species switching from *M. balthica* to *H. diversicolor* when the bivalves are depleted (Atkinson et al., 2010, 2003; Ens, 2006). The corroboration of the model with observed foraging data suggests that these predictions could be a slight over-estimation compared to what happens in nature since modelled birds seem to be having more difficulty meeting their energy requirements than real birds but even then, the predicted impact of a rising water temperature is small.

## 5 CONCLUSION

In this paper we have demonstrated how modelling tools and empirical evidence can be combined in a holistic manner to assess the environmental effects of a thermal discharge. The model predicts that the bird population involved in this instance is generalist enough to withstand the impact of a potential decrease of prey quality. This finding is, however, suspected to be a site-specific situation and a similar protocol applied to another site may not yield the same outcomes. Benthic communities living on intertidal areas and particularly those in estuaries are expected to be tolerant of variations of temperature, but this tolerance will vary from one species to another and this aspect may becomes critical whenever the site is close to the species' geographical limit of distribution. Temperature tolerance of species highly connected within a trophic network must be thoroughly addressed together with the level of specialism of the bird species involved; the relatively simple network studied in this instance allows for a realistic understanding of these two fundamental mechanisms and allowed us to test different impact scenarios resulting from the warm-water discharge of a coastal power station development.

## 6 ACKNOWLEDGEMENTS

The authors would like acknowledge: the Institute of Estuarine and Coastal Sciences for assistance with fieldwork and invertebrate sample processing; David Roberts, Brian Robinson, Bryony Townhill and Berrit Bredemeier from CEFAS for their valuable suggestions to improve the manuscript; Colin Taylor and Stephen Roast for their scientific input. This work was funded by EDF NNB Genco through the BEEMS programme, which provides the marine science base underpinning engineering design and environmental assessment considerations of the Hinkley Point C and Sizewell C new nuclear developments.

# 7 REFERENCES

Anders, N.R., Churchyard, T., Hiddink, J.G., 2009. Predation of the shelduck Tadorna tadorna on the mud snail Hydrobia ulvae. Aquat. Ecol. 43, 1193–1199. doi:10.1007/s10452-008-9216-5

Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A., Ireland, P.L., 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. Biol. Conserv. 114, 127–141. doi:10.1016/S0006-3207(03)00017-X

Atkinson, P.W., Maclean, I.M., Clark, N.A., 2010. Impacts of shellfisheries and nutrient inputs on waterbird communities in the Wash, England. J. Appl. Ecol. 47, 191–199. doi:10.1111/j.1365-2664.2009.01760.x

Azouzi, L., Bourget, E., Borcard, D., 2002. Spatial variation in the intertidal bivalve Macoma balthica: Biotic variables in relation to density and abiotic factors. Mar. Ecol. Prog. Ser. 234, 159–170. doi:10.3354/meps234159

Bachelet, G., Labourg, P.J., Madani, I., 1990. Nouvelles signalisations de Mollusques (Prosobranches et Bivalves) dans le Bassin d'Arcachon. Cah. Biol. Mar. 31, 87–92.

Bamber, R.N., 1995. The influence of rising background temperature on the effects of marine thermal effluents. J. therm. Biol. 20, 105–110.

Beukema, J.J., De Bruin, W., 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve Macoma balthica in the Dutch Wadden Sea. Netherlands J. Sea Res. 11, 42–55. doi:10.1016/0077-7579(77)90020-5

Beukema, J.J., Dekker, R., Jansen, J.M., 2009. Some like it cold: populations of the tellinid bivalve Macoma balthica (L.) suffer in various ways from a warming climate. Mar. Ecol. Prog. Ser. 384, 135–145. doi:10.3354/meps07952

Beukema, J.J., Desprez, M., 1986. Single and dual annual growing seasons in the tellinid bivalve Macoma balthica (L.). J. Exp. Mar. Bio. Ecol. 102, 35–45. doi:10.1016/0022-0981(86)90124-3

Beukema, J.J., Knol, E., Cadee, G.C., 1985. Effects of temperature on the length of the annual growing season in the tellenid bivalve Macoma balthica (L.) living on tidal flats in the Dutch Wadden Sea. J. Exp. Mar. Bio. Ecol. 90, 129–144. doi:10.1016/0022-0981(85)90115-7

Blake, N.J., Doyle, L.J., Pyle, T.E., 1976. Macrobenthic community of a thermally altered area of Tampa Bay, Florida, in: Esch, G.W., McFarlane, R.W. (Eds.), Proceedings of II Thermal Ecology Symposium; Augusta, Georgia, USA. Technical Information Center, Energy Research and Development Administration, Springfield, pp. 296–301.

Bolam, S., Bremner, J., Forster, R., 2011. Ecological characterisation of the intertidal region of Hinkley Point, Severn Estuary: Results from the 2008 Field Survey and Assessment of Risk. Lowestoft.

Boyden, C.R., Little, C., 1973. Faunal distributions in soft sediments of the Severn Estuary. Estuar. Coast. Mar. Sci. 1, 203–223. doi:10.1016/0302-3524(73)90035-2

Bryant, D.M., Leng, J., 1975. Feeding distribution and behaviour of Shelduck in relation to food supply. Wildfowl 26, 20–30.

Burton, N.H.K., Musgrove, A.J., Rehfisch, M.M., Clark, N.A., 2010. Birds of the Severn Estuary and Bristol Channel: Their current status and key environmental issues. Mar. Pollut. Bull. 61, 115–123. doi:10.1016/j.marpolbul.2009.12.018

Clark, N.A., Prys-Jones, R.J., 1994. Low tide distribution of wintering waders and shelduck on the Severn Estuary in relation to the proposed tidal barrage. Biol. J. Linn. Soc. 51, 199–217.

Cowie, P.R., 2007. A synopsis report of the marine biological work carried out in the vicinity of Hunterstone power station and potential habitat sensitivities to thermal effluents withing a 2 - 5 km radius. A report prepared for British Energy.

Cramp, S., Simmons, K.E.L., 1983. Handbook of the birds of Europe, the Middle East and North Africa. Oxford University Press, Oxford.

Crema, R., Bonvicini Pagliai, A.M., 1980. The structure of benthic communities in an area of thermal discharge from a coastal power station. Mar. Pollut. Bull. 11, 221–224. doi:10.1016/0025-326X(80)90410-5

De Jonge, V.N., 1980. Fluctuations in the Organic Carbon to Chlorophyll a Ratios for Estuarine Benthic Diatom Populations. Mar. Ecol. Prog. Ser. 2, 345–353. doi:10.3354/meps002345

De Wilde, P.A.W.J., 1975. The influence of temperature on behaviour, energy metabolism, and growth of Macoma balthica (L.), in: Proceedings of the 9th European Marine Biology Symposium. pp. 239–256.

Del Hoyo, J., Elliott, A., Sargatal, J., Bateman, R., 1996. Handbook of the Birds of the World, Volume 3 (Hoatzin to Auks). Lynx Edicions.

Dit Durell, S.E.A.L. V., Stillman, R.A., Caldow, R.W.G., McGrorty, S., West, A.D., Humphreys, J., 2006. Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, UK. Biol. Conserv. 131, 459–473. doi:10.1016/j.biocon.2006.02.022

Dit Durell, S.E.A.L. V., Stillman, R.A., Triplet, P., Aulert, C., Ono dit Biot, D., Bouchet, A., Duhamel, S., Mayot, S., Goss-Custard, J.D., 2005. Modelling the efficacy of proposed mitigation areas for shorebirds: A case study on the Seine estuary, France. Biol. Conserv. 123, 67–77. doi:10.1016/j.biocon.2004.10.009

Dit Durell, S.E.A.L. V., Stillman, R.A., Triplet, P., Desprez, M., Fagot, C., Loquet, N., Sueur, F., Goss-Custard, J.D., 2008. Using an individual-based model to inform estuary management in the Baie de Somme, France. Oryx 42, 265–277.

Dobrzycka-Krahel, A., Krzak, M., Szaniawska, A., 2014. A laboratory-based comparison of osmoregulatory ability at different water temperatures and salinities in the stenothermic isopod Saduria entomon (Linnaeus, 1758) and the eurythermic amphipod Corophium volutator (Pallas, 1766) from the Baltic Sea. Mar. Freshw. Behav. Physiol. 47, 29–39. doi:10.1080/10236244.2013.874120

Duffy, J.E., Srivastava, D.S., McLaren, J., Sankaran, M., Solan, M., Griffin, J., Emmerson, M., Jones, K.E., 2009. Forecasting decline in ecosystem services under realistic scenarios of extinction, in: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), Biodiversity, Ecosystem Functioning, & Human Wellbeing. Oxford University Press, Oxford, pp. 60–77.

EDF/NNB Genco Entec UK Ltd, 2009. EDF development company Ltd, Hinkley, third interim bird report. Reading.

Ens, B.J., 2006. The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden Sea, in: Boere, G.C., Galbraith, C.A., Stroud, D.A. (Eds.), Waterbirds around the World. The Stationery Office, Edinburg, UK, pp. 806–811.

Ernest, S.K.M., Brown, J.H., 2001. Homeostasis and compensation: The role of species and resources in ecosystem stability. Ecology 82, 2118–2132.

Evans, A., 1987. Relative availability of the prey of wading birds by day and by night. Mar. Ecol. Prog. Ser. 37, 103–107. doi:10.3354/meps037103

Fernand, L., Silva, T., Bacon, J., van Leeuwen, S., 2011. Hinkley Point thermal plume modelling: GETM stage 3a results with the final cooling water configuration. Lowestoft.

Ferns, P.N., Reed, J.P., 2009. Effects of the Cardiff Bay tidal barrage on the abundance, ecology and behaviour of shelducks Tadorna tadorna. Aquat. Conserv. Mar. Freshw. Ecosyst. 19, 466–473. doi:10.1002/aqc.1011

Finlay, B.J., Uhlig, G., 1981. Calorific and carbon values of marine and freshwater Protozoa. Helgoländer Meeresuntersuchungen 34, 401–412.

Fritzsche, D., von Oertzen, J.-A., 1995. Metabolic responses to changing environmental conditions in the brackish water polychaetes Marenzelleria viridis and Hediste diversicolor. Mar. Biol. 121, 693–699.

Goss-Custard, J.D., Stillman, R.A., West, A.D., Caldow, R.W.G., Triplet, P., Dit Durell, S.E.A.L. V., McGrorty, S., 2004. When enough is not enough: shorebirds and shellfishing. Proc. Biol. Sci. 271, 233–237. doi:10.1098/rspb.2003.2602

Goss-Custard, J.D., West, A.D., Yates, M.G., Caldow, R.W.G., Stillman, R.A., Bardsley, L., Castilla, J., Castro, M., Dierschke, V., Dit Durell, S.E.A.L. V., Eichhorn, G., Ens, B.J., Exo, K.-M., Udayangani-Fernando, P.U., Ferns, P.N., Hockey, P.A.R., Gill, J.A., Johnstone, I., Kalejta-Summers, B., Masero, J.A., Moreira, F., Nagarajan, R.V., Owens, I.P.F., Pacheco, C., Perez-Hurtado, A., Rogers, D., Scheiffarth, G., Sitters, H., Sutherland, W.J., Triplet, P., Worrall, D.H., Zharikov, Y., Zwarts, L., Pettifor, R.A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biol. Rev. Camb. Philos. Soc. 81, 501–529. doi:10.1017/S1464793106007093

Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACE. Ecol. Modell. 280, 129–139. doi:10.1016/j.ecolmodel.2014.01.018

Hartmann-Schröder, G., 1996. Annelida, Borstenwürmer, Polychaeta, 2nd ed. Gustav Fisher.

Hiddink, J.G., 2003. Modelling the adaptive value of intertidal migration and nursery use in the bivalve Macoma balthica. Mar. Ecol. Prog. Ser. 252, 173–185. doi:10.3354/meps252173

Honkoop, P.J.., Beukema, J.J., 1997. Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. J. Exp. Mar. Bio. Ecol. 212, 277–297. doi:10.1016/S0022-0981(96)02757-8

Honkoop, P.J.C., Van Der Meer, J., 1998. Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. J. Exp. Mar. Bio. Ecol. 220, 227–246. doi:http://dx.doi.org/10.1016/S0022-0981(97)00107-X

Honkoop, P.J.C., Van Der Meer, J., 1997. Reproductive output of Macoma balthica populations in relation to winter-temperature and intertidal height mediated changes of body mass. Mar. Ecol. Prog. Ser. 149, 155–162. doi:10.3354/meps149155

Honkoop, P.J.C., Van Der Meer, J., Beukema, J.J., Kwast, D., 1998. Does temperature-influenced egg production predict the recruitment in the bivalve Macoma balthica? Mar. Ecol. Prog. Ser. 164, 229–235. doi:10.3354/meps164229

Hummel, H., Bogaards, R., Bek, T., Polishchuk, L., Amiard-Triquet, C., Bachelet, G., Desprez, M., Strelkov, P., Sukhotin, A., Naumov, A., Dahle, S., Denisenko, S., Gantsevich, M., Sokolov, K., De Wolf, L., 1997. Sensitivity to stress in the bivalve Macoma balthica from the most northern (Arctic) to the most southern (French) populations: low sensitivity in Arctic populations because of genetic adaptations? Hydrobiologia 355, 127–138. doi:10.1023/A:1003009524563

Hylleberg, J., 1975. The effect of salinity and temperature on egestion in mud snails (Gastropoda: Hydrobiidae). A study on niche overlap. Oecologia 21, 279–289.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.

