

1 **Nuclear power and coastal birds: predicting the ecological consequences of warm-water**
2 **outflows**

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17 ABSTRACT

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

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

37

38 1.INTRODUCTION

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

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

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

67 The aim of the investigations described by this paper is to explore the ecological consequences of a
68 large thermal discharge on wading birds, including shorebirds and wildfowl. Using high spatial and
69 temporal resolution benthic data and the output from a separately validated numerical

70 hydrodynamic model, these investigations explore how to predict which low-trophic level species
71 (i.e. benthic invertebrate) are most likely to be affected by a direct local thermal discharge over an
72 intertidal mudflat and how best to estimate the cascading, secondary consequences for their main
73 avian predators further up the food chain. We answer these questions in two steps: first, by using an
74 empirical understanding of benthic invertebrate physiology and ecology coupled with the outputs of
75 a validated hydrodynamic model to assess the potential consequences of a local temperature
76 increase on the benthic community; second, by using an understanding of bird physiology and
77 behaviour in individual-based model to predict the knock-on consequences for the birds of changes
78 in their invertebrate prey.

79 2 METHOD

80 2.1 Study site and context

81 The Severn Estuary (UK) is one of the largest estuaries in Europe and has the third largest tidal range
82 in the world. It encompasses several sites supporting bird populations that are of national or
83 international importance. Although the estuary is thought of as species-poor, prey items are found
84 at very high densities across wide areas of intertidal mudflats and sandbanks (Boyden and Little,
85 1973; Mettam et al., 1994; Warwick and Somerfield, 2010; Warwick et al., 1991) which support
86 considerable numbers of wading birds during the winter (Burton et al., 2010). The largest of these
87 areas is Bridgwater Bay, which is composed of two main intertidal mudflats, Stert and Berrow flats
88 respectively on the south and the north side of the River Parret (**Figure 1**). Adjacent to the bay,
89 Hinkley Point (HP) is the location of two existing nuclear power stations (HPA – no longer operating
90 and HPB – operational) and permission has recently been granted for a third (HPC), the operation of
91 which could have impacts on the local marine fauna and flora, including the wading bird and their
92 preys.

93 2.2 Identification of the potential thermal impact on benthic invertebrate species

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

102 2.2.1 Assessment of the sensitivity to elevated temperature for the main benthic taxa

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

114 2.2.2 Thermal sensitivity of *M. balthica*

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

129 2.3 The individual-based model

130 2.3.1 Rationale

131 The selection of an appropriate model for investigating the trophic interactions between the birds
132 and their infaunal preys requires consideration of aspects of the birds' ecology. Mortality and
133 reproductive rate of the birds are the two most important demographic factors to assess (Stillman

134 and Goss-Custard, 2010). Individual-based models (IBM) are considered to be appropriate tools for
135 such tasks since they consider important aspects of species interaction such as interference and
136 competition and incorporation of individual variations (Stillman and Goss-Custard, 2010).

137 MORPH is a flexible IBM platform designed to be used with a wide range of species and
138 environmental issues (freely available at: <http://individualecology.bournemouth.ac.uk/index.html>).

139 The tool is described in detail in Stillman (2008). Briefly, the basic principles of MORPH are as
140 follows: Time progresses in discrete, fixed duration time-steps, the birds arrive on site on their
141 species-specific arrival day, they remain at the same location during a time-step, either on a feeding
142 patch or travelling between patches but cannot move between time-steps. They alter their location
143 and the food they consume in order to maximise their perceived fitness and finally leave the site on
144 their species-specific departure day. During the model period, each day, each model bird aims to
145 meet its temperature-related energy demand by selecting feeding locations, times of the day and
146 tidal zones where the intake rate is highest. Survival is then determined by the balance between
147 daily consumption rate and energy demands.

148 2.3.2 The model global environment

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

152 2.3.3 The model patches

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

160 2.3.4 Patch resources

161 *Benthic data source*

162 A seasonal survey of the intertidal benthic community was conducted in 2010/2011 with one visit
163 per season (April, July and November 2010 and January 2011). For each species ash-free dry weight

164 was calculated either individually or at the species level. Additionally, shell length/total length in mm
165 was measured for most polychaetes and mollusc taxa collected.

166 *Prey size class*

167 Common shorebird species forage mainly across a particular prey size range (Goss-Custard et al.,
168 2006). In order to classify the potential dietary sources in an ecologically realistic manner, the
169 invertebrate species were grouped by size. All taxa whose average length was less than 10mm were
170 attributed to one of the resource categories with no size differences (**Appendix B**); the majority of
171 species recorded from the mudflats belonged to this category. Species whose lengths exceeded
172 10mm – the bivalve *M. balthica* and the polychaetes *H. diversicolor*, *Eunereis longissima*, *Nephtys*
173 *hombergii*, *Nephtys cirrosa* and *Eteone longa/flava* - were divided into resource-specific size-classes,
174 based on published information on size range of prey handling by different bird species (Goss-
175 Custard et al., 2006). Thus, bivalves were divided into two (<10mm and >10mm) and polychaetes
176 into four (<10mm, 10-20mm, 20-50mm and >50mm) size classes (**Appendix B & C**).

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

178 The birds' prey-specific intake rates are not fully defined with respect to all macro-invertebrate
179 species present in the mudflat. Fortunately, they were still available for the most abundant species
180 (Goss-Custard et al., 2006). We however chose not to ignore the potential extra sources of energy
181 from the other, rarer species but, in so doing, had to simplify the prey-species input in MORPH by
182 arranging all species into functional resource groups, referred to as 'resource group' hereafter. Apart
183 from the bivalve group which exclusively contains *M. balthica*, the resource groups were based on
184 the most abundant taxa on site: *P. ulvae*, *Pygospio elegans*, *C. volutator*, *H. diversicolor* and the
185 oligochaete family Enchytraeidae and the remaining species were grouped with one of the closest
186 abundant taxa according to shape, size and life form (**Appendix B**). Their respective initial density
187 was then calculated using the July 2010 abundance data (**Appendix C**). These resource groups¹ were
188 named and defined as follow:

- 189 - "PolErr" (Polychaeta Errantia or motile worms, e.g. *Hediste* spp, *Nephtys* spp): 4 size-classes
190 (<10mm – PolErr0to10, 10-20 – PolErr10to20, 20-50 – PolErr20to50 and >50mm –
191 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. PolErr0to10 resource group.

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

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

- 200 - Benthic invertebrates

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

- 204 - Microphytobenthos

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

213 The grain size of the sediment where infauna samples were collected was therefore used as an
 214 indicator of the biofilm food resource, with an assumed inversely proportional relationship between
 215 chlorophyll and increasing grain size converted to an algal equivalent AFDW per m², assuming the
 216 following relations:

- 217 - 1mg chl *a*=50x1mgC (de Jonge, 1980)
- 218 - 1mg AFDW=0.4x1mgC (Finlay and Uhlig, 1981).

219 However, the way the ingestion rate of birds changes with MPB density (i.e. functional response see
 220 **section 2.3.6**) is unknown which prevents direct inclusion of MPB as an independent resource group
 221 in MORPH. Therefore, MPB was linked to the benthic resource groups, assuming that invertebrate
 222 prey physically covered with MPB would display a higher energy value than would the same type of

223 prey not covered by MPB. Larger individuals are able to burrow deeper in the sediment, but MPB
224 biofilms are mainly found in the upper 2mm of sediment. With this in mind, only the small group
225 resources were considered to benefit from this supplementary energetic value. The average MPB
226 AFDW/m² was apportioned between the six smallest resource groups presented above (i.e.
227 PolErr0to10 resource group, Gastropoda resource group, Interstitial resource group, PolSed resource
228 group, Macoma0to10 resource group and Crustacea resource group) (see **Appendix C**).

229 *Resource dynamics*

230 - Densities

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

239 - Average Ash-free dry weight per individual

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

248 2.3.5 The bird assemblage

249 The bird assemblage data needed to parameterise MORPH are overall mean monthly count, arrival
250 day and departure day for each forager species. Data used for the present MORPH model were
251 obtained from the Wetland Bird Survey (WeBS) Core Counts scheme
252 (<http://www.bto.org/volunteer-surveys/webs/taking-part/core-counts>, data obtained in August
253 2012). In Bridgwater Bay bird data were available from four areas (Berrow flats, Berrow, Burnham-

254 on-Sea and Bridgwater Bay). These areas have been surveyed for several consecutive years and have
255 been summarised in order to build a generic September to March period.

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

273 2.3.6 Forager feeding ecology

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

276 *Diet*

277 There is an abundant literature on feeding of coastal birds (see e.g. Anders et al., 2009; Evans, 1987;
278 Goss-Custard et al., 2006; Quaintenne et al., 2010; Scheiffarth and Nehls, 1997; Zwarts and Wanink,
279 1993). This information was used to characterise a bird-specific diet for all the forager species
280 selected in the model based on a specific selection of the resource groups, in other words, a bird diet
281 group² was defined as a combination of one or more resource groups (**Table 4a and b**).

282 *Day and night variation in foraging efficiency*

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. PolErr20plus diet group

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

297 *Bird functional response*

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

305 - Shorebirds

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

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

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

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

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

316 - Shelduck

317 Using the shorebird functional response equation “as it is” for shelduck was inappropriate because it
 318 was developed for shorebirds but shelduck is a wildfowl and this would result in an underestimation
 319 of its intake rate calculation. However, since no functional response value existed for shelduck, we
 320 adapted the shorebird equation to account for the different way of feeding. The classic shorebirds
 321 functional response follows the general forms of the ‘disc equation’, which is a theoretical model of
 322 a decelerating rate of intake (see e.g., Goss-Custard et al., 2006, Hiddink, 2003 and Smart and Gill,
 323 2003) where the maximum (or asymptotic) intake rate is determined by how long it takes the
 324 forager to capture and swallow prey items, the ‘handling time’. At the asymptote of the functional
 325 response, the prey items are so abundant that the forager finds another prey immediately after it
 326 swallows the preceding, the intake rate being only limited by the rate at which the gut can process
 327 food. However, instead of probing or pecking for individual prey items as shorebirds do, shelduck
 328 sweeps the surface of the mud in broad arcs (‘scything’) which results in an omnivorous diet (Ferns
 329 and Reed, 2009) that may include MPB (Meininger and Snoek, 1992), *P. ulvae*, young *M. balthica*,
 330 young mussels, young cockles and many kind of worms (including *H. diversicolor*) (Anders et al.,
 331 2009; Ferns and Reed, 2009; Leopold et al., 2004a, 2004b). Additionally, shelduck is the largest
 332 species of all the birds considered in the present study and feeds on rather small prey sizes with
 333 respect to its own body mass. This is a very wildfowl-specific characteristic since amongst the
 334 shorebirds, the larger the bird species, the larger the prey size (Goss-Custard et al., 2006; Johnson,
 335 1985). The long-term trend of shelduck winter counts suggests a slightly increasing overwintering
 336 population in Bridgwater Bay (Burton et al., 2010); this means that the current observed survival for
 337 the species in the area must be high. Consequently, the shorebird equation, which underestimates
 338 shelduck intake rate (and overestimate its mortality), was corrected by progressively increasing to
 339 the value of the *IFIR* until the resulting modelled survival reached values very close to 100% - this
 340 happened after a 50% increase of the *IFIR* coefficient for shelduck.

341 2.4 Simulation procedures

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

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

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

351 The length of the growing season was estimated using bottom water temperature values from a run
352 of an existing validated and calibrated numerical hydrodynamic model utilising the General Estuarine
353 Transport Model (GETM, the model was obtained from <https://www.getm.eu>) (Stips et al., 2004).
354 This model was run in 3D with 100m resolution and 15 depth intervals, providing simulated
355 temperature outputs for the intertidal areas covering periods of both immersion and emersion. The
356 3D domain included the Severn Estuary and the inner Bristol Channel up to the line between
357 Minehead and Cowbridge. The elevation and current boundary conditions were supplied from a
358 larger 2D GETM run and the meteorological forcing from ECMWF (European Centre for Medium-
359 Range Weather Forecasts: <http://www.ecmwf.int/en/research/climate-reanalysis/era-interim>) ERA
360 interim reanalysis data. The GETM model was run at 1.5 second internal time steps for one full year
361 and includes the cooling water discharge from HPB power station, which has a flow of 33m.s^{-1} and a
362 temperature increase at the outfall of 11°C . The GETM model was successfully validated against
363 measurements from tidal gauges in the Severn and Acoustic Doppler Current Profilers (ADCP) data
364 and temperature sensors previously deployed in the Bridgwater Bay area. For more details of this
365 model and its corroboration see Fernand et al. (2011).