Jansen, J.M., Pronker, A.E., Bonga, S.W., Hummel, H., 2007. Macoma balthica in Spain, a few decades back in climate history. J. Exp. Mar. Bio. Ecol. 344, 161–169. doi:10.1016/j.jembe.2006.12.014

Johnson, C., 1985. Patterns of seasonal weight variation in waders on the wash. Ringing Migr. 6, 19–32. doi:10.1080/03078698.1985.9673850

Kalejta, B., 1992. Time budget and predatory impact of waders at the Berg river estuary, South Africa. Ardea 80, 327–342.

Kater, B.J., Jol, J.G., Smit, M.G.D., 2008. Growth of Corophium volutator under laboratory conditions. Arch. Environ. Contam. Toxicol. 54, 440–446.

Kuwae, T., Beninger, P.G., Decottignies, P., Mathot, K.J., Lund, D.R., Elner, R.W., 2008. Biofilm grazing in a higher vertebrate: the western sandpiper, Calidris mauri. Ecology 89, 599–606. doi:10.1890/07-1442.1

Kuwae, T., Miyoshi, E., Hosokawa, S., Ichimi, K., Hosoya, J., Amano, T., Moriya, T., Kondoh, M., Ydenberg, R.C., Elner, R.W., 2012. Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. Ecol. Lett. 15, 347–356. doi:10.1111/j.1461-0248.2012.01744.x

Langston, W.J., Chesman, B.S., Burt, G.R., Campbell, M., Manning, A., Jonas, P.J.C., 2007. The Severn estuary: sediments, contaminants and biota. Occas. Publ. Mar. Biol. Assoc. United Kingdom 19, 176.

Leopold, M.F., Dijkman, E.M., Cremer, J.S.M., Meijboom, A., Goedhart, P.W., 2004a. De effecten van mechanische kokkelvisserij op de benthische macrofauna en hun habitat; eindverslag EVA II (evaluatie schelpdiervisserij tweede fase) deelproject C1/3. Wageningen.

Leopold, M.F., Smit, C.J., Goedhart, P.W., van Roomen, M.W.J., van Winden, A.J., van Turnhout, C., 2004b. Langjarige trends in aantallen wadvogels, in relatie tot de kokkelvisserij en het gevoerde beleid in deze; eindverslag EVA II (evaluatie schelpdiervisserij tweede fase) deelproject C2. Wageningen.

Lincoln, R.J., 1979. British Marine Amphipoda: Gammaridea. Natural History Museum Publications.

Little, C., 2000. The Biology of Soft Shores and Estuaries. Oxford University Press.

Lourenço, P.M., Silva, A., Santos, C.D., Miranda, A.C., Granadeiro, J.P., Palmeirim, J.M., 2008. The energetic importance of night foraging for waders wintering in a temperate estuary. Acta Oecologica 34, 122–129. doi:10.1016/j.actao.2008.04.005

Mathot, K.J., Lund, D.R., Elner, R.W., 2010. Sediment in Stomach Contents of Western Sandpipers and Dunlin Provide Evidence of Biofilm Feeding. Waterbirds 33, 300–306. doi:10.1675/063.033.0305

Meadows, P.S., Ruagh, A.A., 1981. Temperature preferences and activity of Corophium volutator (Pallas) in a new choice apparatus. Sarsia 66, 67–72. doi:10.1080/00364827.1981.10414522

Meininger, P.L., Snoek, H., 1992. Non-breeding shelduck Tadorna tadorna in the southwest Netherlands: effects of habitat changes on distribution, numbers, moulting sites and food. Wildfowl 43, 139–151.

Mettam, C., Conneely, M.E., White, S.J., 1994. Benthic macrofauna and sediments in the Severn estuary. Biol. J. Linn. Soc. 51, 71–81.

Musk, W., Leighton, A., Thomson, S., 2011a. Hinkley Point, Intertidal survey & analysis report November 2010. Hull.

Musk, W., Leighton, A., Thomson, S., 2011b. Hinkley Intertidal survey and analysis report January 2011. Hull.

Musk, W., Leighton, A., Thomson, S., 2010a. Hinkley Point; Intertidal survey and analysis report, April 2010. Hull.

Musk, W., Leighton, A., Thomson, S., 2010b. Hinkley Point; Intertidal survey and analysis report, July 2010. Hull.

Olney, P.J.S., 1965. The food and feeding habits of shelduck Tadorna tadorna. Ibis (Lond. 1859). 107, 527–532.

Ozoh, P.T.E., Jones, N.V., 1990. Capacity adaptation of Hediste (Nereis) diversicolor embryogenesis to salinity, temperature and copper. Mar. Environ. Res. 29, 227–243. doi:10.1016/0141-1136(90)90035-M

Paterson, D.M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnol. Oceanogr. 34, 223–234. doi:10.4319/lo.1989.34.1.0223

Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve Macoma balthica. Limnol. Oceanogr. 48, 2171–2185. doi:10.4319/lo.2003.48.6.2171

Pimm, S.L., 1980. Food web design and the effects of species deletion. Oikos 35, 139–149.

Quaintenne, G., Van Gils, J.A., Bocher, P., Dekinga, A., Piersma, T., 2010. Diet selection in a molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-maximization? J. Anim. Ecol. 79, 53–62. doi:10.1111/j.1365-2656.2009.01608.x

Raffaelli, D., Hawkins, S.J., 1996. Intertidal Ecology. Springer.

Robinson, K.I.M., 2010. Effects of thermal power station effluent on the seagrass benthic communities of Lake Macquarie, a New South Wales coastal lagoon. Wetl.

Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. Sci. Mar. 65, 107–119. doi:10.3989/scimar.2001.65s2107

Scheiffarth, G., Nehls, G., 1997. Consumption of benthic fauna by carnivorous birds in the Wadden Sea. Helgoländer Meeresuntersuchungen 51, 373–387.

Schiel, D.R., Steinbeck, J.R., Foster, M.S., 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. Ecology 85, 1833–1839. doi:10.1890/03-3107

Sitters, H., 2000. The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding oystercatchers. Oxford University.

Smart, J., Gill, J.A., 2003. Non-intertidal habitat use by shorebirds: a reflection of inadequate intertidal resources? Biol. Conserv. 111, 359–369. doi:10.1016/S0006-3207(02)00304-X

Smith, R.I., 1977. Physiological and reproductive adaptations of Nereis diversicolor to life in the Baltic Sea and adjacent waters, in: Reish, D.J., Fauchald, K. (Eds.), Essays on Polychaetous Annelids. University of Southern California Press, Los Angeles, pp. 373–390.

Stillman, R.A., 2008. MORPH-An individual-based model to predict the effect of environmental change on foraging animal populations. Ecol. Modell. 216, 265–276. doi:10.1016/j.ecolmodel.2008.04.014

Stillman, R.A., Caldow, R.W.G., Alexander, M.J., 2000. Individual variation in intake rate : the relative importance of foraging efficiency and dominance. J. Anim. Ecol. 69, 484–493.

Stillman, R.A., Goss-Custard, J.D., 2010. Individual-based ecology of coastal birds. Biol. Rev. 85, 413–434. doi:10.1111/j.1469-185X.2009.00106.x

Stillman, R.A., Moore, J.J., Woolmer, A.P., Murphy, M.D., Walker, P., Vanstaen, K.R., Palmer, D., Sanderson, W.G., 2010. Assessing waterbird conservation objectives: an example for the Burry Inlet, UK. Biol. Conserv. 143, 2617–2630. doi:10.1016/j.biocon.2010.07.004

Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G., Triplet, P., 2002. Predicting the strength of interference more quickly using behaviour-based models. J. Anim. Ecol. 71, 532–541. doi:10.1046/j.1365-2656.2002.00621.x

Stillman, R.A., West, A.D., Caldow, R.W.G., Dit Durell, S.E.A.L. V., 2007. Predicting the effect of disturbance on coastal birds. Ibis (Lond. 1859). 149, 73–81. doi:10.1111/j.1474-919X.2007.00649.x

Stillman, R.A., West, A.D., Goss-Custard, J.D., McGrorty, S., Frost, N.J., Morrisey, D.J., Kenny, A.J., Drewitt, A.L., 2005. Predicting site quality for shorebird communities: A case study on the Humber estuary, UK. Mar. Ecol. Prog. Ser. 305, 203–217. doi:10.3354/meps305203

Stips, A., Bolding, K., Pohlman, T., Burchard, H., 2004. Simulating the temporal and spatial dynamics of the North Sea using the new model GETM (general estuarine transport model). Ocean Dyn. 54, 266–283.

Suh, S., 2014. Massive cooling water dispersion behavior in a shallow macro-tidal coastal zone in Korea. J. Coast. Res. 70, 360–365. doi:10.2112/SI70-061.1

Thompson, D.B.A., 1981. Feeding behaviour of wintering shelduck on the Clyde estuary. Wildfowl 32, 88–98.

Triplet, P., Stillman, R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference in a foraging shorebird. J. Anim. Ecol. 68, 254–265. doi:10.1046/j.1365-2656.1999.00280.x

Turpie, J.K., Hockey, P.A.R., 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory grey plovers Pluvialis squatarola and whimbrels Numenius phaeopus in South Africa. Ibis (Lond. 1859). 135, 156–165. doi:10.1111/j.1474-919X.1993.tb02827.x

Van der Wal, D., Wielemaker-van den Dool, A., Herman, P.M.J., 2010. Spatial synchrony in intertidal benthic algal biomass in temperate coastal and estuarine ecosystems. Ecosystems 13, 338–351.

Warwick, R.M., Goss-Custard, J.D., Kirby, R., George, C.L., Pope, N.D., Rowden, A.A., 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? J. Appl. Ecol. 28, 329–345.

Warwick, R.M., Somerfield, P.J., 2010. The structure and functioning of the benthic macrofauna of the Bristol channel and Severn estuary, with predicted effects of a tidal barrage. Mar. Pollut. Bull. 61, 92–99. doi:10.1016/j.marpolbul.2009.12.016

Wilson, W.H., Parker, K., 1996. The life history of the amphipod, Corophium volutator: The effects of temperature and shorebird predation. J. Exp. Mar. Bio. Ecol. 196, 239–250. doi:10.1016/0022-0981(95)00133-6

World Nuclear Association, 2015. Information Library [WWW Document]. World Energy Needs Nucl. Power. URL http://www.world-nuclear.org/info/Current-and-Future-Generation/World-Energy-Needs-and-Nuclear-Power/

Zwarts, L., Blomert, A.M., 1992. Why knot Calidris canutus take medium-sized Macoma balthica when six prey species are available. Mar. Ecol. Prog. Ser. 83, 113–128. doi:10.3354/meps083113

Zwarts, L., Wanink, J., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Netherlands J. Sea Res. 31, 441–476.

TABLES

**Table 1**. Review of the temperature sensitivity of the main intertidal benthic taxa in Bridgwater Bay.

| **Species** | **Distribution** | **Physiology measured** | **Sensitive?** | **References** |
|---|---|---|---|---|
| ***Hediste diversicolor*** | North east Atlantic to Mediterranean and Black Sea lagoons | Reproduction<br>Metabolism | Unlikely | (Fritzsche and von Oertzen, 1995; Hartmann-Schröder, 1996; Ozoh and Jones, 1990; Smith, 1977) |
| ***Corophium volutator*** | North east Atlantic to Mediterranean and Black Sea lagoons, Azov sea | Osmoregulation<br>Growth rate | Unlikely | (Dobrzycka-Krahel et al., 2014; Kater et al., 2008; Lincoln, 1979; Meadows and Ruagh, 1981; Wilson and Parker, 1996) |
| ***Peringia (Hydrobia) ulvae*** | Northern Norway to Senegal | Metabolism | Unlikely | (Hylleberg, 1975) |
| ***Macoma balthica*** | Eastern Atlantic, Pechora Sea to the Gironde estuary | Fecundity<br>Recruitment<br>Stress conditions | Likely | (Honkoop and Beukema, 1997; Honkoop and Van Der Meer, 1998, 1997; Honkoop et al., 1998; Hummel et al., 1997; Philippart et al., 2003) |

**Table 2**. Modelled decrease in density and individual energetic value of group resources throughout the model period.

| Resource group | Density curve | Mortality | AFDW curve | AFDW decrease |
|---|---|---|---|---|
| **PolErr0to10** | Exponential | 29.20% | Linear | 0% |
| **PolErr10to20** | Exponential | 29.20% | Linear | 0% |
| **PolErr20to50** | Exponential | 29.20% | Linear | 0% |
| **PolErr50plus** | Exponential | 29.20% | Linear | 0% |
| **Crustacea** | Exponential | 25.52% | Linear | 4.71% |
| **Gastropoda** | Exponential | 0% | Linear | 62.1% |
| **Macoma0to10** | Exponential | 0% | Linear | 71.02% |
| **Macoma10plus** | Exponential | 26.49% | Linear | 22.65% |
| **PolSed** | Exponential | 11.81% | Linear | 87.27% |
| **Interstitial** | Exponential | 0% | Linear | 44.99% |

**Table 3**. Bird population descriptive parameters.

| Forager | Scientific name | Population number | Model number | Arrival day | Departure day |
|---|---|---|---|---|---|
| Dunlin | *Calidris alpina* | 4695 | 7803 | 62 | 182 |
| Ringed plover | *Charadrius hiaticula* | 29 | 29 | 1 | 212 |
| Turnstone | *Arenaria interpres* | 43 | 43 | 1 | 212 |
| Knot | *Calidris canuta* | 313 | 358 | 31 | 212 |
| Redshank | *Tringa totanus* | 354 | 354 | 1 | 212 |
| Grey plover | *Pluvialis squatarola* | 93 | 108 | 31 | 212 |
| Black-tailed godwit | *Limosa limosa* | 18 | 42 | 1 | 92 |
| Oystercatcher | *Haematopus ostralegus* | 139 | 139 | 1 | 212 |
| Curlew | *Numenius arquata* | 614 | 614 | 1 | 212 |
| Shelduck | *Tadorna tadorna* | 977 | 977 | 1 | 212 |

**Table 4.**

(a) Relation between group resource and bird diet.

| **Diet** | **Resource** |
|---|---|
| PolErr10to50 | PolErr10to20 |
| PolErr10to50 | PolErr20to50 |
| PolErr20plus | PolErr20to50 |
| PolErr20plus | PolErr50plus |
| PolErr50plus | PolErr50plus |
| Gastropoda | Gastropoda |
| Macoma0to10 | Macoma0to10 |
| Macoma10plus | Macoma10plus |
| Crustacea | Crustacea |
| Worms0to10 | PolErr0to10 |
| Worms0to10 | PolSed |
| Worms0to10 | Interstitial |

(b) Diet matrix of bird species. PE: PolErr, G: Gastropoda, M: Macoma, C: Crustacea and W: Worms

| **Forager** | **PE10-50** | **PE20+** | **PE50+** | **G** | **M0-10** | **M10+** | **C** | **W0-10** |
|---|---|---|---|---|---|---|---|---|
| Dunlin | **√** | X | X | **√** | **√** | X | **√** | X |
| Ringed plover | **√** | X | X | **√** | X | X | **√** | X |
| Turnstone | X | **√** | X | **√** | **√** | **√** | **√** | X |
| Knot | **√** | X | X | **√** | X | **√** | X | X |
| Redshank | X | **√** | X | **√** | **√** | **√** | **√** | X |
| Grey plover | X | **√** | X | **√** | X | **√** | X | X |
| Black-tailed godwit | X | **√** | X | X | X | **√** | X | X |
| Oystercatcher | **√** | X | **√** | X | X | **√** | X | **√** |
| Curlew | X | X | **√** | X | X | **√** | X | X |
| Shelduck | **√** | X | **√** | **√** | **√** | X | **√** | **√** |

**Table 5.** Modelled input scenarios for *M. balthica* average energy content in proportion per individual.

| **Scenario** | **Decrease in *M. balthica* energy content (%)** | |
|---|---|---|
| | Stert Flats | Berrow Flats |
| A – Current conditions | 0 | 0 |
| B | 9 | 3 |
| C | 50 | 10 |
| D | 50 | 20 |

**Table 6.** Survival and body condition of each bird species and on average at the end of the winter (in percentage) in relation to food availability.

| **Forager** | **Resources (gAFDW/m$^2$)** | **Survival (%)** | **Body condition (%)** |
|---|---|---|---|
| Dunlin | 7.79 | 100 | 99.9 |
| Ringed plover | 5.80 | 100 | 98.5 |
| Turnstone | 8.71 | 100 | 99.2 |
| Knot | 5.92 | 100 | 99.08 |
| Redshank | 8.71 | 100 | 99.29 |
| Grey plover | 6.84 | 100 | 99.17 |
| Black-tailed godwit | 3.79 | 100 | 99.9 |
| Oystercatcher | 8.35 | 90.64 | 91.76 |
| Curlew | 3.79 | 64.7 | 73.31 |
| Shelduck | 13.27 | 100 | 96.86 |
| Total | 14.49 | 97.75 | 91.64 |

FIGURES

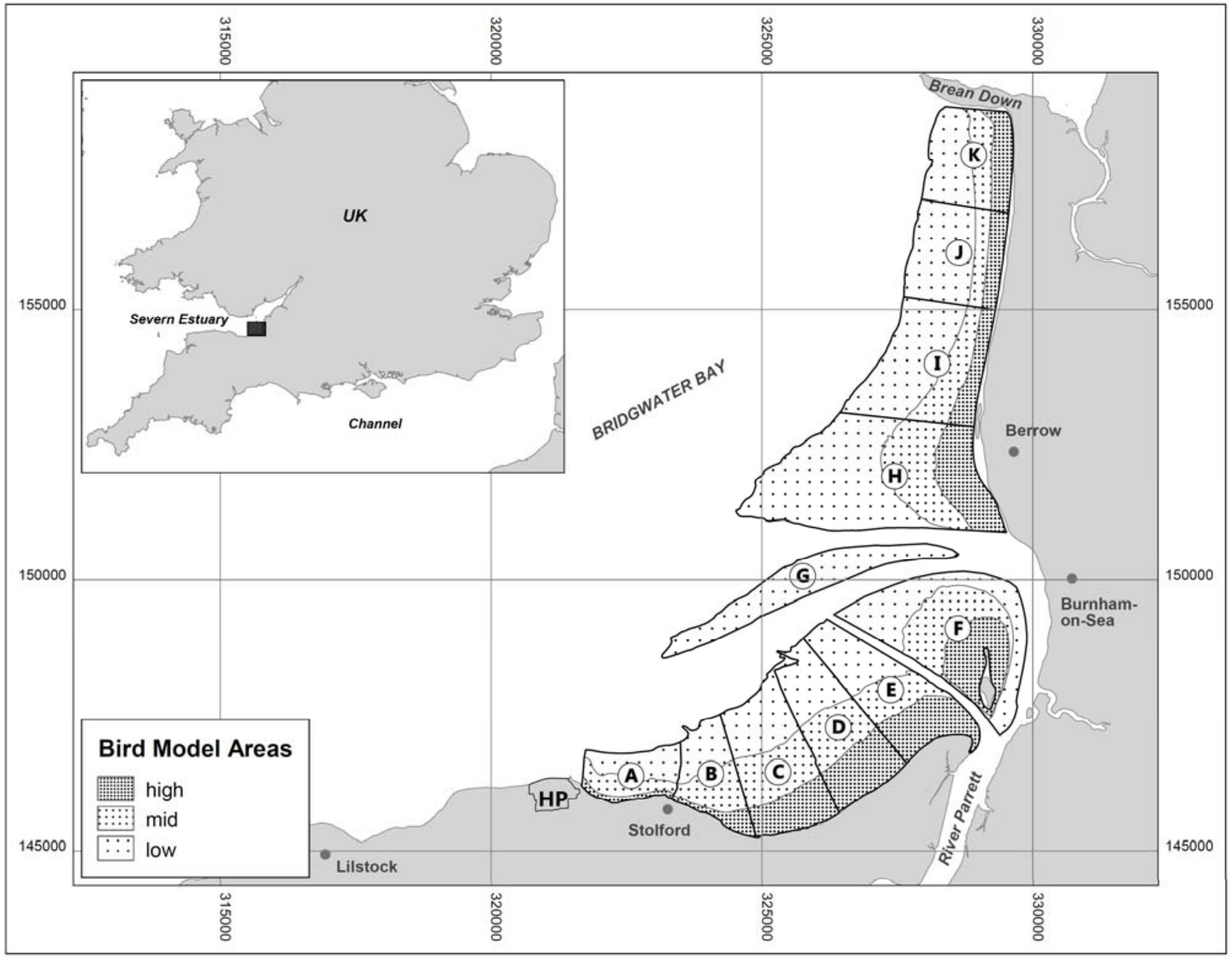


**Figure 1.** Bridgwater Bay and the 16 feeding patches defined by the combination of profile zones based on benthic invertebrates data (e.g. A, B) and broadly shore-parallel divisions based on tidal elevation areas (High, Mid, Low). Stert flats: Profile zones from A to F; Berrow flats: Profile zones from H to K; HP: complex of power stations at Hinkley Point.

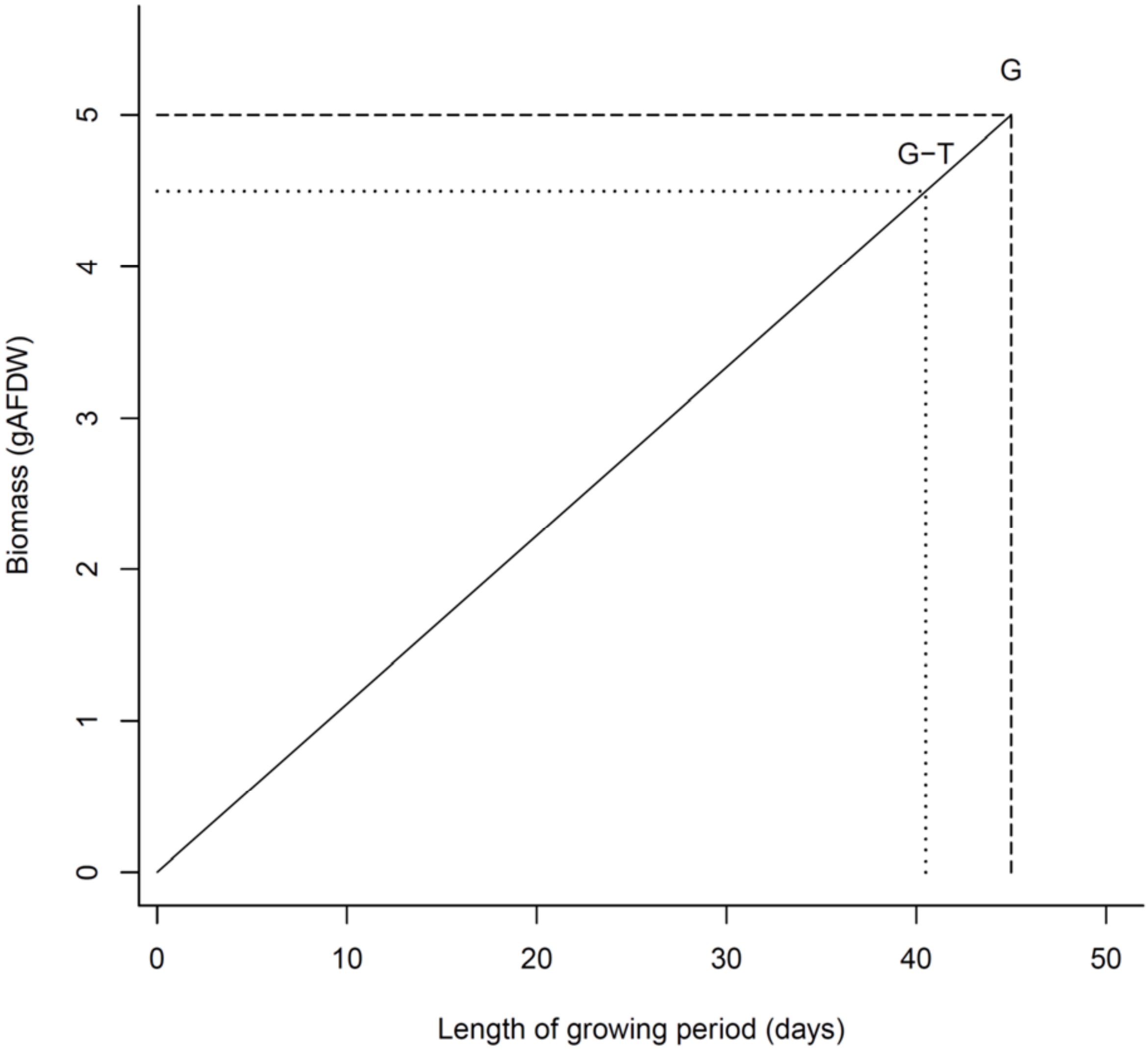
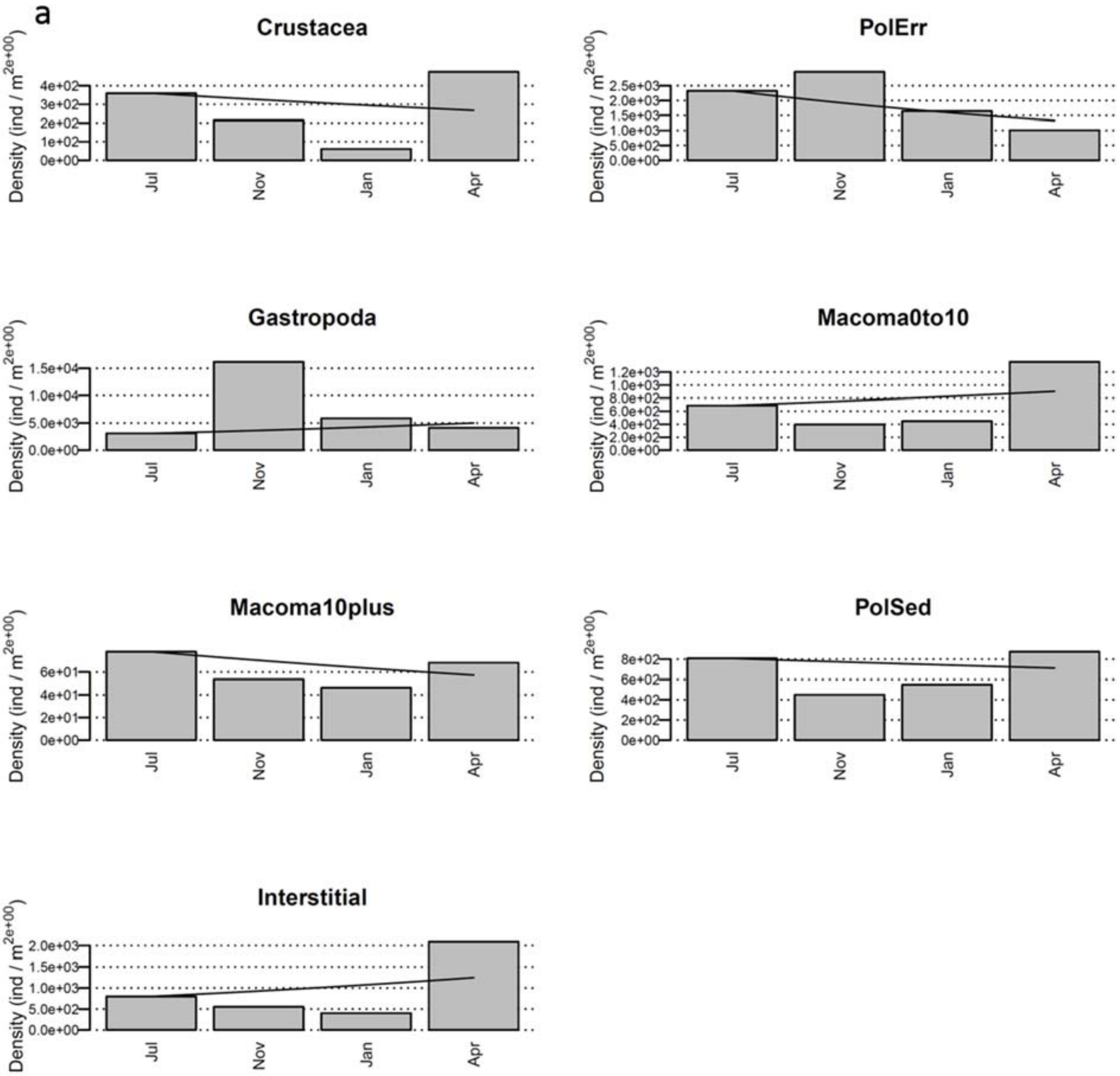