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

372 The reduction in biomass accrued over a single growing season was translated into MORPH by
373 decreasing the average AFDW content of individual *M. balthica* and therefore the temperature

374 effect concerns only the two model resource groups including this species (Macoma0to10 resource
375 group and Macoma10plus resource group). Three scenarios of biomass reduction were simulated (B,
376 C and D in **Table 5**) and compared against the reference conditions (A in **Table 5**).

377 3.RESULTS

378 3.1 Corroboration of the MORPH model

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

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

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

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

400 The primary purpose of the WeBS scheme is to investigate relative distributions averaged over
401 several dates, which makes it an ideal dataset for validating spatial prediction. The observed winter
402 low tide counts (November 2009 to February 2010) were compared against predicted bird
403 distribution on the patches (i.e., A, B-C, D-E, F, G, H, I, J, K) (**Figure 6**). Most modelled bird species
404 show the same pattern of distribution spending most of their time on the same two main patches, a

405 primary and a secondary one. Overall, MORPH runs predicted the bird distribution among patches
406 with a high degree of accuracy especially for the primary feeding patches. The two main
407 discrepancies concern: (i) knot, for which the model predicted foraging on Berrow flats (i.e. I and K)
408 whilst observations showed that the actual preference was for Stert flats (i.e. A, B-C and D-E) and (ii)
409 oystercatcher for which the primary feeding ground was predicted to be Stert flats whilst
410 observations showed a preference for Berrow flats (i.e. from patch G to K). Additionally, the
411 observed secondary feeding patches on Berrow flats by curlew (~10%) and shelduck (~20%) were
412 not well predicted by the model.

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

415 3.2 Model simulations outputs

416 3.2.1 Bird survival and prey selection

417 Food availability, as average biomass density (i.e. mean biomass multiplied by the density), mainly
418 controls the survival and body condition (respectively expressed as the percentage of the number of
419 birds alive / total and the final average bird mass / target mass – the average mass of a healthy bird)
420 of the birds on site. These bird-specific values recorded at the end of the winter season are two of
421 the major outputs of MORPH (**Table 6**). With an average of 14.49 gAFDW/m² of benthic
422 invertebrates and MPB prey supply, Bridgwater Bay is predicted to sustain in excess of 97% of the
423 overall overwintering bird population under reference (i.e. current) conditions. Of the 10 bird
424 species selected, 7 had a survival rate of over 99% and body condition over 98%. Of the 3 remaining
425 species, MORPH predicted shelduck, oystercatcher and curlew body condition to be 91, 90 and
426 73.3% and survival rates to be 100, 91.6 and 64.7% respectively.

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

436 3.2.2 Effects of changes in prey biomass across all patches

437 In order to test how sustainable Bridgwater Bay is for the bird feeding on the mudflats, prey biomass
438 densities, encompassing all resource groups, were varied between 0 and 250% of the current (2010)
439 mean (in gAFDW/m²) to determine the threshold below which survival would be adversely affected
440 (**Figure 8**). As a result, dunlin, turnstone, knot, redshank, grey plover and black-tailed godwit were
441 predicted to show a survival rate >94% until the food supply was reduced to 25%. Ringed plover
442 remained at 100% survival when food supply was reduced to 75%. Shelduck survival was shown to
443 decrease immediately after the food supply was reduced (83% survival rate at 75% AFDW). Finally,
444 survival for oystercatcher and curlew within Bridgwater Bay was predicted to be lower than 100%
445 with the current food supply (100%). Oystercatcher reaches 100% survival with an extra 25% food
446 supply but even with up to 250% of the reference biomass condition curlew survival only reaches
447 97%. Thus, for all species except oystercatcher and curlew, the available data suggest that the
448 current observed food supply within Bridgwater Bay is sufficient or more than sufficient to support
449 the observed number of birds. Shelduck and ringed plover are predicted to be the most sensitive
450 species to reductions in food supply.

451 3.2.3 Effects of changes in prey biomass due to warm-water outflow

452 The body condition and survival of dunlin, ringed plover, turnstone, redshank, grey plover, black-
453 tailed godwit, oystercatcher, curlew and shelduck are not predicted to be adversely impacted by
454 reductions in *M. balthica* average AFDW brought on by any of the four tested scenarios (**Figures 9 &**
455 **10**). Knot, on the other hand, is predicted to be slightly affected by scenario B (1.2% reduction in
456 survival), C (1.5% reduction in survival) and D (3% reduction in survival).

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

462 4.DISCUSSION

463 4.1 Predicting the ecological consequences of a warm-water outflow

464 In this paper, we used empirical evidence coupled with two models, a previously validated
465 hydrodynamic model and an IBM – MORPH – to predict the secondary consequences of a future
466 heated effluent on bird populations. Efforts were made to incorporate observational data on all of
467 the main bird species overwintering on our study site, Bridgwater bay; this includes shorebirds and
468 wildfowl. Additionally, the model was implemented using high spatial and temporal resolution

469 benthic data and a microphytobenthic component was included in order to build the most accurate
470 estimation of prey stock and change through time for MORPH use. Model outputs for a reference
471 case were also corroborated against independantly sourced field data not utilised in model
472 development. To our knowledge, this is the first time that this has been done. We first endeavoured
473 to qualitatively identify potential temperature sensitivity among the prey species living on the
474 mudflat (i.e. benthic invertebrate). Then, an existing validated and calibrated numerical
475 hydrodynamic model (GETM) was used to assess the quantitative extent of the thermal and seasonal
476 sensitivity and its inherent consequences on the populations of the clam *M. balthica*, the only
477 species suspected to be adversely affected by a warm-water outflow. The biological link between
478 benthic prey species and their avian predators was formalised by implementing a Bridgwater Bay-
479 specific version of MORPH. GETM outputs which described *M. balthica* growth period shortening
480 were then fed into MORPH and different prey decrease scenarios were thus simulated. MORPH
481 predicted that a local temperature increase due to the the proposed power station development
482 (HPC) would cause little difference for worm-feeding birds and that even primarily bivalve-feeding
483 species would have the ability to shift to a more worm-based diet if necessary.

484 4.2 Understanding the effects of thermal impact on benthic invertebrates

485 Depending upon the precise disposition of the discharge and the local tidal regime, warm-water
486 discharges from coastal power stations can be expected to have an effect that extends to local
487 intertidal areas. Infaunal communities living between the low and the high water marks will already
488 experience daily variations in environmental stress (e.g. wave-induced sediment remobilisation,
489 temperature, salinity, dessication) (Raffaelli and Hawkins, 1996) and this can be even more
490 pronounced if the area is also located in or close to an estuary due to the presence of and variance
491 in freshwater discharge (Little, 2000) or where the tidal range is extreme leading to higher levels of
492 superficial sediment disturbance (Raffaelli and Hawkins, 1996). Consequently, most benthic species
493 living on the intertidal mudflats are ecologically adapted to such varying environments.

494 Understandably, all dominant benthic species in Bridgwater Bay are euryhaline and eurythermic and
495 present some form of resistance to most stresses caused by their intertidal and estuarine medium
496 (Little, 2000). As a result these species are not expected to be readily sensitive to thermal stress
497 unless they are already close to their warmer limit of geographic distribution and are already
498 undergoing some sort of stress (temperature or otherwise), whereby an extra thermal pressure
499 during a critical period of the year could “push them over the edge”. In first considering possible
500 thermal effects of a new power station development on the intertidal area of Bridgwater Bay,
501 through published evidence from field and laboratory studies and due to its reported southern limit

502 of distribution (see **section 2.2.1**), we identified the cold-water clam *M. balthica* as potentially
503 temperature sensitive. The study that has been reported here suggests, however, that this will not
504 be of great concern because the direct thermal impact on the *M. balthica* population will be
505 somewhat local (mostly on Stert flat) and the indirect effect on its bird predators attenuated by the
506 availability of alternative choices of prey. Beside, competitive release means that this local loss may
507 lead to a structural reorganisation of the community *via* compensatory mechanisms (Duffy et al.,
508 2009; Ernest and Brown, 2001); the outcome of which cannot be known for certain until it occurs
509 but scenarios of benthic succession along various environmental gradient, together with the
510 knowledge of the other locally dominant species suggest that a shift to polychaetes-dominated
511 community might happen (Rosenberg, 2001). This, in turn, could potentially account for the extra
512 predatory pressure forecast by the model on these taxa. In Bridgwater Bay *M. balthica* is not
513 predicted to be the main prey for the birds normally present, hence the negligible cascade effects on
514 bird predators. It cannot, however, be assumed that this will consistently remain the case since
515 prey/predator linkages are known to differ between sites. For example, a study in the Wash,
516 England, showed that a similar local depression of two clams the cockle *Cerastoderma edule* and the
517 mussel *Mytilus edulis* (due to fishery activity) progressively changed the population of birds from a
518 bivalve-diet species to a worm-based species thus qualitatively changing the bird populations
519 (Atkinson et al., 2010).

520 4.3 Model corroboration

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

533 In Bridgwater Bay, predictions were corroborated with field data from different sources than those
534 used in developing the model itself. Overall, MORPH accurately predicted the present-day

535 distribution of dunlin, ringed plover, turnstone, redshank and black-tailed godwit between the two
536 main mudflats. However, knot, oystercatcher and, to a lesser extent, shelduck and curlew
537 distributions were less well predicted. Modelled knot were predicted to feed entirely in high shore
538 Berrow flats due to a high density of the Macoma10plus diet group in these areas. Observations,
539 however, show that knot primarily fed on Stert flats which would have corresponded to a
540 preferential use of the PolErr10to50 diet group and/or Gastropoda diet group. High-density patches
541 of bivalves may have been missed despite our high spatial resolution surveys since *M. balthica*
542 density has been observed to vary widely over a rather short spatial scale in other intertidal
543 locations (Azouzi et al., 2002) and the medium-large *M. balthica* standing-stock of Stert flats could
544 have been underestimated. Oystercatcher, curlew and shelduck's main feeding patches were
545 correctly predicted but some of the secondary ones much less so. Realistically, not all parameters
546 included in MORPH can be site-specific and some had to be derived from generic relationships
547 defined with data from other areas (see **section 2.3.6** and **Appendix D**) (Stillman and Goss-Custard,
548 2010). These relationships, combined with the uncertainties of food abundance records, can explain
549 some of the differences between predictions and observations. This is consistent with previously
550 published applications, where MORPH sometimes failed to predict spatial occupation of some
551 species, curlew and oystercatcher in Poole Harbour (Dit Durell et al., 2006) and dunlin and curlew in
552 the Humber estuary (Stillman et al., 2005). These shortcomings have not prevented these models to
553 make useful predictions.

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

569 representation of the real system in this instance with perhaps a slight over-estimation of the energy
570 needs when compared with what happens in nature.

571 4.4 Site quality

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

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

601 energetic requirements which seem to be unsustainable by the mudflats alone, a behaviour that has
602 indeed been observed within the Severn Estuary by Stillman (Com. Pers.).

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

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

615 4.5 Effect of warm-water outflows on birds

616 The MORPH model simulated the effects of reduced *M. balthica* individual average AFDW due to a
617 contraction of its growth period resulting from a warm-water discharge from a proposed new
618 nuclear build within Bridgwater Bay. The exact effect of the future thermal impact on the clam's
619 population dynamics cannot be confirmed until the station begins to operate. Some assumptions
620 used in the present paper were not based on local field observations but instead on the authors'
621 knowledge on the species' physiology, previously published temperature-related population
622 dynamic studies and existing numerical hydrodynamic model outputs: one result was that we were
623 obliged to use a wide range of potential AFDW decreases from that model to bracket the possible
624 impact of the thermal influence on that particular parameter value. The simulation scenarios show
625 that (i) eight of the 10 bird species included in the model did not differ in their survival and body
626 condition under even the most conservative impact scenarios, most of these species being found to
627 feed predominantly on worms and (ii) the progressive decrease of *M. balthica* attractiveness
628 triggered a switch to the PolErr resource group (mix size-classes). The only bird species amongst
629 those selected whose survival was predicted to be reduced by a *M. balthica* AFDW decrease was
630 knot. Knot has been observed to feed on the worm *H. diversicolor*, but only on individuals ranging
631 from 10 to 59mm (Goss-Custard et al., 2006); an older study even states that this species cannot
632 feed on such prey larger than 30mm (Zwarts and Blomert, 1992). The model did not show knot

633 turning to *H. diversicolor* to compensate for the loss of *M. balthica*. This could be because large *M.*
634 *balthica* may be a better quality food source than small and medium size-classes of *H. diversicolor*.
635 The drop in predicted survival was mild , at 3%, but is consistent with other studies documenting
636 cases of bird species switching from *M. balthica* to *H. diversicolor* when the bivalves are depleted
637 (Atkinson et al., 2010, 2003; Ens, 2006). The corroboration of the model with observed foraging data
638 suggests that these predictions could be a slight over-estimation compared to what happens in
639 nature since modelled birds seem to be having more difficulty meeting their energy requirements
640 than real birds but even then, the predicted impact of a rising water temperature is small.