**Figure 2.** Conceptual diagram of the effects of increased seawater temperature on biomass accrual by *Macoma balthica*. AFDW: ash-free dry weight; G: dashed line: growth period in current conditions; G-T: dotted line: growth period shortened by an extra thermal pressure. Calculations are based on a linear growth rate.


a
Crustacea
Density (ind / m^2e+00)
4e+02
3e+02
2e+02
1e+02
0e+00
Jul
Nov
Jan
Apr
PolErr
Density (ind / m^2e+00)
2.5e+03
2.0e+03
1.5e+03
1.0e+03
5.0e+02
0.0e+00
Jul
Nov
Jan
Apr
Gastropoda
Density (ind / m^2e+00)
1.5e+04
1.0e+04
5.0e+03
0.0e+00
Jul
Nov
Jan
Apr
Macoma0to10
Density (ind / m^2e+00)
1.2e+03
1.0e+03
8.0e+02
6.0e+02
4.0e+02
2.0e+02
0.0e+00
Jul
Nov
Jan
Apr
Macoma10plus
Density (ind / m^2e+00)
6e+01
4e+01
2e+01
0e+00
Jul
Nov
Jan
Apr
PolSed
Density (ind / m^2e+00)
8e+02
6e+02
4e+02
2e+02
0e+00
Jul
Nov
Jan
Apr
Interstitial
Density (ind / m^2e+00)
2.0e+03
1.5e+03
1.0e+03
5.0e+02
0.0e+00
Jul
Nov
Jan
Apr

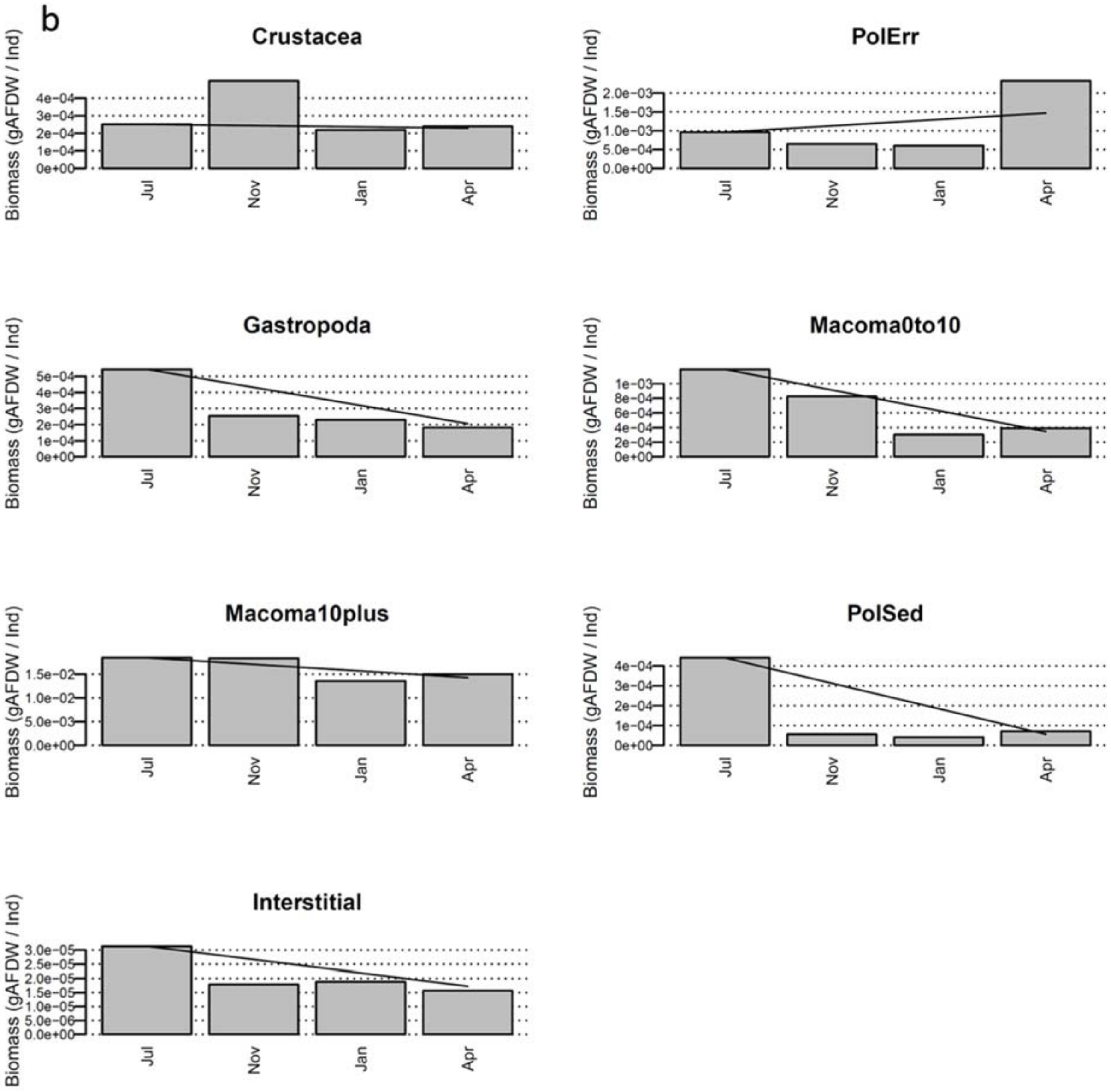


**Figure 3.** Generic temporal dynamics of the (**a**) density and (**b**) average individual biomass of each functional resource group throughout the model period. The solid line represents the decrease coefficient used in the model: the decrease follows (**a**) an exponential and (**b**) a linear model respectively.

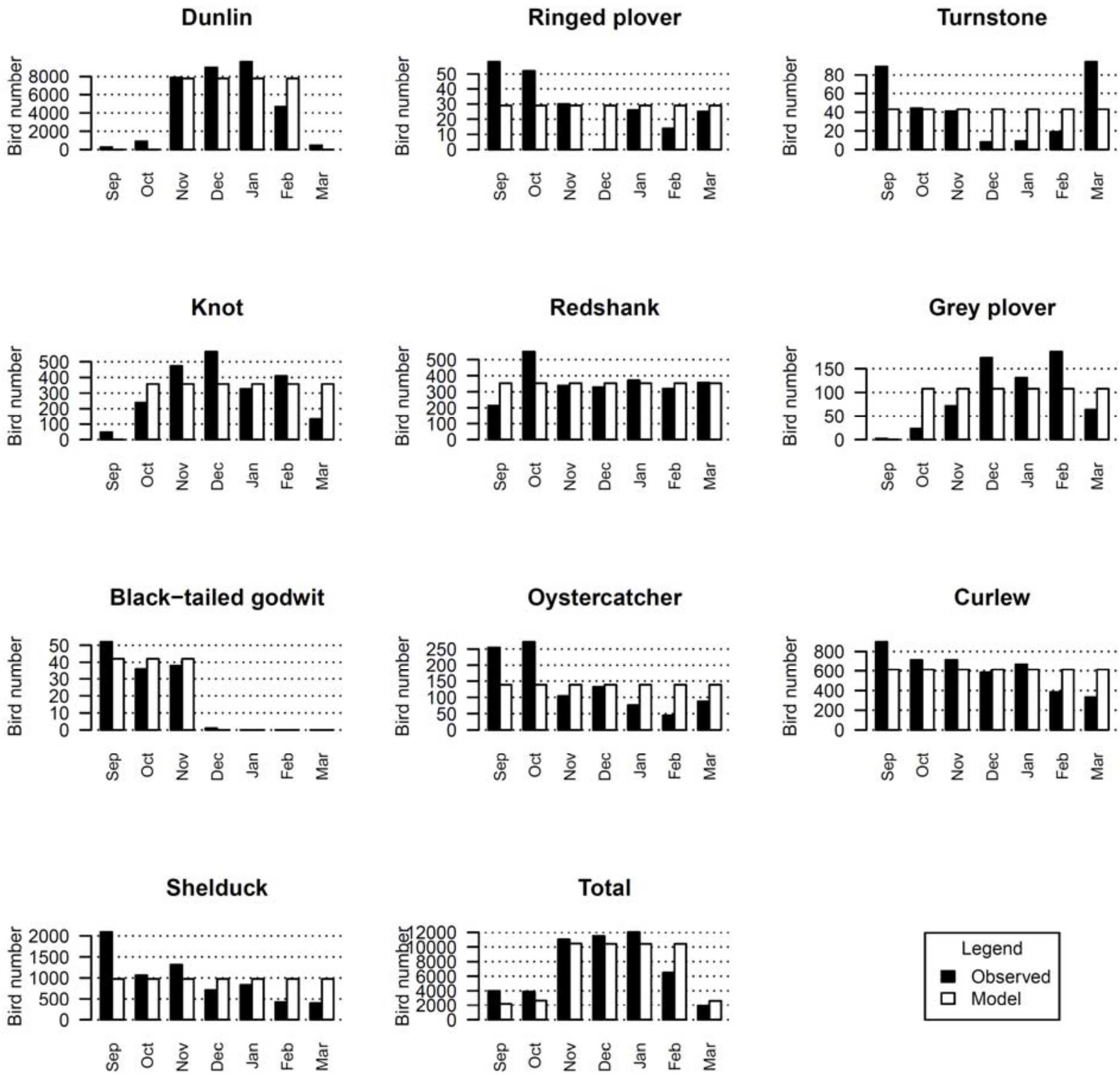


**Figure 4.** Bird counts as a monthly average per species. Observed numbers (black bars) were modified (open bars) (see **section 2.3.5**) in order to best describe the population changes throughout the model period.