641 5 CONCLUSION

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

655

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664

665 7 REFERENCES

- 666 Anders, N.R., Churchyard, T., Hiddink, J.G., 2009. Predation of the shelduck *Tadorna tadorna* on the
667 mud snail *Hydrobia ulvae*. *Aquat. Ecol.* 43, 1193–1199. doi:10.1007/s10452-008-9216-5
- 668 Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A., Ireland, P.L., 2003. Changes in
669 commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biol.*
670 *Conserv.* 114, 127–141. doi:10.1016/S0006-3207(03)00017-X
- 671 Atkinson, P.W., Maclean, I.M., Clark, N.A., 2010. Impacts of shellfisheries and nutrient inputs on
672 waterbird communities in the Wash, England. *J. Appl. Ecol.* 47, 191–199. doi:10.1111/j.1365-
673 2664.2009.01760.x
- 674 Azouzi, L., Bourget, E., Borcard, D., 2002. Spatial variation in the intertidal bivalve *Macoma balthica*:
675 Biotic variables in relation to density and abiotic factors. *Mar. Ecol. Prog. Ser.* 234, 159–170.
676 doi:10.3354/meps234159
- 677 Bachelet, G., Labourg, P.J., Madani, I., 1990. Nouvelles signalisations de Mollusques (Prosobranches
678 et Bivalves) dans le Bassin d’Arcachon. *Cah. Biol. Mar.* 31, 87–92.
- 679 Bamber, R.N., 1995. The influence of rising background temperature on the effects of marine
680 thermal effluents. *J. therm. Biol.* 20, 105–110.
- 681 Beukema, J.J., De Bruin, W., 1977. Seasonal changes in dry weight and chemical composition of the
682 soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. *Netherlands J. Sea*
683 *Res.* 11, 42–55. doi:10.1016/0077-7579(77)90020-5
- 684 Beukema, J.J., Dekker, R., Jansen, J.M., 2009. Some like it cold: populations of the tellinid bivalve
685 *Macoma balthica* (L.) suffer in various ways from a warming climate. *Mar. Ecol. Prog. Ser.* 384,
686 135–145. doi:10.3354/meps07952
- 687 Beukema, J.J., Desprez, M., 1986. Single and dual annual growing seasons in the tellinid bivalve
688 *Macoma balthica* (L.). *J. Exp. Mar. Bio. Ecol.* 102, 35–45. doi:10.1016/0022-0981(86)90124-3
- 689 Beukema, J.J., Knol, E., Cadee, G.C., 1985. Effects of temperature on the length of the annual
690 growing season in the tellinid bivalve *Macoma balthica* (L.) living on tidal flats in the Dutch
691 Wadden Sea. *J. Exp. Mar. Bio. Ecol.* 90, 129–144. doi:10.1016/0022-0981(85)90115-7
- 692 Blake, N.J., Doyle, L.J., Pyle, T.E., 1976. Macrobenthic community of a thermally altered area of
693 Tampa Bay, Florida, in: Esch, G.W., McFarlane, R.W. (Eds.), *Proceedings of II Thermal Ecology*
694 *Symposium; Augusta, Georgia, USA.* Technical Information Center, Energy Research and
695 Development Administration, Springfield, pp. 296–301.
- 696 Bolam, S., Bremner, J., Forster, R., 2011. Ecological characterisation of the intertidal region of
697 Hinkley Point, Severn Estuary: Results from the 2008 Field Survey and Assessment of Risk.
698 Lowestoft.
- 699 Boyden, C.R., Little, C., 1973. Faunal distributions in soft sediments of the Severn Estuary. *Estuar.*
700 *Coast. Mar. Sci.* 1, 203–223. doi:10.1016/0302-3524(73)90035-2

- 701 Bryant, D.M., Leng, J., 1975. Feeding distribution and behaviour of Shelduck in relation to food
702 supply. *Wildfowl* 26, 20–30.
- 703 Burton, N.H.K., Musgrove, A.J., Rehfisch, M.M., Clark, N.A., 2010. Birds of the Severn Estuary and
704 Bristol Channel: Their current status and key environmental issues. *Mar. Pollut. Bull.* 61, 115–
705 123. doi:10.1016/j.marpolbul.2009.12.018
- 706 Clark, N.A., Prys-Jones, R.J., 1994. Low tide distribution of wintering waders and shelduck on the
707 Severn Estuary in relation to the proposed tidal barrage. *Biol. J. Linn. Soc.* 51, 199–217.
- 708 Cowie, P.R., 2007. A synopsis report of the marine biological work carried out in the vicinity of
709 Hunterstone power station and potential habitat sensitivities to thermal effluents withing a 2 -
710 5 km radius. A report prepared for British Energy.
- 711 Cramp, S., Simmons, K.E.L., 1983. Handbook of the birds of Europe, the Middle East and North
712 Africa. Oxford University Press, Oxford.
- 713 Crema, R., Bonvicini Pagliai, A.M., 1980. The structure of benthic communities in an area of thermal
714 discharge from a coastal power station. *Mar. Pollut. Bull.* 11, 221–224. doi:10.1016/0025-
715 326X(80)90410-5
- 716 De Jonge, V.N., 1980. Fluctuations in the Organic Carbon to Chlorophyll a Ratios for Estuarine
717 Benthic Diatom Populations. *Mar. Ecol. Prog. Ser.* 2, 345–353. doi:10.3354/meps002345
- 718 De Wilde, P.A.W.J., 1975. The influence of temperature on behaviour, energy metabolism, and
719 growth of *Macoma balthica* (L.), in: Proceedings of the 9th European Marine Biology
720 Symposium. pp. 239–256.
- 721 Del Hoyo, J., Elliott, A., Sargatal, J., Bateman, R., 1996. Handbook of the Birds of the World, Volume 3
722 (Hoatzin to Auks). Lynx Edicions.
- 723 Dit Durell, S.E.A.L. V., Stillman, R.A., Caldow, R.W.G., McGroarty, S., West, A.D., Humphreys, J., 2006.
724 Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour,
725 UK. *Biol. Conserv.* 131, 459–473. doi:10.1016/j.biocon.2006.02.022
- 726 Dit Durell, S.E.A.L. V., Stillman, R.A., Triplet, P., Aulert, C., Ono dit Biot, D., Bouchet, A., Duhamel, S.,
727 Mayot, S., Goss-Custard, J.D., 2005. Modelling the efficacy of proposed mitigation areas for
728 shorebirds: A case study on the Seine estuary, France. *Biol. Conserv.* 123, 67–77.
729 doi:10.1016/j.biocon.2004.10.009
- 730 Dit Durell, S.E.A.L. V., Stillman, R.A., Triplet, P., Desprez, M., Fagot, C., Loquet, N., Sueur, F., Goss-
731 Custard, J.D., 2008. Using an individual-based model to inform estuary management in the Baie
732 de Somme, France. *Oryx* 42, 265–277.
- 733 Dobrzycka-Kraheil, A., Krzak, M., Szaniawska, A., 2014. A laboratory-based comparison of
734 osmoregulatory ability at different water temperatures and salinities in the stenothermic
735 isopod *Saduria entomon* (Linnaeus, 1758) and the eurythermic amphipod *Corophium volutator*
736 (Pallas, 1766) from the Baltic Sea. *Mar. Freshw. Behav. Physiol.* 47, 29–39.
737 doi:10.1080/10236244.2013.874120

- 738 Duffy, J.E., Srivastava, D.S., McLaren, J., Sankaran, M., Solan, M., Griffin, J., Emmerson, M., Jones,
739 K.E., 2009. Forecasting decline in ecosystem services under realistic scenarios of extinction, in:
740 Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), *Biodiversity, Ecosystem*
741 *Functioning, & Human Wellbeing*. Oxford University Press, Oxford, pp. 60–77.
- 742 EDF/NNB Genco Entec UK Ltd, 2009. EDF development company Ltd, Hinkley, third interim bird
743 report. Reading.
- 744 Ens, B.J., 2006. The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden
745 Sea, in: Boere, G.C., Galbraith, C.A., Stroud, D.A. (Eds.), *Waterbirds around the World*. The
746 Stationery Office, Edinburgh, UK, pp. 806–811.
- 747 Ernest, S.K.M., Brown, J.H., 2001. Homeostasis and compensation: The role of species and resources
748 in ecosystem stability. *Ecology* 82, 2118–2132.
- 749 Evans, A., 1987. Relative availability of the prey of wading birds by day and by night. *Mar. Ecol. Prog.*
750 *Ser.* 37, 103–107. doi:10.3354/meps037103
- 751 Fernand, L., Silva, T., Bacon, J., van Leeuwen, S., 2011. Hinkley Point thermal plume modelling: GETM
752 stage 3a results with the final cooling water configuration. Lowestoft.
- 753 Ferns, P.N., Reed, J.P., 2009. Effects of the Cardiff Bay tidal barrage on the abundance, ecology and
754 behaviour of shelducks *Tadorna tadorna*. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 19, 466–473.
755 doi:10.1002/aqc.1011
- 756 Finlay, B.J., Uhlig, G., 1981. Calorific and carbon values of marine and freshwater Protozoa.
757 *Helgoländer Meeresuntersuchungen* 34, 401–412.
- 758 Fritzsche, D., von Oertzen, J.-A., 1995. Metabolic responses to changing environmental conditions in
759 the brackish water polychaetes *Marenzelleria viridis* and *Hediste diversicolor*. *Mar. Biol.* 121,
760 693–699.
- 761 Goss-Custard, J.D., Stillman, R.A., West, A.D., Caldow, R.W.G., Triplet, P., Dit Durell, S.E.A.L. V.,
762 McGrorty, S., 2004. When enough is not enough: shorebirds and shellfishing. *Proc. Biol. Sci.*
763 271, 233–237. doi:10.1098/rspb.2003.2602
- 764 Goss-Custard, J.D., West, A.D., Yates, M.G., Caldow, R.W.G., Stillman, R.A., Bardsley, L., Castilla, J.,
765 Castro, M., Dierschke, V., Dit Durell, S.E.A.L. V., Eichhorn, G., Ens, B.J., Exo, K.-M., Udayangani-
766 Fernando, P.U., Ferns, P.N., Hockey, P.A.R., Gill, J.A., Johnstone, I., Kalejta-Summers, B.,
767 Masero, J.A., Moreira, F., Nagarajan, R.V., Owens, I.P.F., Pacheco, C., Perez-Hurtado, A., Rogers,
768 D., Scheiffarth, G., Sitters, H., Sutherland, W.J., Triplet, P., Worrall, D.H., Zharikov, Y., Zwartz, L.,
769 Pettifor, R.A., 2006. Intake rates and the functional response in shorebirds (Charadriiformes)
770 eating macro-invertebrates. *Biol. Rev. Camb. Philos. Soc.* 81, 501–529.
771 doi:10.1017/S1464793106007093
- 772 Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli,
773 M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards better modelling and decision
774 support: Documenting model development, testing, and analysis using TRACE. *Ecol. Modell.*
775 280, 129–139. doi:10.1016/j.ecolmodel.2014.01.018
- 776 Hartmann-Schröder, G., 1996. *Annelida, Borstenwürmer, Polychaeta*, 2nd ed. Gustav Fisher.

- 777 Hiddink, J.G., 2003. Modelling the adaptive value of intertidal migration and nursery use in the
778 bivalve *Macoma balthica*. *Mar. Ecol. Prog. Ser.* 252, 173–185. doi:10.3354/meps252173
- 779 Honkoop, P.J., Beukema, J.J., 1997. Loss of body mass in winter in three intertidal bivalve species: an
780 experimental and observational study of the interacting effects between water temperature,
781 feeding time and feeding behaviour. *J. Exp. Mar. Bio. Ecol.* 212, 277–297. doi:10.1016/S0022-
782 0981(96)02757-8
- 783 Honkoop, P.J.C., Van Der Meer, J., 1998. Experimentally induced effects of water temperature and
784 immersion time on reproductive output of bivalves in the Wadden Sea. *J. Exp. Mar. Bio. Ecol.*
785 220, 227–246. doi:http://dx.doi.org/10.1016/S0022-0981(97)00107-X
- 786 Honkoop, P.J.C., Van Der Meer, J., 1997. Reproductive output of *Macoma balthica* populations in
787 relation to winter-temperature and intertidal height mediated changes of body mass. *Mar.*
788 *Ecol. Prog. Ser.* 149, 155–162. doi:10.3354/meps149155
- 789 Honkoop, P.J.C., Van Der Meer, J., Beukema, J.J., Kwast, D., 1998. Does temperature-influenced egg
790 production predict the recruitment in the bivalve *Macoma balthica*? *Mar. Ecol. Prog. Ser.* 164,
791 229–235. doi:10.3354/meps164229
- 792 Hummel, H., Bogaards, R., Bek, T., Polishchuk, L., Amiard-Triquet, C., Bachelet, G., Desprez, M.,
793 Strelkov, P., Sukhotin, A., Naumov, A., Dahle, S., Denisenko, S., Gantsevich, M., Sokolov, K., De
794 Wolf, L., 1997. Sensitivity to stress in the bivalve *Macoma balthica* from the most northern
795 (Arctic) to the most southern (French) populations: low sensitivity in Arctic populations
796 because of genetic adaptations? *Hydrobiologia* 355, 127–138. doi:10.1023/A:1003009524563
- 797 Hylleberg, J., 1975. The effect of salinity and temperature on egestion in mud snails (Gastropoda:
798 Hydrobiidae). A study on niche overlap. *Oecologia* 21, 279–289.
- 799 IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to
800 the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva,
801 Switzerland.
- 802 Jansen, J.M., Pronker, A.E., Bonga, S.W., Hummel, H., 2007. *Macoma balthica* in Spain, a few decades
803 back in climate history. *J. Exp. Mar. Bio. Ecol.* 344, 161–169. doi:10.1016/j.jembe.2006.12.014
- 804 Johnson, C., 1985. Patterns of seasonal weight variation in waders on the wash. *Ringed Migr.* 6, 19–
805 32. doi:10.1080/03078698.1985.9673850
- 806 Kalejta, B., 1992. Time budget and predatory impact of waders at the Berg river estuary, South
807 Africa. *Ardea* 80, 327–342.
- 808 Kater, B.J., Jol, J.G., Smit, M.G.D., 2008. Growth of *Corophium volutator* under laboratory conditions.
809 *Arch. Environ. Contam. Toxicol.* 54, 440–446.
- 810 Kuwae, T., Beninger, P.G., Decottignies, P., Mathot, K.J., Lund, D.R., Elner, R.W., 2008. Biofilm grazing
811 in a higher vertebrate: the western sandpiper, *Calidris mauri*. *Ecology* 89, 599–606.
812 doi:10.1890/07-1442.1
- 813 Kuwae, T., Miyoshi, E., Hosokawa, S., Ichimi, K., Hosoya, J., Amano, T., Moriya, T., Kondoh, M.,
814 Ydenberg, R.C., Elner, R.W., 2012. Variable and complex food web structures revealed by

- 815 exploring missing trophic links between birds and biofilm. *Ecol. Lett.* 15, 347–356.
816 doi:10.1111/j.1461-0248.2012.01744.x
- 817 Langston, W.J., Chesman, B.S., Burt, G.R., Campbell, M., Manning, A., Jonas, P.J.C., 2007. The Severn
818 estuary: sediments, contaminants and biota. *Occas. Publ. Mar. Biol. Assoc. United Kingdom* 19,
819 176.
- 820 Leopold, M.F., Dijkman, E.M., Cremer, J.S.M., Meijboom, A., Goedhart, P.W., 2004a. De effecten van
821 mechanische kokkelvisserij op de benthische macrofauna en hun habitat; eindverslag EVA II
822 (evaluatie schelpdiervisserij tweede fase) deelproject C1/3. Wageningen.
- 823 Leopold, M.F., Smit, C.J., Goedhart, P.W., van Roomen, M.W.J., van Winden, A.J., van Turnhout, C.,
824 2004b. Langjarige trends in aantallen wadvogels, in relatie tot de kokkelvisserij en het gevoerde
825 beleid in deze; eindverslag EVA II (evaluatie schelpdiervisserij tweede fase) deelproject C2.
826 Wageningen.
- 827 Lincoln, R.J., 1979. *British Marine Amphipoda: Gammaridea*. Natural History Museum Publications.
- 828 Little, C., 2000. *The Biology of Soft Shores and Estuaries*. Oxford University Press.
- 829 Lourenço, P.M., Silva, A., Santos, C.D., Miranda, A.C., Granadeiro, J.P., Palmeirim, J.M., 2008. The
830 energetic importance of night foraging for waders wintering in a temperate estuary. *Acta*
831 *Oecologica* 34, 122–129. doi:10.1016/j.actao.2008.04.005
- 832 Mathot, K.J., Lund, D.R., Elnor, R.W., 2010. Sediment in Stomach Contents of Western Sandpipers
833 and Dunlin Provide Evidence of Biofilm Feeding. *Waterbirds* 33, 300–306.
834 doi:10.1675/063.033.0305
- 835 Meadows, P.S., Ruagh, A.A., 1981. Temperature preferences and activity of *Corophium volutator*
836 (Pallas) in a new choice apparatus. *Sarsia* 66, 67–72. doi:10.1080/00364827.1981.10414522
- 837 Meininger, P.L., Snoek, H., 1992. Non-breeding shelduck *Tadorna tadorna* in the southwest
838 Netherlands: effects of habitat changes on distribution, numbers, moulting sites and food.
839 *Wildfowl* 43, 139–151.
- 840 Mettam, C., Conneely, M.E., White, S.J., 1994. Benthic macrofauna and sediments in the Severn
841 estuary. *Biol. J. Linn. Soc.* 51, 71–81.
- 842 Musk, W., Leighton, A., Thomson, S., 2011a. Hinkley Point, Intertidal survey & analysis report
843 November 2010. Hull.
- 844 Musk, W., Leighton, A., Thomson, S., 2011b. Hinkley Intertidal survey and analysis report January
845 2011. Hull.
- 846 Musk, W., Leighton, A., Thomson, S., 2010a. Hinkley Point; Intertidal survey and analysis report, April
847 2010. Hull.
- 848 Musk, W., Leighton, A., Thomson, S., 2010b. Hinkley Point; Intertidal survey and analysis report, July
849 2010. Hull.

- 850 Olney, P.J.S., 1965. The food and feeding habits of shelduck *Tadorna tadorna*. *Ibis* (Lond. 1859). 107,
851 527–532.
- 852 Ozoh, P.T.E., Jones, N.V., 1990. Capacity adaptation of *Hediste* (*Nereis*) *diversicolor* embryogenesis
853 to salinity, temperature and copper. *Mar. Environ. Res.* 29, 227–243. doi:10.1016/0141-
854 1136(90)90035-M
- 855 Paterson, D.M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related
856 to the migratory behavior of epipelagic diatoms. *Limnol. Oceanogr.* 34, 223–234.
857 doi:10.4319/lo.1989.34.1.0223
- 858 Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C., Dekker, R., 2003. Climate-
859 related changes in recruitment of the bivalve *Macoma balthica*. *Limnol. Oceanogr.* 48, 2171–
860 2185. doi:10.4319/lo.2003.48.6.2171
- 861 Pimm, S.L., 1980. Food web design and the effects of species deletion. *Oikos* 35, 139–149.
- 862 Quaintenne, G., Van Gils, J.A., Bocher, P., Dekinga, A., Piersma, T., 2010. Diet selection in a
863 molluscivore shorebird across Western Europe: does it show short- or long-term intake rate-
864 maximization? *J. Anim. Ecol.* 79, 53–62. doi:10.1111/j.1365-2656.2009.01608.x
- 865 Raffaelli, D., Hawkins, S.J., 1996. *Intertidal Ecology*. Springer.
- 866 Robinson, K.I.M., 2010. Effects of thermal power station effluent on the seagrass benthic
867 communities of Lake Macquarie, a New South Wales coastal lagoon. *Wetl.*
- 868 Rosenberg, R., 2001. Marine benthic faunal successional stages and related sedimentary activity. *Sci.*
869 *Mar.* 65, 107–119. doi:10.3989/scimar.2001.65s2107
- 870 Scheiffarth, G., Nehls, G., 1997. Consumption of benthic fauna by carnivorous birds in the Wadden
871 Sea. *Helgoländer Meeresuntersuchungen* 51, 373–387.
- 872 Schiel, D.R., Steinbeck, J.R., Foster, M.S., 2004. Ten years of induced ocean warming causes
873 comprehensive changes in marine benthic communities. *Ecology* 85, 1833–1839.
874 doi:10.1890/03-3107
- 875 Sitters, H., 2000. The role of night-feeding in shorebirds in an estuarine environment with specific
876 reference to mussel-feeding oystercatchers. Oxford University.
- 877 Smart, J., Gill, J.A., 2003. Non-intertidal habitat use by shorebirds: a reflection of inadequate
878 intertidal resources? *Biol. Conserv.* 111, 359–369. doi:10.1016/S0006-3207(02)00304-X
- 879 Smith, R.I., 1977. Physiological and reproductive adaptations of *Nereis diversicolor* to life in the
880 Baltic Sea and adjacent waters, in: Reish, D.J., Fauchald, K. (Eds.), *Essays on Polychaetous*
881 *Annelids*. University of Southern California Press, Los Angeles, pp. 373–390.
- 882 Stillman, R.A., 2008. MORPH-An individual-based model to predict the effect of environmental
883 change on foraging animal populations. *Ecol. Modell.* 216, 265–276.
884 doi:10.1016/j.ecolmodel.2008.04.014

- 885 Stillman, R.A., Caldow, R.W.G., Alexander, M.J., 2000. Individual variation in intake rate : the relative
886 importance of foraging efficiency and dominance. *J. Anim. Ecol.* 69, 484–493.
- 887 Stillman, R.A., Goss-Custard, J.D., 2010. Individual-based ecology of coastal birds. *Biol. Rev.* 85, 413–
888 434. doi:10.1111/j.1469-185X.2009.00106.x
- 889 Stillman, R.A., Moore, J.J., Woolmer, A.P., Murphy, M.D., Walker, P., Vanstaen, K.R., Palmer, D.,
890 Sanderson, W.G., 2010. Assessing waterbird conservation objectives: an example for the Burry
891 Inlet, UK. *Biol. Conserv.* 143, 2617–2630. doi:10.1016/j.biocon.2010.07.004
- 892 Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G., Triplet, P., 2002.
893 Predicting the strength of interference more quickly using behaviour-based models. *J. Anim.*
894 *Ecol.* 71, 532–541. doi:10.1046/j.1365-2656.2002.00621.x
- 895 Stillman, R.A., West, A.D., Caldow, R.W.G., Ditt Durell, S.E.A.L. V., 2007. Predicting the effect of
896 disturbance on coastal birds. *Ibis (Lond. 1859)*. 149, 73–81. doi:10.1111/j.1474-
897 919X.2007.00649.x
- 898 Stillman, R.A., West, A.D., Goss-Custard, J.D., McGorrtly, S., Frost, N.J., Morrissey, D.J., Kenny, A.J.,
899 Drewitt, A.L., 2005. Predicting site quality for shorebird communities: A case study on the
900 Humber estuary, UK. *Mar. Ecol. Prog. Ser.* 305, 203–217. doi:10.3354/meps305203
- 901 Stips, A., Bolding, K., Pohlman, T., Burchard, H., 2004. Simulating the temporal and spatial dynamics
902 of the North Sea using the new model GETM (general estuarine transport model). *Ocean Dyn.*
903 54, 266–283.
- 904 Suh, S., 2014. Massive cooling water dispersion behavior in a shallow macro-tidal coastal zone in
905 Korea. *J. Coast. Res.* 70, 360–365. doi:10.2112/SI70-061.1
- 906 Thompson, D.B.A., 1981. Feeding behaviour of wintering shelduck on the Clyde estuary. *Wildfowl* 32,
907 88–98.
- 908 Triplet, P., Stillman, R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference
909 in a foraging shorebird. *J. Anim. Ecol.* 68, 254–265. doi:10.1046/j.1365-2656.1999.00280.x
- 910 Turpie, J.K., Hockey, P.A.R., 1993. Comparative diurnal and nocturnal foraging behaviour and energy
911 intake of premigratory grey plovers *Pluvialis squatarola* and whimbrels *Numenius phaeopus* in
912 South Africa. *Ibis (Lond. 1859)*. 135, 156–165. doi:10.1111/j.1474-919X.1993.tb02827.x
- 913 Van der Wal, D., Wielemaker-van den Dool, A., Herman, P.M.J., 2010. Spatial synchrony in intertidal
914 benthic algal biomass in temperate coastal and estuarine ecosystems. *Ecosystems* 13, 338–351.
- 915 Warwick, R.M., Goss-Custard, J.D., Kirby, R., George, C.L., Pope, N.D., Rowden, A.A., 1991. Static and
916 dynamic environmental factors determining the community structure of estuarine
917 macrobenthos in SW Britain: why is the Severn estuary different? *J. Appl. Ecol.* 28, 329–345.
- 918 Warwick, R.M., Somerfield, P.J., 2010. The structure and functioning of the benthic macrofauna of
919 the Bristol channel and Severn estuary, with predicted effects of a tidal barrage. *Mar. Pollut.*
920 *Bull.* 61, 92–99. doi:10.1016/j.marpolbul.2009.12.016