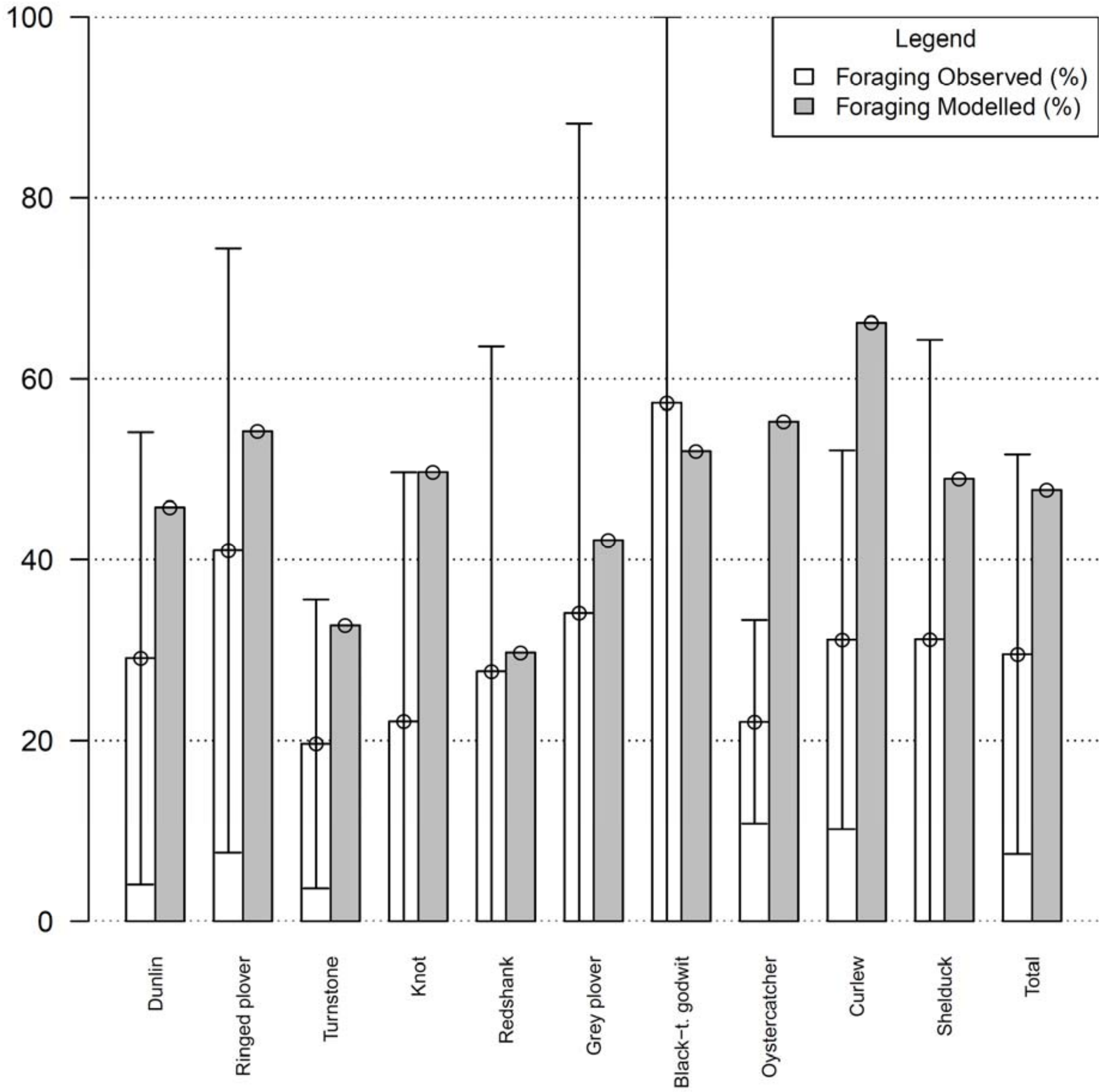


**Figure 5.** Observed (open bars) and predicted (grey bars) proportions of bird time spent foraging.

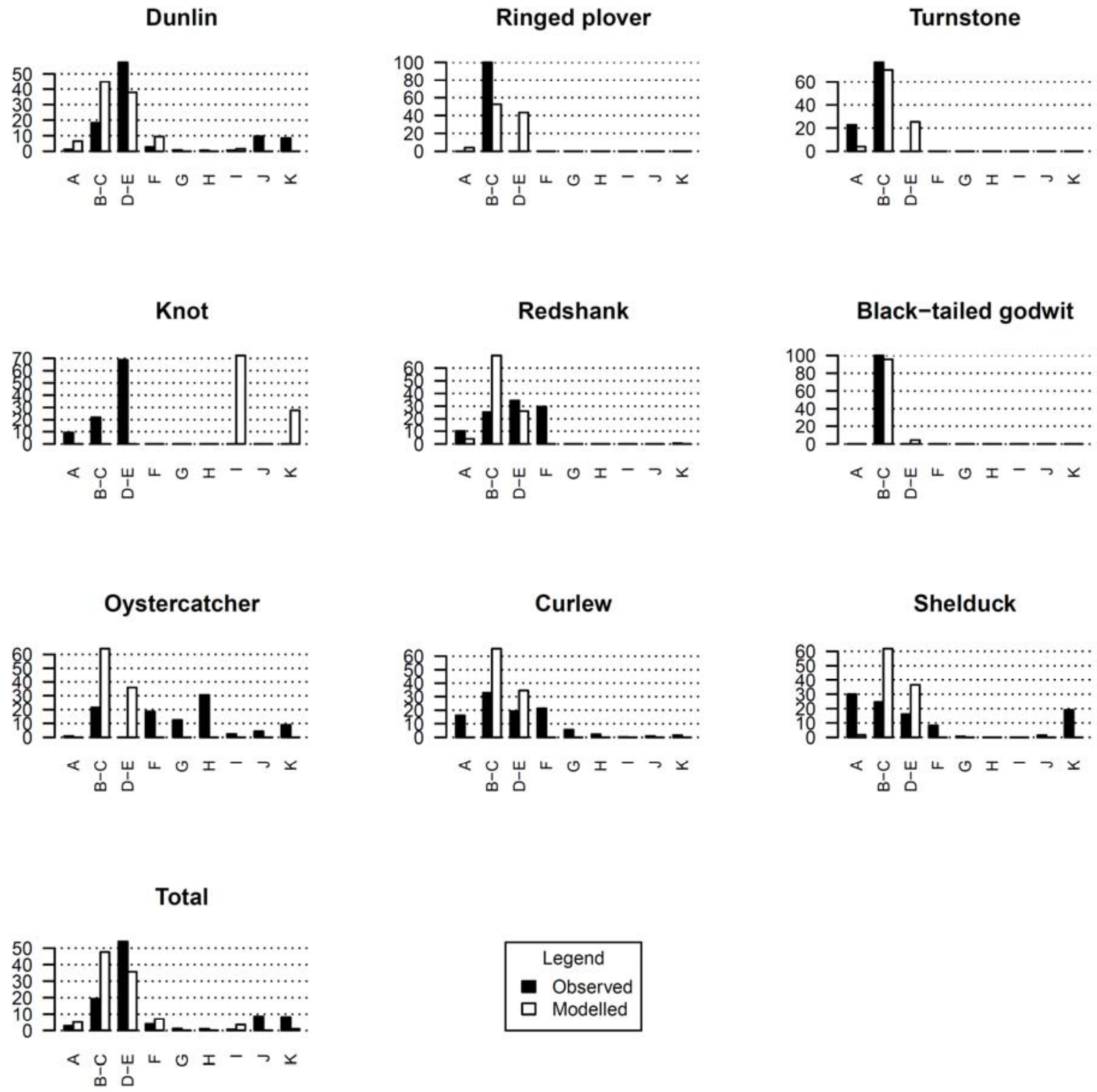


**Figure 6.** Observed (black bars) and predicted (open bars) average distribution of birds across the different feeding patches.

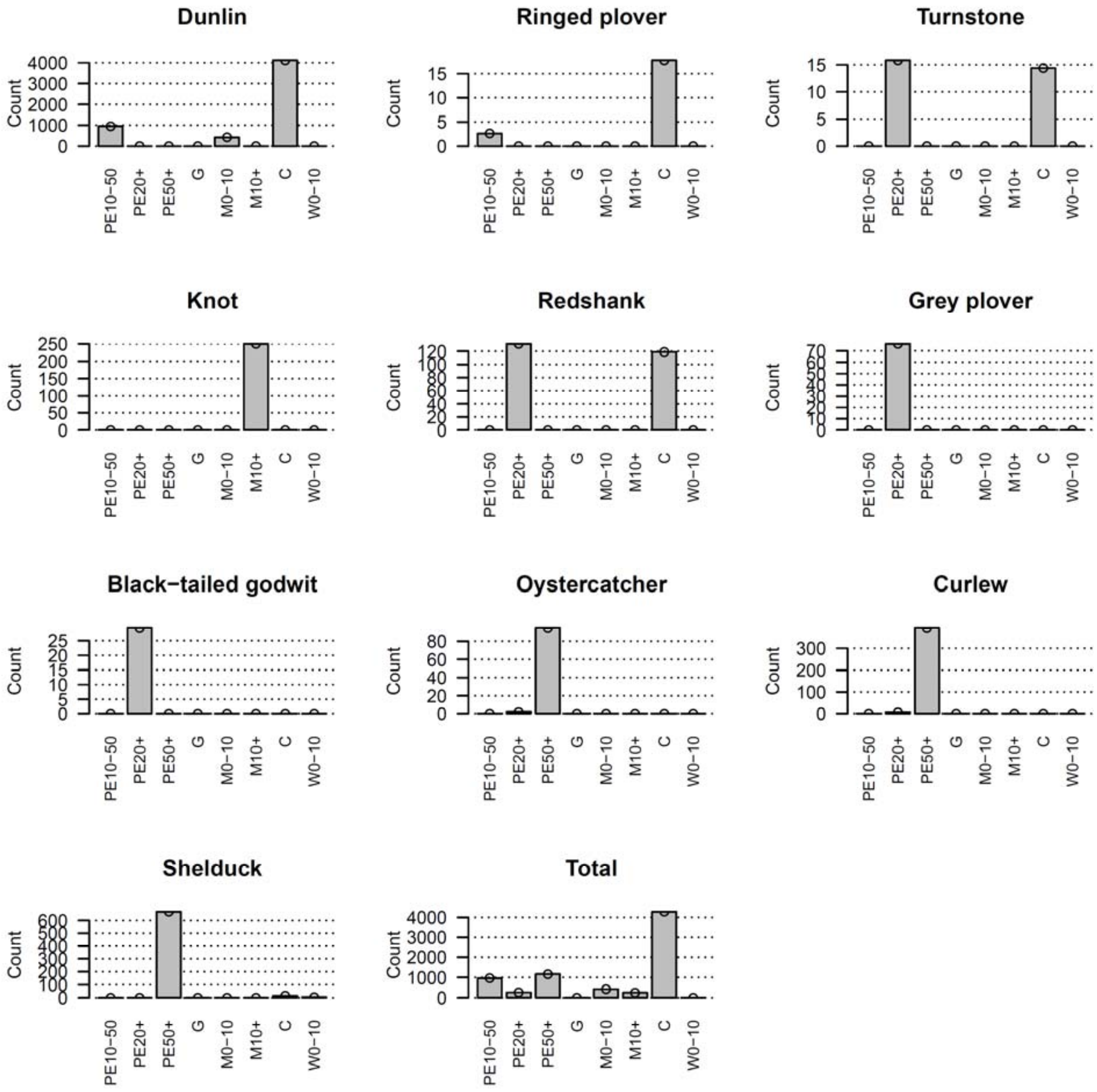


**Figure 7.** Functional diet groups for each bird species and in total (in number of birds feeding) as predicted by the model. PE10-50 (PolErr10to50 diet group), PE20+ (PolErr20plus diet group), PE50+ (PolErr50plus diet group), G (Gastropoda diet group), M0-10 (Macoma0to10 diet group), M10+ (Macoma10plus diet group), C (Crustacea diet group) and W0-10 (Worms0to10 diet group)

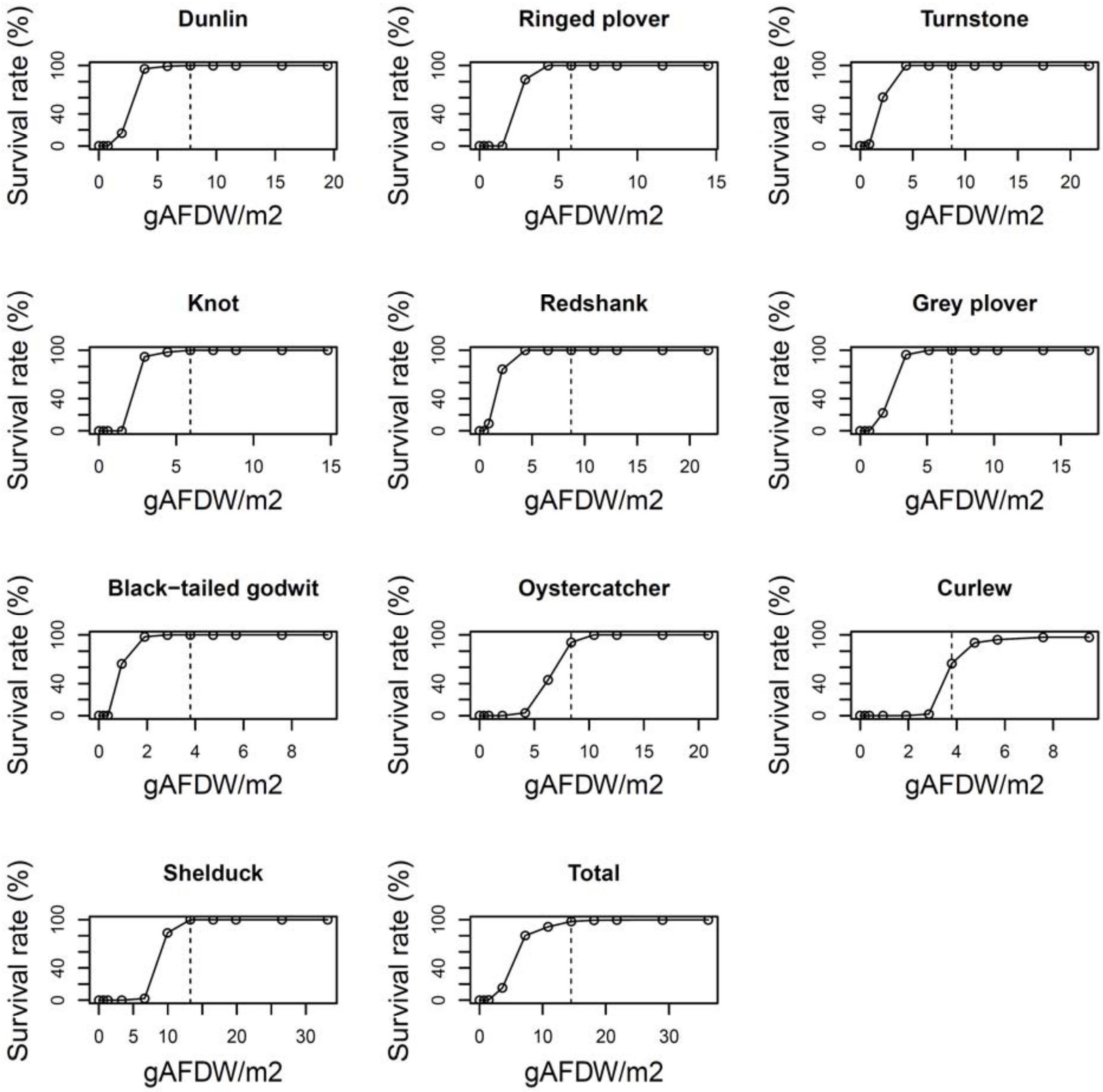


**Figure 8.** Predicted effects of change in prey biomass densities on overwinter survival rate of the selected bird species in Bridgwater Bay (in percentages). The vertical dashed line represents the actual prey biomass density values.