- 921 Wilson, W.H., Parker, K., 1996. The life history of the amphipod, *Corophium volutator*: The effects of
922 temperature and shorebird predation. *J. Exp. Mar. Bio. Ecol.* 196, 239–250. doi:10.1016/0022-
923 0981(95)00133-6
- 924 World Nuclear Association, 2015. Information Library [WWW Document]. World Energy Needs Nucl.
925 Power. URL [http://www.world-nuclear.org/info/Current-and-Future-Generation/World-](http://www.world-nuclear.org/info/Current-and-Future-Generation/World-Energy-Needs-and-Nuclear-Power/)
926 [Energy-Needs-and-Nuclear-Power/](http://www.world-nuclear.org/info/Current-and-Future-Generation/World-Energy-Needs-and-Nuclear-Power/)
- 927 Zwarts, L., Blomert, A.M., 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica*
928 when six prey species are available. *Mar. Ecol. Prog. Ser.* 83, 113–128.
929 doi:10.3354/meps083113
- 930 Zwarts, L., Wanink, J., 1993. How the food supply harvestable by waders in the Wadden Sea depends
931 on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-
932 flat invertebrates. *Netherlands J. Sea Res.* 31, 441–476.
- 933

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

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

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944 **Table 2.** Modelled decrease in density and individual energetic value of group resources throughout
 945 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%

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

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

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953 **Table 4.**

954 (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

955 (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	✓	✓

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959

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

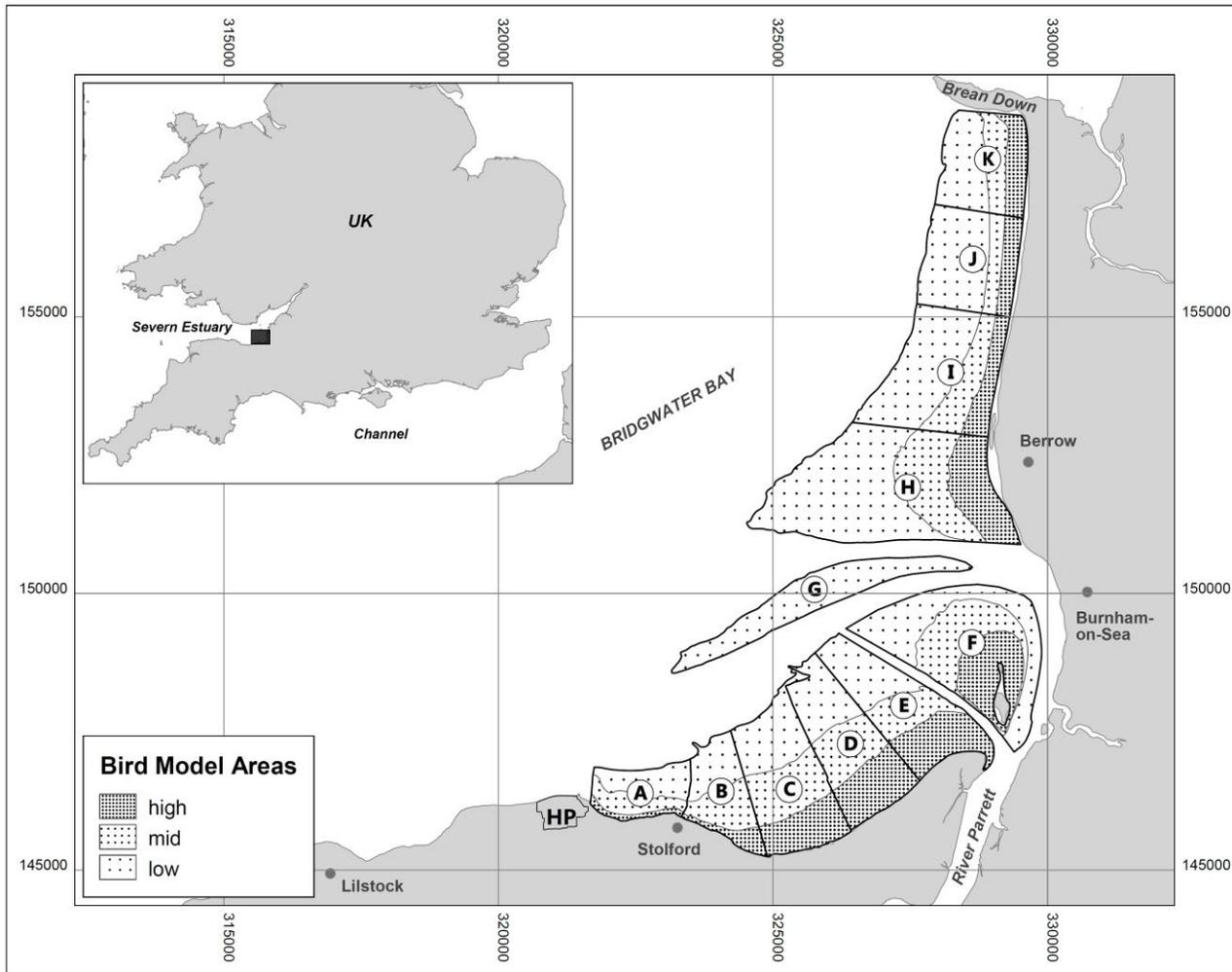
Scenario	Decrease in <i>M. balthica</i> energy content (%)	
	Stert Flats	Berrow Flats
A – Current conditions	0	0
B	9	3
C	50	10
D	50	20

962

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

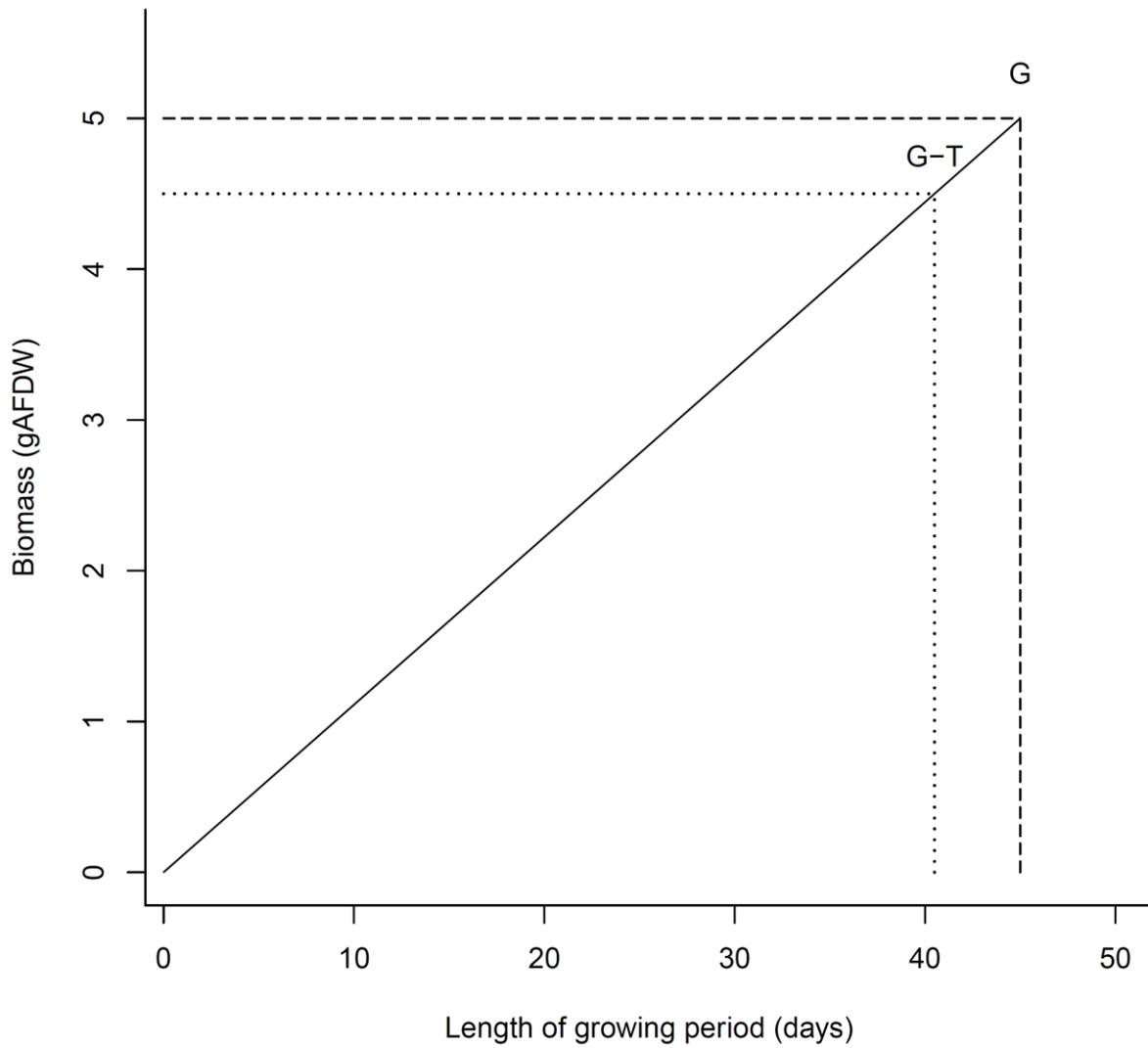
Forager	Resources (gAFDW/m ²)	Survival (%)	Body condition (%)
Dunlin	7.79	100	99.9
Ringed plover	5.80	100	98.5
Turnstone	8.71	100	99.2
Knot	5.92	100	99.08
Redshank	8.71	100	99.29
Grey plover	6.84	100	99.17
Black-tailed godwit	3.79	100	99.9
Oystercatcher	8.35	90.64	91.76
Curlew	3.79	64.7	73.31
Shelduck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

965



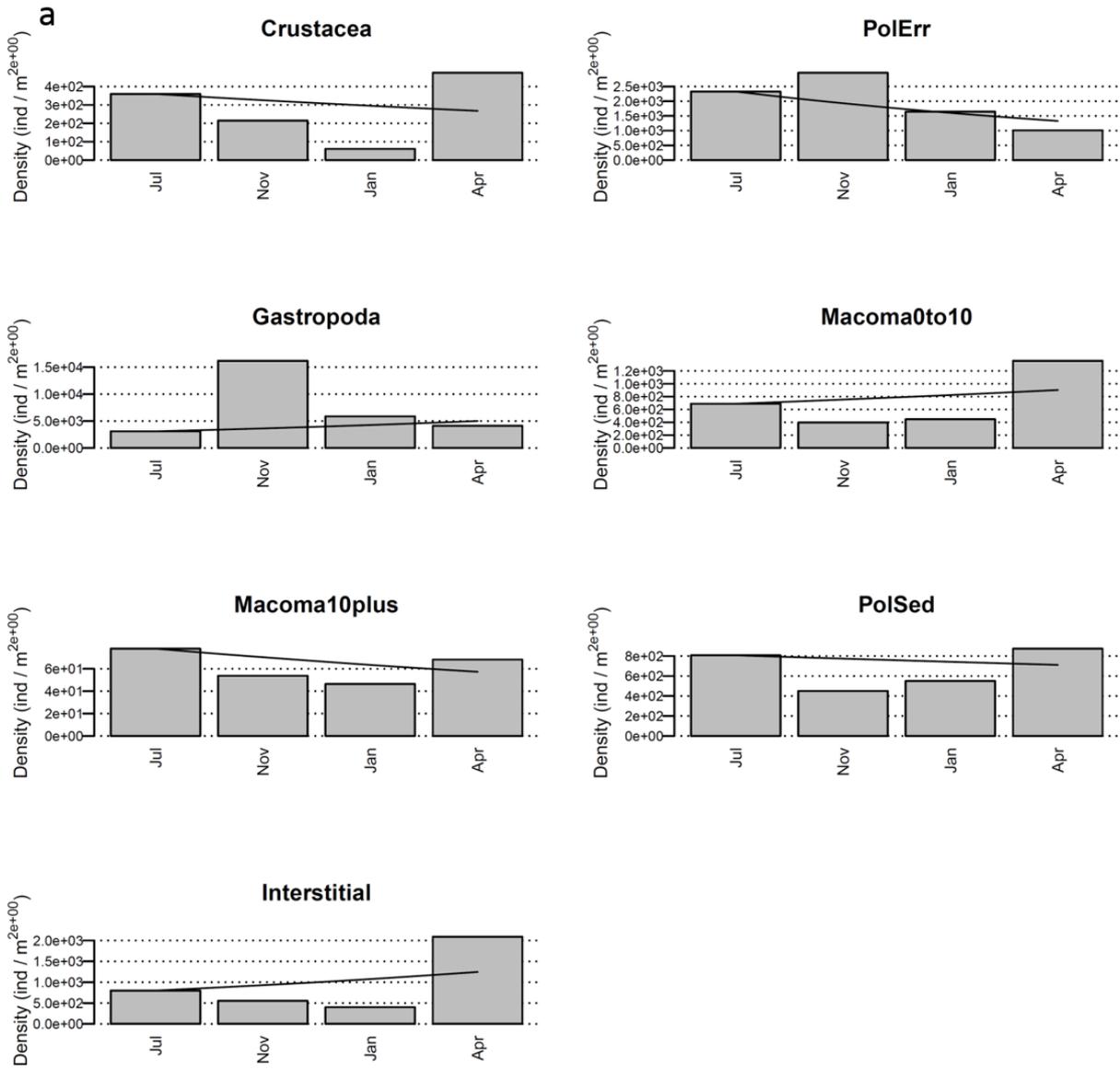
967

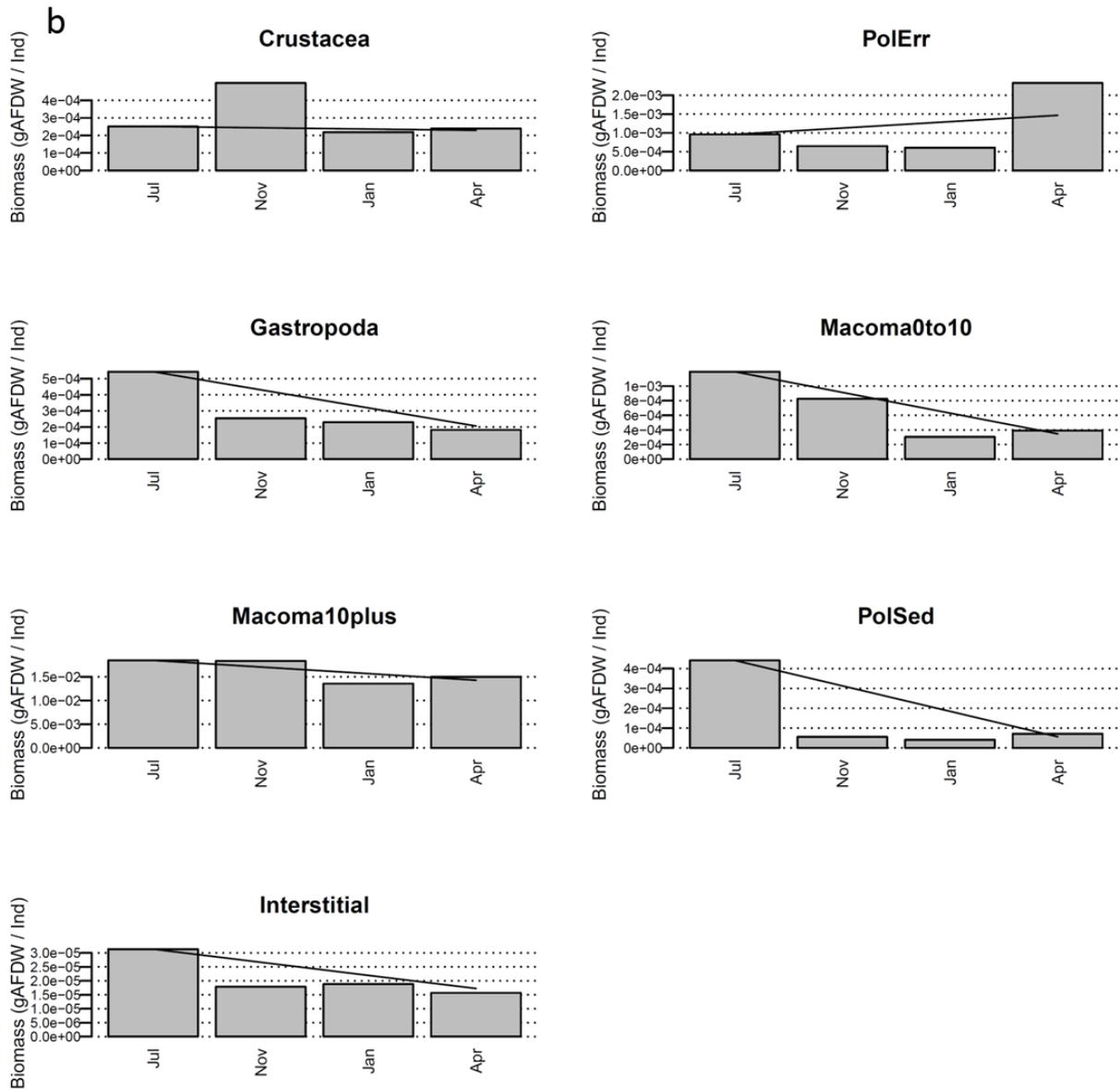
968 **Figure 1.** Bridgwater Bay and the 16 feeding patches defined by the combination of profile zones based on benthic invertebrates data (e.g. A, B) and broadly
 969 shore-parallel divisions based on tidal elevation areas (High, Mid, Low). Stert flats: Profile zones from A to F; Berrow flats: Profile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



971

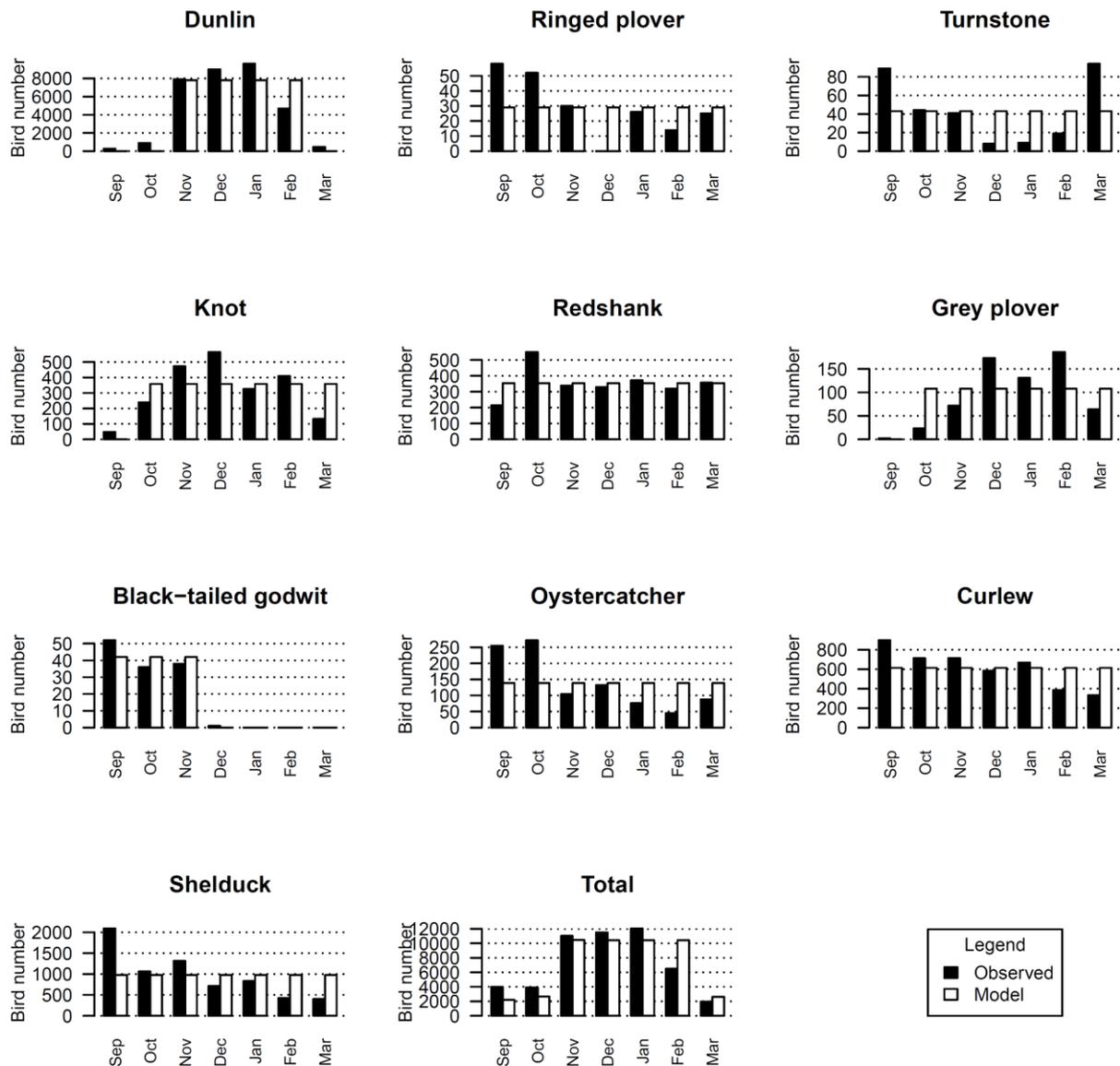
972 **Figure 2.** Conceptual diagram of the effects of increased seawater temperature on biomass accrual
 973 by *Macoma balthica*. AFDW: ash-free dry weight; G: dashed line: growth period in current
 974 conditions; G-T: dotted line: growth period shortened by an extra thermal pressure. Calculations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