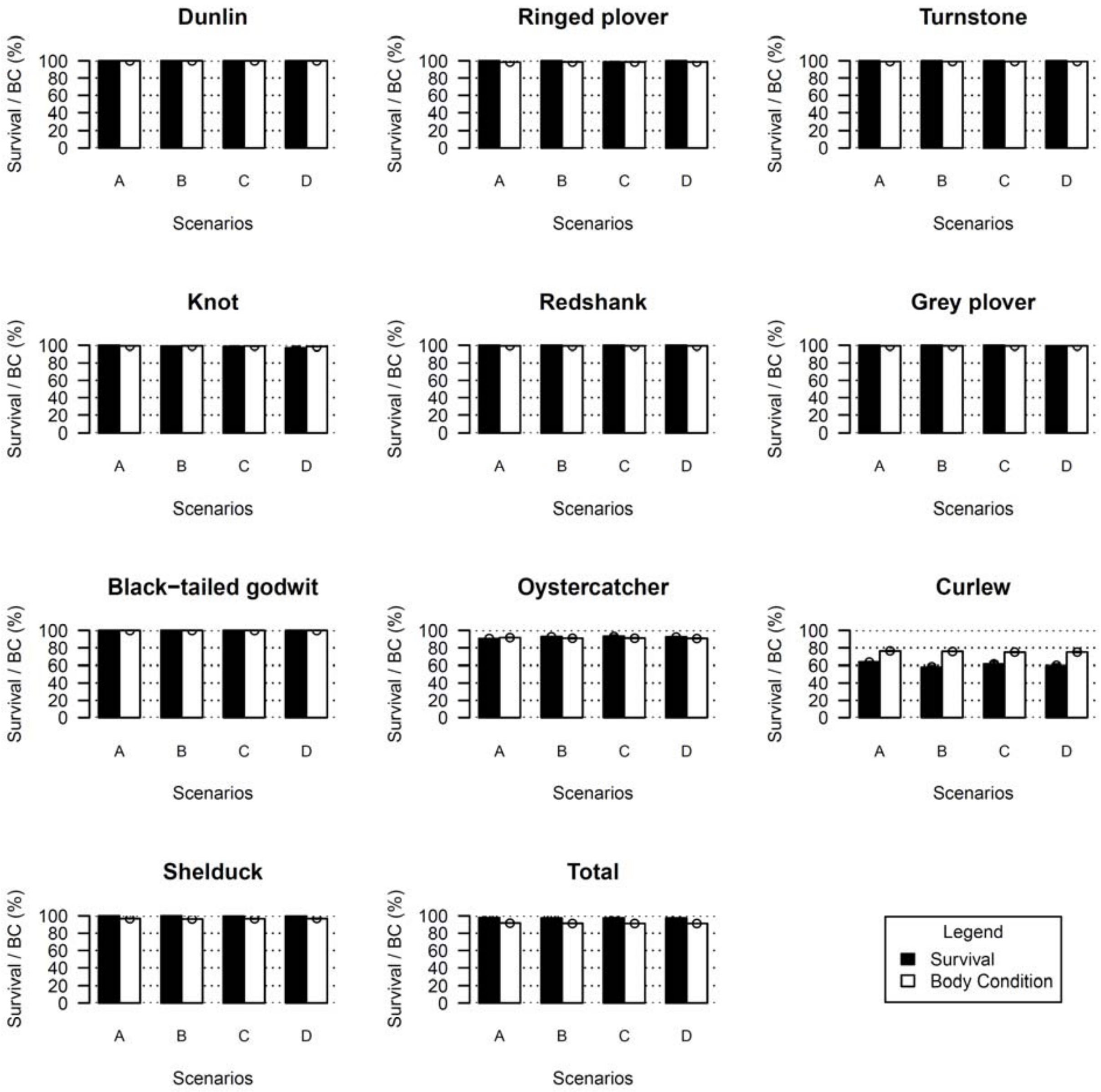


**Figure 9.** Predicted annual survival rate and body condition change (in percentages) of the selected birds under three scenarios of decrease in *M. balthica* energy content on Stert flats and Berrow flats respectively (in %). A: current (reference) conditions, B: 9% and 3%, C: 50% and 10% and D: 50% and 20%.

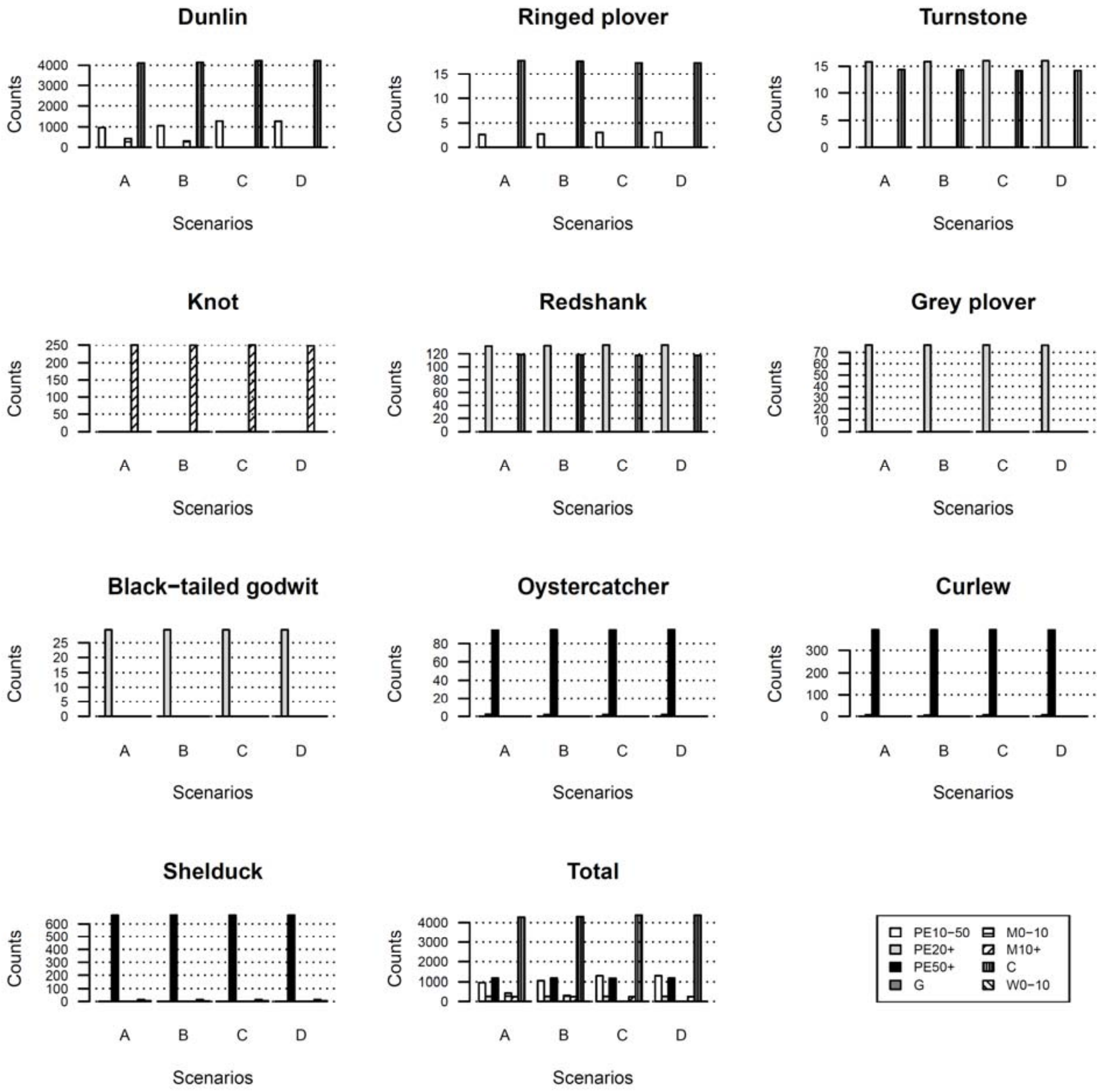


**Figure 10**. Predicted change in functional diet groups selection under scenarios B, C and D compared to the reference condition A. A: current (reference) conditions, B: 9% and 3%, C: 50% and 10% and D: 50% and 20%.

# GLOSSARY

Cascade (secondary) effects: The effects of species depletion (or loss) on subsequent depletion (or loss) of additional species.

Diet (MORPH): Collection of one or more resources from a patch consumed simultaneously by a forager.

Forager (MORPH): Animal which forage within the system consuming diets and assimilating energy. Here the foragers are the nine species of shorebird and the wildfowl.

Global environment (MORPH): State variables which apply throughout the modelled system.

Overwintering: Process by which some organisms pass through or wait out the winter season (or the period of the year) when winter-like conditions make normal activities and survival difficult.

Patch (MORPH): Locations with local, patch-specific state variables containing resources and foragers.

Resource (MORPH): The food consumed by the foragers.

Shorebird/Wader: Bird species members of the Charadriiformes order that includes plovers, sandpipers, godwit or curlews; excluding the more marine web-footed seabird group (gulls). They are a group of various ground-nesting bird of small to moderate size that live near the water.

Wildfowl: Bird species members of the Anatidae family that includes ducks, geese and swans. These birds are adapted for swimming, floating on the surface, and in some cases diving in shallow water.

## APPENDIX

**Appendix A.** Patch-specific variables. The patch names combine the profile zones (e.g. A, B) and elevation areas (high, mid, low). Shore levels are relative to British National Grid (Ordonnance Datum Newlyn).

| Patch number | Patch name | Shore level (m) | Patch area ($m^2$) | Patch number | Patch name | Shore level (m) | Patch area ($m^2$) |
|---|---|---|---|---|---|---|---|
| 1 | Roost | >5 | 1000000 | 17 | Fhigh | 1 – 5 | 1391447 |
| 2 | Ahigh | 1 – 5 | 166834 | 18 | Fmid | -1 – 1 | 1682610 |
| 3 | Amid | -1 – 1 | 527362 | 19 | Flow | <-1 | 2433889 |
| 4 | Alow | <-1 | 848064 | 20 | Glow | <-1 | 2538660 |
| 5 | Bhigh | 1 – 5 | 317716 | 21 | Hhigh | 1 – 5 | 1411444 |
| 6 | Bmid | -1 – 1 | 774230 | 22 | Hmid | -1 – 1 | 1748902 |
| 7 | Blow | <-1 | 806393 | 23 | Hlow | <-1 | 4513673 |
| 8 | Chigh | 1 – 5 | 1053357 | 24 | Ihigh | 1 – 5 | 674536 |
| 9 | Cmid | -1 – 1 | 1285203 | 25 | Imid | -1 – 1 | 1038085 |
| 10 | Clow | <-1 | 1381339 | 26 | Ilow | <-1 | 2671851 |
| 11 | Dhigh | 1 – 5 | 1216332 | 27 | Jhigh | 1 – 5 | 524879 |
| 12 | Dmid | -1 – 1 | 1046195 | 28 | Jmid | -1 – 1 | 459288 |
| 13 | Dlow | <-1 | 1154361 | 29 | Jlow | <-1 | 2107134 |
| 14 | Ehigh | 1 – 5 | 1272711 | 30 | Khigh | 1 – 5 | 684267 |
| 15 | Emid | -1 – 1 | 857551 | 31 | Kmid | -1 – 1 | 664495 |
| 16 | Elow | <-1 | 1267852 | 32 | Klow | <-1 | 1374216 |

**Appendix B.** List of the benthic species from the 2010 - 2011 surveys included in the functional resource groups.

| Taxa | Resource group | Abundance (%) | Number of class |
|---|---|---:|---|
| *Eteone longa/flava* | PolErr | 0.049529 | 1 |
| *Hediste diversicolor* | PolErr | 8.927601 | 4 |
| *Nephtys* (juvenile) | PolErr | 3.244149 | 2 |
| *Nephtys hombergii* | PolErr | 7.145522 | 4 |
| Nereididae (juvenile) | PolErr | 0.074293 | 1 |
| *Hydrobia ulvae* | Gastropoda | 49.5909 | 1 |
| *Retusa obtusa* | Gastropoda | 0.60673 | 1 |
| *Macoma balthica* | Macoma | 11.28023 | 2 |
| Tellinoidea (juv) | Macoma | 0.297174 | 1 |
| *Bathyporeia pilosa* | Crustacea | 0.012382 | 1 |
| *Bathyporeia sarsi* | Crustacea | 1.10202 | 1 |
| *Corophium volutator* | Crustacea | 1.832573 | 1 |
| *Cumopsis goodsir* | Crustacea | 0.024764 | 1 |
| *Diastylis rathkei* | Crustacea | 0.037147 | 1 |
| *Gastosaccus spinifer* | Crustacea | 0.012382 | 1 |
| *Idotea neglecta* | Crustacea | 0.012382 | 1 |
| *Melita* spp | Crustacea | 0.012382 | 1 |
| *Pontocrates altamarinus* | Crustacea | 0.012382 | 1 |
| *Sphaeroma monodi* | Crustacea | 0.024764 | 1 |
| *Arenicola* (juvenile) | PolSed | 0.024764 | 1 |
| *Arenicola marina* | PolSed | 0.012382 | 1 |
| *Aricidea minuta* | PolSed | 0.916286 | 1 |
| *Capitella* sp | PolSed | 1.844955 | 1 |
| *Eupolymnia nebulosa* | PolSed | 0.024764 | 1 |
| *Levinsenia gracilis* | PolSed | 0.012382 | 1 |
| *Polydora cornuta* | PolSed | 0.136205 | 1 |
| *Pygospio elegans* | PolSed | 2.538361 | 1 |
| *Sabellaria spinulosa* | PolSed | 0.123822 | 1 |
| *Scoloplos armiger* | PolSed | 0.061911 | 1 |
| *Streblospio shrubsolii* | PolSed | 0.841993 | 1 |
| Enchytraeidae | Interstitial | 5.770128 | 1 |
| *Grania* spp | Interstitial | 0.198116 | 1 |
| Nematoda | Interstitial | 0.829611 | 1 |
| Nemertina | Interstitial | 0.235263 | 1 |
| *Tubificoides amplivasatus* | Interstitial | 2.117364 | 1 |