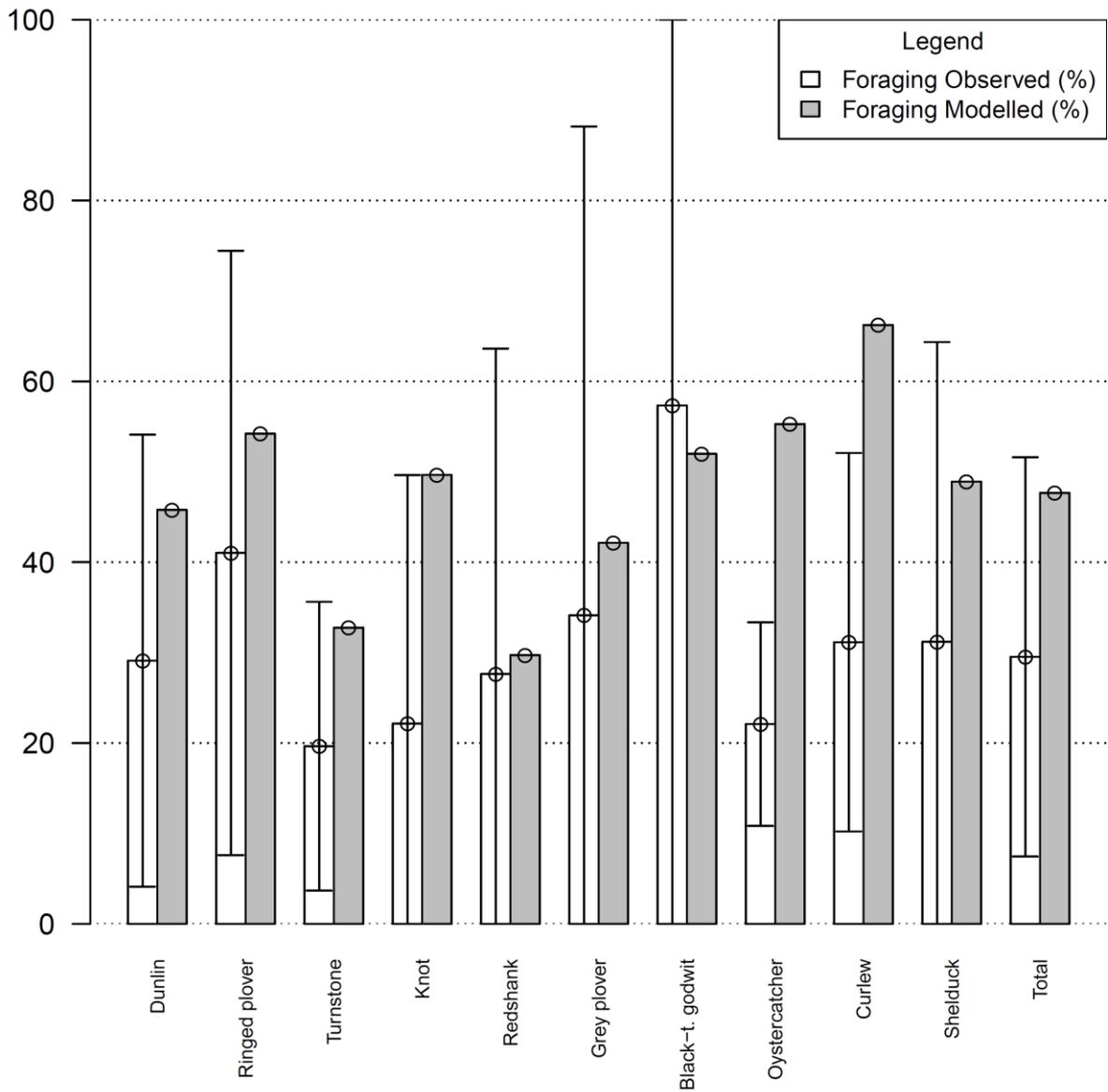
977

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



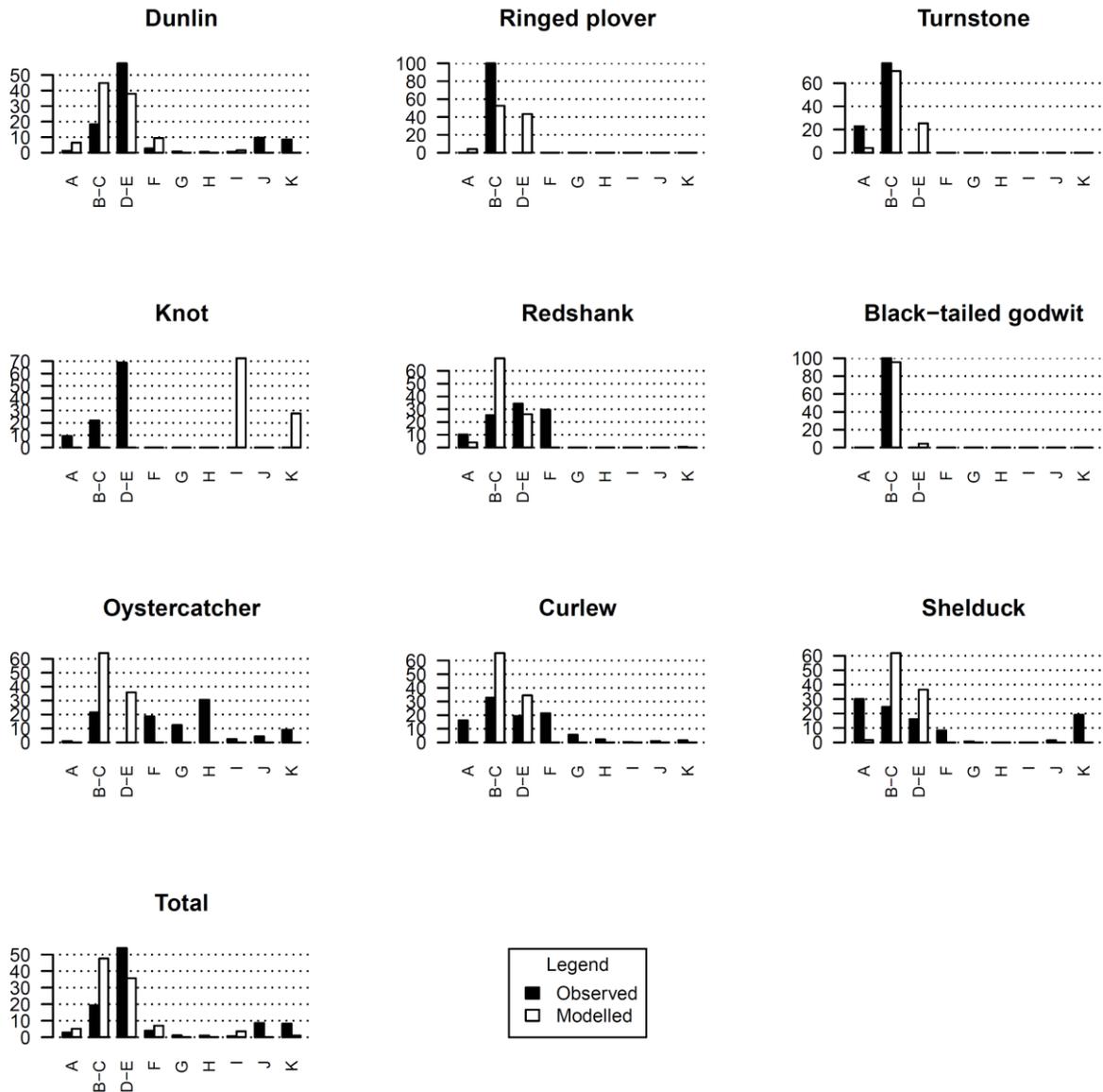
982

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



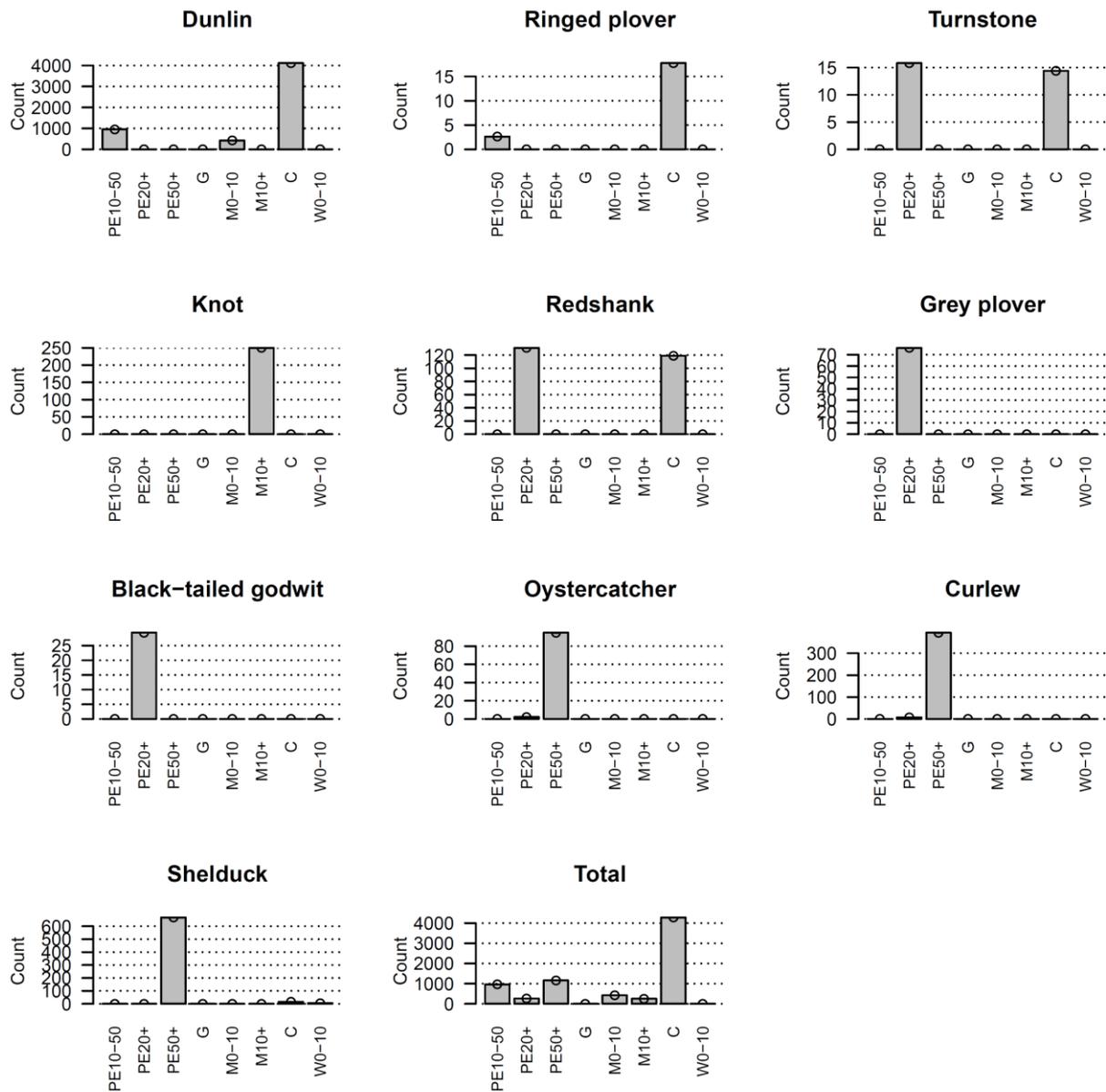
986

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



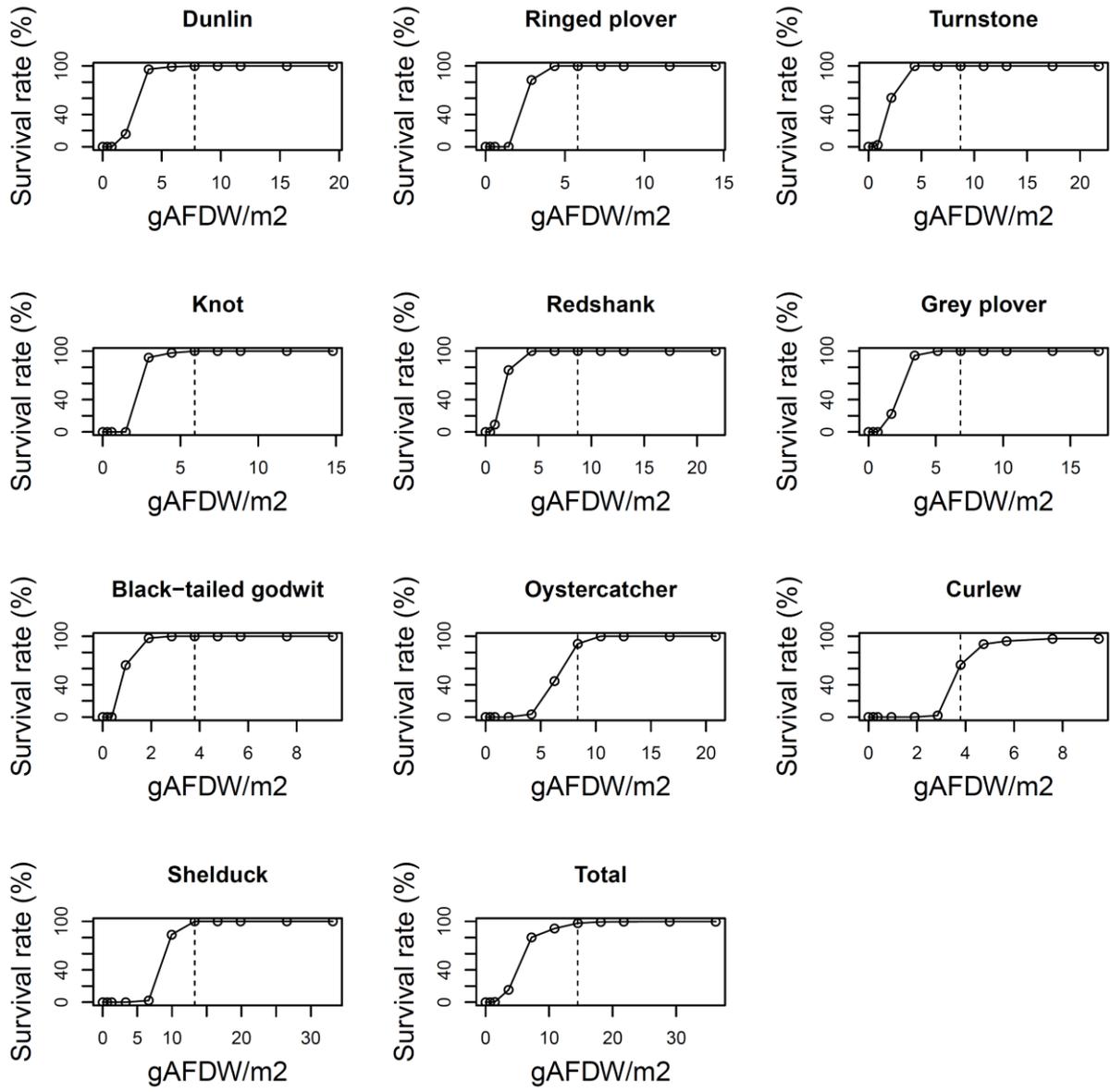
988

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



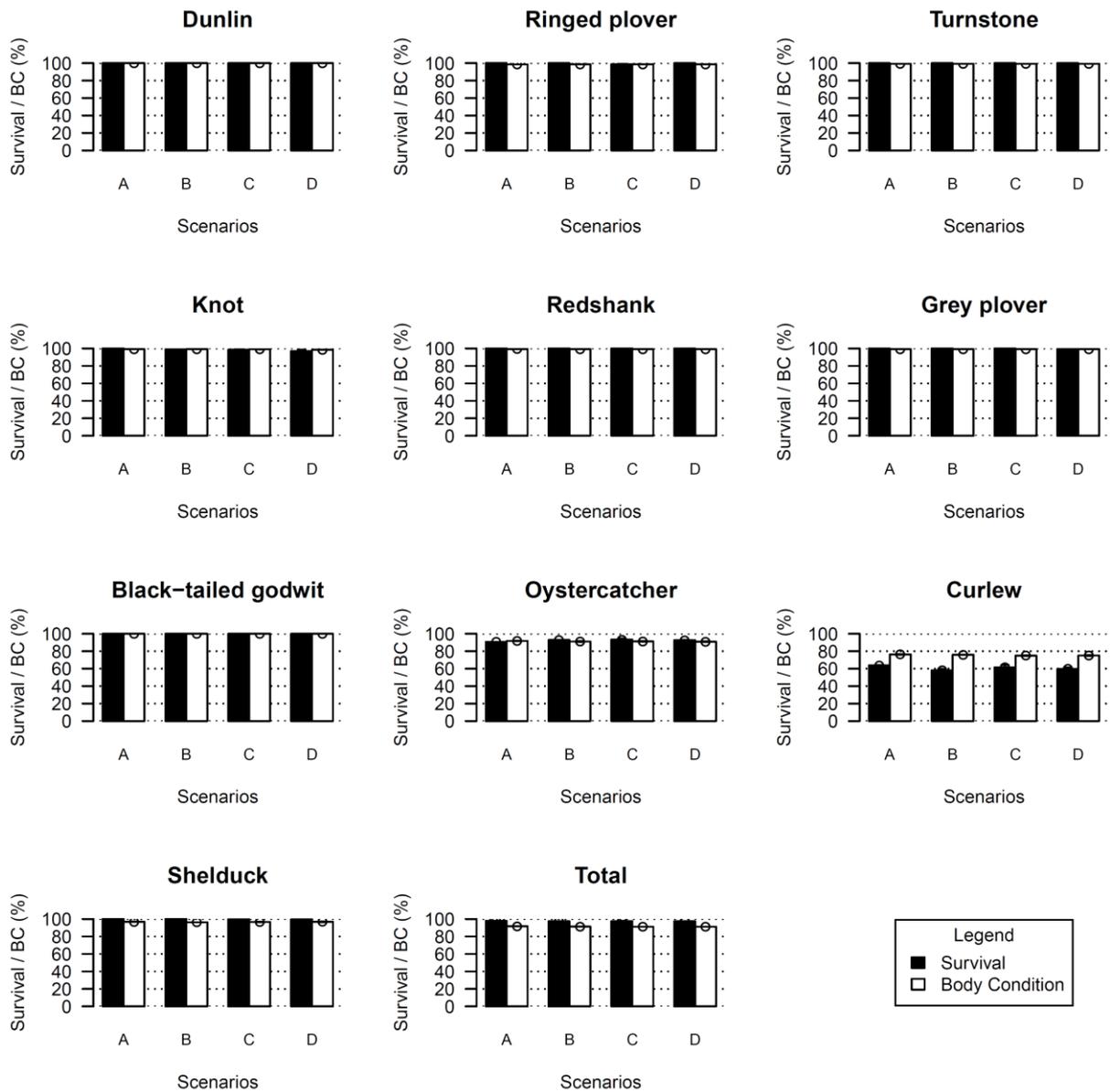
991

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



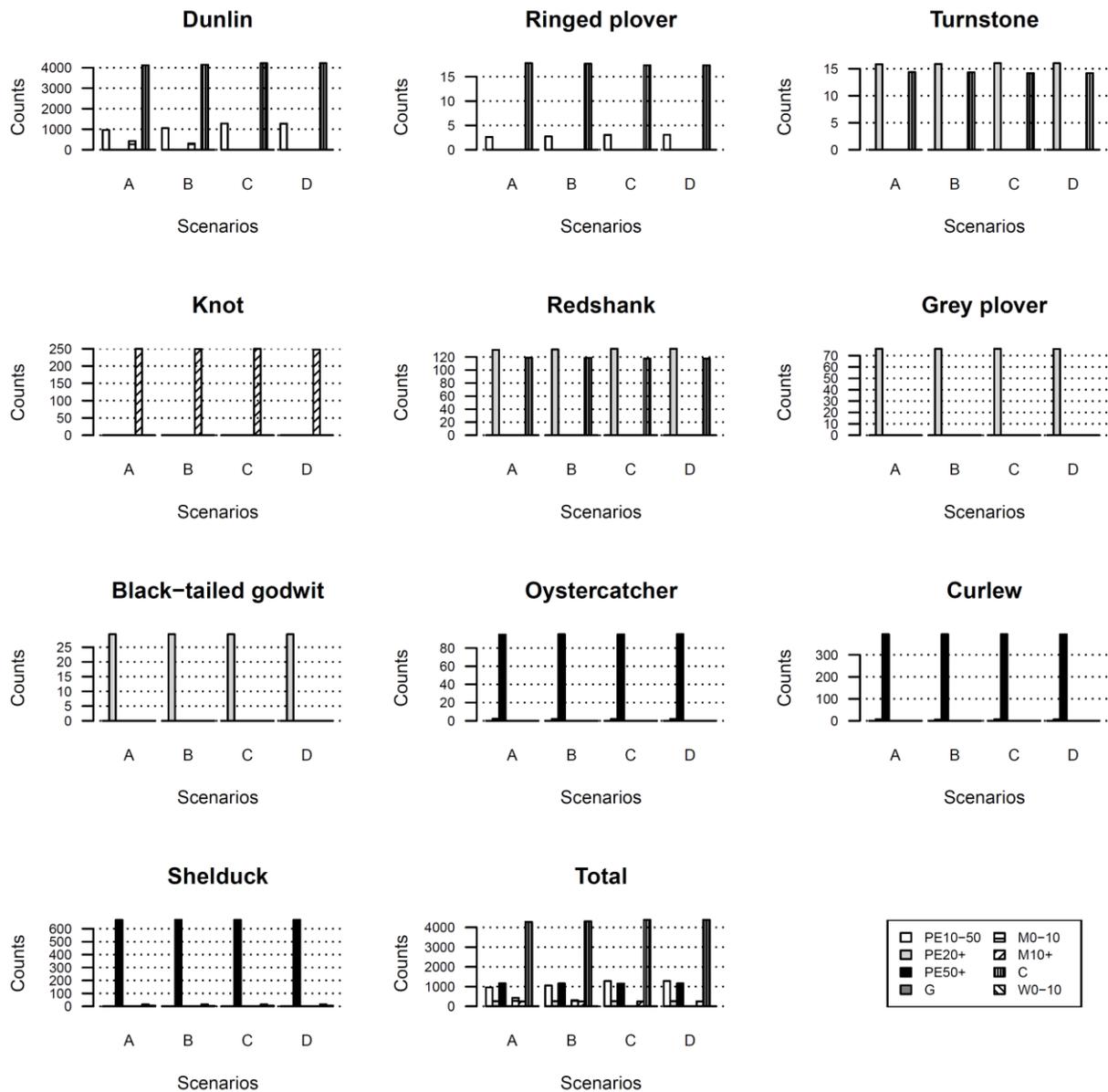
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997 **Figure 8.** Predicted effects of change in prey biomass densities on overwinter survival rate of the
 998 selected bird species in Bridgwater Bay (in percentages). The vertical dashed line represents the
 999 actual prey biomass density values.



1000

1001 **Figure 9.** Predicted annual survival rate and body condition change (in percentages) of the selected
 1002 birds under three scenarios of decrease in *M. balthica* energy content on Stert flats and Berrow flats
 1003 respectively (in %). A: current (reference) conditions, B: 9% and 3%, C: 50% and 10% and D: 50% and
 1004 20%.



1005

1006 **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
 1007 to the reference condition A. A: current (reference) conditions, B: 9% and 3%, C: 50% and 10% and
 1008 D: 50% and 20%.

1009

1010

1011 GLOSSARY

1012 Cascade (secondary) effects: The effects of species depletion (or loss) on subsequent depletion (or
1013 loss) of additional species.

1014 Diet (MORPH): Collection of one or more resources from a patch consumed simultaneously by a
1015 forager.

1016 Forager (MORPH): Animal which forage within the system consuming diets and assimilating energy.
1017 Here the foragers are the nine species of shorebird and the wildfowl.

1018 Global environment (MORPH): State variables which apply throughout the modelled system.

1019 Overwintering: Process by which some organisms pass through or wait out the winter season (or the
1020 period of the year) when winter-like conditions make normal activities and survival difficult.

1021 Patch (MORPH): Locations with local, patch-specific state variables containing resources and
1022 foragers.

1023 Resource (MORPH): The food consumed by the foragers.

1024 Shorebird/Wader: Bird species members of the Charadriiformes order that includes plovers,