**Appendix C**. Resources per patch (individuals per $m^2$) and by ash-free dry weight (g per individual) (* denotes groups with added microphytobenthic biomass).

| Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Roost | PolErr0to10* | 0 | 0 | Amid | Macoma10plus | 51.96 | 0.018463 | Chigh | PolErr20to50 | 1094.00 | 0.009509 |
| Roost | PolErr10to20 | 0 | 0 | Amid | Crustacea* | 25.98 | 0.047569 | Chigh | PolErr50plus | 320.33 | 0.045279 |
| Roost | PolErr20to50 | 0 | 0 | Amid | PolSed* | 684.16 | 0.002238 | Chigh | Gastropoda* | 4598.60 | 0.000874 |
| Roost | PolErr50plus | 0 | 0 | Amid | Interstitial* | 34.64 | 0.03552 | Chigh | Macoma0to10* | 1117.17 | 0.002559 |
| Roost | Gastropoda* | 0 | 0 | Bhigh | PolErr0to10* | 1082.93 | 0.002137 | Chigh | Macoma10plus | 51.96 | 0.018463 |
| Roost | Macoma0to10* | 0 | 0 | Bhigh | PolErr10to20 | 1444.29 | 0.000868 | Chigh | Crustacea* | 51.96 | 0.029538 |
| Roost | Macoma10plus | 0 | 0 | Bhigh | PolErr20to50 | 617.49 | 0.009509 | Chigh | PolSed* | 701.48 | 0.002611 |
| Roost | Crustacea* | 0 | 0 | Bhigh | PolErr50plus | 179.80 | 0.045279 | Chigh | Interstitial* | 818.39 | 0.001891 |
| Roost | PolSed* | 0 | 0 | Bhigh | Gastropoda* | 1195.12 | 0.001616 | Clow | PolErr0to10* | 551.00 | 0.003602 |
| Roost | Interstitial* | 0 | 0 | Bhigh | Macoma0to10* | 77.94 | 0.017644 | Clow | PolErr10to20 | 383.27 | 0.000868 |
| Ahigh | PolErr0to10* | 207.85 | 0.009126 | Bhigh | Macoma10plus | 207.85 | 0.018463 | Clow | PolErr20to50 | 65.96 | 0.009509 |
| Ahigh | PolErr10to20 | 597.56 | 0.000868 | Bhigh | Crustacea* | 0.00 | 0.000251 | Clow | PolErr50plus | 26.03 | 0.045279 |
| Ahigh | PolErr20to50 | 77.94 | 0.009509 | Bhigh | PolSed* | 181.87 | 0.00749 | Clow | Gastropoda* | 259.81 | 0.005157 |
| Ahigh | PolErr50plus | 0.00 | 0.045279 | Bhigh | Interstitial* | 77.94 | 0.016479 | Clow | Macoma0to10* | 207.85 | 0.006964 |
| Ahigh | Gastropoda* | 39438.82 | 0.000575 | Blow | PolErr0to10* | 558.59 | 0.003647 | Clow | Macoma10plus | 51.96 | 0.018463 |
| Ahigh | Macoma0to10* | 1896.60 | 0.001845 | Blow | PolErr10to20 | 363.73 | 0.000868 | Clow | Crustacea* | 25.98 | 0.046389 |
| Ahigh | Macoma10plus | 51.96 | 0.018463 | Blow | PolErr20to50 | 77.94 | 0.009509 | Clow | PolSed* | 935.31 | 0.001723 |
| Ahigh | Crustacea* | 0.00 | 0.000251 | Blow | PolErr50plus | 0.00 | 0.045279 | Clow | Interstitial* | 272.80 | 0.004426 |
| Ahigh | PolSed* | 1532.87 | 0.001243 | Blow | Gastropoda* | 2121.76 | 0.001124 | Cmid | PolErr0to10* | 582.97 | 0.005132 |
| Ahigh | Interstitial* | 51.96 | 0.023691 | Blow | Macoma0to10* | 320.43 | 0.005042 | Cmid | PolErr10to20 | 483.68 | 0.000868 |
| Alow | PolErr0to10* | 940.71 | 0.002751 | Blow | Macoma10plus | 51.96 | 0.018463 | Cmid | PolErr20to50 | 92.41 | 0.009509 |
| Alow | PolErr10to20 | 110.48 | 0.000868 | Blow | Crustacea* | 25.98 | 0.047679 | Cmid | PolErr50plus | 8.81 | 0.045279 |
| Alow | PolErr20to50 | 14.00 | 0.009509 | Blow | PolSed* | 5715.77 | 0.000657 | Cmid | Gastropoda* | 1047.89 | 0.00233 |
| Alow | PolErr50plus | 0.05 | 0.045279 | Blow | Interstitial* | 1039.23 | 0.001217 | Cmid | Macoma0to10* | 164.54 | 0.012574 |
| Alow | Gastropoda* | 3325.54 | 0.000996 | Bmid | PolErr0to10* | 415.69 | 0.004651 | Cmid | Macoma10plus | 95.26 | 0.018463 |
| Alow | Macoma0to10* | 623.54 | 0.00361 | Bmid | PolErr10to20 | 389.71 | 0.000868 | Cmid | Crustacea* | 25.98 | 0.072308 |
| Alow | Macoma10plus | 155.88 | 0.018463 | Bmid | PolErr20to50 | 25.98 | 0.009509 | Cmid | PolSed* | 64.95 | 0.029264 |
| Alow | Crustacea* | 25.98 | 0.058169 | Bmid | PolErr50plus | 0.00 | 0.045279 | Cmid | Interstitial* | 441.67 | 0.00427 |
| Alow | PolSed* | 259.81 | 0.006233 | Bmid | Gastropoda* | 1130.16 | 0.001605 | Dhigh | PolErr0to10* | 298.78 | 0.012342 |
| Alow | Interstitial* | 86.60 | 0.017407 | Bmid | Macoma0to10* | 389.71 | 0.004275 | Dhigh | PolErr10to20 | 324.76 | 0.000868 |
| Amid | PolErr0to10* | 493.63 | 0.004067 | Bmid | Macoma10plus | 116.91 | 0.018463 | Dhigh | PolErr20to50 | 181.87 | 0.009509 |
| Amid | PolErr10to20 | 389.71 | 0.000868 | Bmid | Crustacea* | 25.98 | 0.046423 | Dhigh | PolErr50plus | 51.96 | 0.045279 |
| Amid | PolErr20to50 | 51.96 | 0.009509 | Bmid | PolSed* | 25.98 | 0.046614 | Dhigh | Gastropoda* | 1247.08 | 0.002482 |
| Amid | PolErr50plus | 0.00 | 0.045279 | Bmid | Interstitial* | 51.96 | 0.023118 | Dhigh | Macoma0to10* | 155.88 | 0.016706 |
| Amid | Gastropoda* | 16445.83 | 0.000618 | Chigh | PolErr0to10* | 1606.08 | 0.001788 | Dhigh | Macoma10plus | 25.98 | 0.018463 |
| Amid | Macoma0to10* | 1125.83 | 0.002288 | Chigh | PolErr10to20 | 2115.07 | 0.000868 | Dhigh | Crustacea* | 2130.42 | 0.001385 |

**Appendix C *(continued)*.**

| Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dhigh | PolSed* | 0.00 | 0.000441 | Elow | Gastropoda* | 1402.96 | 0.001368 | Fmid | PolErr0to10* | 2248.76 | 0.001003 |
| Dhigh | Interstitial* | 1688.75 | 0.001463 | Elow | Macoma0to10* | 415.69 | 0.00398 | Fmid | PolErr10to20 | 361.09 | 0.000868 |
| Dlow | PolErr0to10* | 719.31 | 0.003131 | Elow | Macoma10plus | 0.00 | 0.018463 | Fmid | PolErr20to50 | 38.42 | 0.009509 |
| Dlow | PolErr10to20 | 254.97 | 0.000868 | Elow | Crustacea* | 0.00 | 0.000251 | Fmid | PolErr50plus | 1.77 | 0.045279 |
| Dlow | PolErr20to50 | 43.30 | 0.009509 | Elow | PolSed* | 25.98 | 0.044984 | Fmid | Gastropoda* | 545.60 | 0.002259 |
| Dlow | PolErr50plus | 0.00 | 0.045279 | Elow | Interstitial* | 25.98 | 0.044574 | Fmid | Macoma0to10* | 259.81 | 0.0048 |
| Dlow | Gastropoda* | 2260.33 | 0.001134 | Emid | PolErr0to10* | 1122.49 | 0.001909 | Fmid | Macoma10plus | 0.00 | 0.018463 |
| Dlow | Macoma0to10* | 402.70 | 0.004513 | Emid | PolErr10to20 | 1025.65 | 0.000868 | Fmid | Crustacea* | 129.90 | 0.007458 |
| Dlow | Macoma10plus | 25.98 | 0.018463 | Emid | PolErr20to50 | 470.38 | 0.009509 | Fmid | PolSed* | 2156.40 | 0.000875 |
| Dlow | Crustacea* | 51.96 | 0.025957 | Emid | PolErr50plus | 114.99 | 0.045279 | Fmid | Interstitial* | 129.90 | 0.007238 |
| Dlow | PolSed* | 51.96 | 0.026148 | Emid | Gastropoda* | 1493.89 | 0.001317 | Glow | PolErr0to10* | 0.00 | 0.000388 |
| Dlow | Interstitial* | 558.59 | 0.002423 | Emid | Macoma0to10* | 337.75 | 0.004619 | Glow | PolErr10to20 | 0.00 | 0.000868 |
| Dmid | PolErr0to10* | 412.38 | 0.009049 | Emid | Macoma10plus | 0.00 | 0.018463 | Glow | PolErr20to50 | 0.00 | 0.009509 |
| Dmid | PolErr10to20 | 444.99 | 0.000868 | Emid | Crustacea* | 1325.02 | 0.001123 | Glow | PolErr50plus | 25.98 | 0.045279 |
| Dmid | PolErr20to50 | 77.94 | 0.009509 | Emid | PolSed* | 25.98 | 0.044934 | Glow | Gastropoda* | 103.92 | 0.001671 |
| Dmid | PolErr50plus | 0.00 | 0.045279 | Emid | Interstitial* | 4325.80 | 0.000299 | Glow | Macoma0to10* | 0.00 | 0.001196 |
| Dmid | Gastropoda* | 1913.92 | 0.001807 | Fhigh | PolErr0to10* | 2248.76 | 0.001279 | Glow | Macoma10plus | 0.00 | 0.018463 |
| Dmid | Macoma0to10* | 571.58 | 0.005426 | Fhigh | PolErr10to20 | 361.09 | 0.000868 | Glow | Crustacea* | 51.96 | 0.002505 |
| Dmid | Macoma10plus | 77.94 | 0.018463 | Fhigh | PolErr20to50 | 38.42 | 0.009509 | Glow | PolSed* | 25.98 | 0.004951 |
| Dmid | Crustacea* | 51.96 | 0.04678 | Fhigh | PolErr50plus | 1.77 | 0.045279 | Glow | Interstitial* | 25.98 | 0.004541 |
| Dmid | PolSed* | 25.98 | 0.093499 | Fhigh | Gastropoda* | 545.60 | 0.003031 | Hhigh | PolErr0to10* | 161.32 | 0.018105 |
| Dmid | Interstitial* | 38.97 | 0.06207 | Fhigh | Macoma0to10* | 259.81 | 0.00642 | Hhigh | PolErr10to20 | 163.43 | 0.000868 |
| Ehigh | PolErr0to10* | 1205.74 | 0.001803 | Fhigh | Macoma10plus | 0.00 | 0.018463 | Hhigh | PolErr20to50 | 56.51 | 0.009509 |
| Ehigh | PolErr10to20 | 1557.67 | 0.000868 | Fhigh | Crustacea* | 129.90 | 0.010697 | Hhigh | PolErr50plus | 8.45 | 0.045279 |
| Ehigh | PolErr20to50 | 914.79 | 0.009509 | Fhigh | PolSed* | 2156.40 | 0.001071 | Hhigh | Gastropoda* | 11743.31 | 0.000708 |
| Ehigh | PolErr50plus | 114.99 | 0.045279 | Fhigh | Interstitial* | 129.90 | 0.010478 | Hhigh | Macoma0to10* | 4104.96 | 0.001668 |
| Ehigh | Gastropoda* | 1584.83 | 0.001272 | Flow | PolErr0to10* | 2248.76 | 0.00047 | Hhigh | Macoma10plus | 25.98 | 0.018463 |
| Ehigh | Macoma0to10* | 259.81 | 0.005641 | Flow | PolErr10to20 | 361.09 | 0.000868 | Hhigh | Crustacea* | 0.00 | 0.000251 |
| Ehigh | Macoma10plus | 0.00 | 0.018463 | Flow | PolErr20to50 | 38.42 | 0.009509 | Hhigh | PolSed* | 1117.17 | 0.002173 |
| Ehigh | Crustacea* | 1325.02 | 0.001122 | Flow | PolErr50plus | 1.77 | 0.045279 | Hhigh | Interstitial* | 155.88 | 0.012442 |
| Ehigh | PolSed* | 0.00 | 0.000441 | Flow | Gastropoda* | 545.60 | 0.000773 | Hlow | PolErr0to10* | 482.42 | 0.001141 |
| Ehigh | Interstitial* | 8625.62 | 0.000165 | Flow | Macoma0to10* | 259.81 | 0.001679 | Hlow | PolErr10to20 | 69.95 | 0.000868 |
| Elow | PolErr0to10* | 1039.23 | 0.002033 | Flow | Macoma10plus | 0.00 | 0.018463 | Hlow | PolErr20to50 | 6.07 | 0.009509 |
| Elow | PolErr10to20 | 493.63 | 0.000868 | Flow | Crustacea* | 129.90 | 0.001216 | Hlow | PolErr50plus | 0.14 | 0.045279 |
| Elow | PolErr20to50 | 25.98 | 0.009509 | Flow | PolSed* | 2156.40 | 0.000499 | Hlow | Gastropoda* | 233.83 | 0.001596 |
| Elow | PolErr50plus | 0.00 | 0.045279 | Flow | Interstitial* | 129.90 | 0.000996 | Hlow | Macoma0to10* | 1727.72 | 0.001339 |

**Appendix C *(continued)*.**

| Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g | Patch | Resource | ind. /m2 | AFDW/ind g |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Hlow | Macoma10plus | 116.91 | 0.018463 | Imid | PolErr20to50 | 12.14 | 0.009509 | Jmid | PolSed* | 389.71 | 0.001148 |
| Hlow | Crustacea* | 51.96 | 0.004985 | Imid | PolErr50plus | 0.28 | 0.045279 | Jmid | Interstitial* | 324.76 | 0.00088 |
| Hlow | PolSed* | 0.00 | 0.000441 | Imid | Gastropoda* | 1584.83 | 0.000632 | Khigh | PolErr0to10* | 142.01 | 0.002145 |
| Hlow | Interstitial* | 0.00 | 3.14E-05 | Imid | Macoma0to10* | 883.35 | 0.001354 | Khigh | PolErr10to20 | 159.43 | 0.000868 |
| Hmid | PolErr0to10* | 1110.87 | 0.000543 | Imid | Macoma10plus | 168.88 | 0.018463 | Khigh | PolErr20to50 | 90.79 | 0.009509 |
| Hmid | PolErr10to20 | 93.98 | 0.000868 | Imid | Crustacea* | 1182.13 | 0.000369 | Khigh | PolErr50plus | 15.50 | 0.045279 |
| Hmid | PolErr20to50 | 14.13 | 0.009509 | Imid | PolSed* | 220.84 | 0.001074 | Khigh | Gastropoda* | 1905.26 | 0.000632 |
| Hmid | PolErr50plus | 2.11 | 0.045279 | Imid | Interstitial* | 311.77 | 0.000479 | Khigh | Macoma0to10* | 2381.57 | 0.001267 |
| Hmid | Gastropoda* | 2000.52 | 0.000602 | Jhigh | PolErr0to10* | 36.02 | 0.006684 | Khigh | Macoma10plus | 259.81 | 0.018463 |
| Hmid | Macoma0to10* | 597.56 | 0.001391 | Jhigh | PolErr10to20 | 0.00 | 0.000868 | Khigh | Crustacea* | 259.81 | 0.000901 |
| Hmid | Macoma10plus | 0.00 | 0.018463 | Jhigh | PolErr20to50 | 0.00 | 0.009509 | Khigh | PolSed* | 346.41 | 0.000929 |
| Hmid | Crustacea* | 51.96 | 0.002493 | Jhigh | PolErr50plus | 0.00 | 0.045279 | Khigh | Interstitial* | 6105.48 | 5.9E-05 |
| Hmid | PolSed* | 0.00 | 0.000441 | Jhigh | Gastropoda* | 1299.04 | 0.000662 | Klow | PolErr0to10* | 18.01 | 0.122607 |
| Hmid | Interstitial* | 0.00 | 3.14E-05 | Jhigh | Macoma0to10* | 1861.96 | 0.001279 | Klow | PolErr10to20 | 0.00 | 0.000868 |
| Ihigh | PolErr0to10* | 0.00 | 0.000388 | Jhigh | Macoma10plus | 86.60 | 0.018463 | Klow | PolErr20to50 | 0.00 | 0.009509 |
| Ihigh | PolErr10to20 | 0.00 | 0.000868 | Jhigh | Crustacea* | 6451.89 | 0.000274 | Klow | PolErr50plus | 0.00 | 0.045279 |
| Ihigh | PolErr20to50 | 0.00 | 0.009509 | Jhigh | PolSed* | 389.71 | 0.000835 | Klow | Gastropoda* | 3983.72 | 0.000918 |
| Ihigh | PolErr50plus | 0.00 | 0.045279 | Jhigh | Interstitial* | 303.11 | 0.000538 | Klow | Macoma0to10* | 433.01 | 0.004637 |
| Ihigh | Gastropoda* | 25.98 | 0.005919 | Jlow | PolErr0to10* | 155.35 | 0.013117 | Klow | Macoma10plus | 0.00 | 0.018463 |
| Ihigh | Macoma0to10* | 493.63 | 0.001479 | Jlow | PolErr10to20 | 548.82 | 0.000868 | Klow | Crustacea* | 1926.91 | 0.001024 |
| Ihigh | Macoma10plus | 311.77 | 0.018463 | Jlow | PolErr20to50 | 84.30 | 0.009509 | Klow | PolSed* | 129.90 | 0.011912 |
| Ihigh | Crustacea* | 2338.27 | 0.00031 | Jlow | PolErr50plus | 1.92 | 0.045279 | Klow | Interstitial* | 86.60 | 0.017237 |
| Ihigh | PolSed* | 415.69 | 0.000777 | Jlow | Gastropoda* | 909.33 | 0.002015 | Kmid | PolErr0to10* | 108.06 | 0.023474 |
| Ihigh | Interstitial* | 571.58 | 0.000276 | Jlow | Macoma0to10* | 129.90 | 0.0115 | Kmid | PolErr10to20 | 0.00 | 0.000868 |
| Ilow | PolErr0to10* | 870.26 | 0.002351 | Jlow | Macoma10plus | 0.00 | 0.018463 | Kmid | PolErr20to50 | 0.00 | 0.009509 |
| Ilow | PolErr10to20 | 108.73 | 0.000868 | Jlow | Crustacea* | 173.21 | 0.007978 | Kmid | PolErr50plus | 0.00 | 0.045279 |
| Ilow | PolErr20to50 | 8.09 | 0.009509 | Jlow | PolSed* | 0.00 | 0.000441 | Kmid | Gastropoda* | 4893.05 | 0.000889 |
| Ilow | PolErr50plus | 0.18 | 0.045279 | Jlow | Interstitial* | 1212.44 | 0.001135 | Kmid | Macoma0to10* | 541.27 | 0.004316 |
| Ilow | Gastropoda* | 1623.80 | 0.001256 | Jmid | PolErr0to10* | 126.07 | 0.003616 | Kmid | Macoma10plus | 0.00 | 0.018463 |
| Ilow | Macoma0to10* | 714.47 | 0.002815 | Jmid | PolErr10to20 | 0.00 | 0.000868 | Kmid | Crustacea* | 4373.43 | 0.000637 |
| Ilow | Macoma10plus | 25.98 | 0.018463 | Jmid | PolErr20to50 | 0.00 | 0.009509 | Kmid | PolSed* | 4568.29 | 0.000811 |
| Ilow | Crustacea* | 25.98 | 0.044766 | Jmid | PolErr50plus | 0.00 | 0.045279 | Kmid | Interstitial* | 303.11 | 0.0056 |
| Ilow | PolSed* | 25.98 | 0.044957 | Jmid | Gastropoda* | 1104.18 | 0.000793 |  |  |  |  |
| Ilow | Interstitial* | 1195.12 | 0.000999 | Jmid | Macoma0to10* | 1039.23 | 0.001461 |  |  |  |  |
| Imid | PolErr0to10* | 1621.61 | 0.000515 | Jmid | Macoma10plus | 86.60 | 0.018463 |  |  |  |  |
| Imid | PolErr10to20 | 184.63 | 0.000868 | Jmid | Crustacea* | 3290.90 | 0.000334 |  |  |  |  |

**Appendix D.** Foragers feeding parameters not specific to the Bridgwater Bay version of MORPH.

| Feeding parameters | Principle | Reference |
|---|---|---|
| Competition | Interference is assumed to reduce intake rate when the number of birds is above 100 birds per hectare with less interference for dominant birds. | (Stillman et al., 2002, 2000; Triplet et al., 1999) |
| Foraging efficiency | Assumed to follow a normal distribution in absence of competitors with a standard deviation of 0.125 | (Stillman et al., 2000) |
| Dominance | Uniform distribution value that influence the sensitivity of foraging efficiency to other competitors | (Stillman et al., 2000) |
| Maximum intake rate | Limits the maximum amount of food a bird can consume within a time-step | (Kirkwood, 1983) |
| Metabolic rate | Amount of energy expended per time-step per bird | (Nagy et al., 1999) |
| Energy density of birds | Amount of energy (KJ) contained in a gram of bird fat reserve (33.4 KJ.g$^{-1}$) | (Kersten and Visser, 1996) |
| Assimilation efficiency | Proportion of energy within the prey consumed that is assimilated into the bird's body: 0.75 for all resources for each bird except 0.85 for Macoma and Peracarida for oystercatcher | (Dit Durell et al., 2006; Stillman et al., 2005) |

**Appendix E.** Night-time foraging efficiency coefficient used in the model, *information found in the literature.

| Forager | Scientific name | Night-time coefficient |
|---|---|---|
| Dunlin | *Calidris alpina* | 0.82 |
| Ringed plover | *Charadrius hiaticula* | 0.49* |
| Turnstone | *Arenaria interpres* | 0.82 |
| Knot | *Calidris canuta* | 0.82 |
| Redshank | *Tringa totanus* | 0.95* |
| Grey plover | *Pluvialis squatarola* | 1.00* |
| Black-tailed godwit | *Limosa limosa* | 0.87* |
| Oystercatcher | *Haematopus ostralegus* | 0.81* |
| Curlew | *Numenius arquata* | 0.82 |
| Shelduck | *Tadorna tadorna* | 0.82 |

**Appendix F.** Bird size in relation to their favourite size-class preys.

| **Bird** | **Weight** | **Preferential preys** |
|---|---|---|
| Dunlin, ringed plover | 48 – 64 g | *P. ulvae*, *C. volutator*, *M. balthica* (3 – 6 mm), *H. diversicolor* (10 – 50 mm) |
| Grey plover, black-tailed godwit | 240 – 310 g | *P. ulvae*, *C. volutator*, *M. balthica* (8 – 20 mm), *H. diversicolor* (>25 mm) |
| Oystercatcher, curlew | 540 – 885 g | *M. balthica* (> 8mm), *H. diversicolor* (>50 mm), *C. maenas* (10 – 50 mm) |
| Shelduck | 1051 g | Small preys or small size-classes of prey |

**Appendix G.** Appendix References

Dit Durell, S.E.A.L. V., Stillman, R.A., Caldow, R.W.G., McGrorty, S., West, A.D., Humphreys, J., 2006. Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, UK. Biol. Conserv. 131, 459–473. doi:10.1016/j.biocon.2006.02.022

Kersten, M., Visser, W., 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. Funct. Ecol. 10, 440–448.

Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. Comp. Biochem. Physiol. 75, 1–3.

Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds. Annu. Rev. Nutr. 19, 247–277. doi:10.1146/annurev.nutr.19.1.247

Stillman, R.A., Caldow, R.W.G., Alexander, M.J., 2000. Individual variation in intake rate : the relative importance of foraging efficiency and dominance. J. Anim. Ecol. 69, 484–493.

Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G., Triplet, P., 2002. Predicting the strength of interference more quickly using behaviour-based models. J. Anim. Ecol. 71, 532–541. doi:10.1046/j.1365-2656.2002.00621.x

Stillman, R.A., West, A.D., Goss-Custard, J.D., McGrorty, S., Frost, N.J., Morrisey, D.J., Kenny, A.J., Drewitt, A.L., 2005. Predicting site quality for shorebird communities: A case study on the Humber estuary, UK. Mar. Ecol. Prog. Ser. 305, 203–217. doi:10.3354/meps305203

Triplet, P., Stillman, R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference in a foraging shorebird. J. Anim. Ecol. 68, 254–265. doi:10.1046/j.1365-2656.1999.00280.x