1025 sandpipers, godwit or curlews; excluding the more marine web-footed seabird group (gulls). They
1026 are a group of various ground-nesting bird of small to moderate size that live near the water.

1027 Wildfowl: Bird species members of the Anatidae family that includes ducks, geese and swans. These
1028 birds are adapted for swimming, floating on the surface, and in some cases diving in shallow water.

1029 APPENDIX

1030 **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
1031 British National Grid (Ordnance 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	Flo	<-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	Blo	<-1	806393	23	Hlo	<-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	Ilo	<-1	2671851
11	Dhigh	1 – 5	1216332	27	Jhigh	1 – 5	524879
12	Dmid	-1 – 1	1046195	28	Jmid	-1 – 1	459288
13	Dlo	<-1	1154361	29	Jlo	<-1	2107134
14	Ehigh	1 – 5	1272711	30	Khigh	1 – 5	684267
15	Emid	-1 – 1	857551	31	Kmid	-1 – 1	664495
16	Elo	<-1	1267852	32	Klo	<-1	1374216

1032 **Appendix B.** List of the benthic species from the 2010 - 2011 surveys included in the functional
 1033 resource groups.

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

1034

1035 **Appendix C.** Resources per patch (individuals per m²) and by ash-free dry weight (g per individual) (* denotes groups with added microphytobenthic
1036 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

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

1039 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				

1040 **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)

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1042 **Appendix E.** Night-time foraging efficiency coefficient used in the model, *information found in the
 1043 literature.

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

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1045 **Appendix F.** Bird size in relation to their favourite size-class preys.

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

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1047 **Appendix G.** Appendix References

1048 Dit Durell, S.E.A.L. V., Stillman, R.A., Caldow, R.W.G., McGrorty, S., West, A.D., Humphreys, J., 2006.
 1049 Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour,
 1050 UK. *Biol. Conserv.* 131, 459–473. doi:10.1016/j.biocon.2006.02.022

1051 Kersten, M., Visser, W., 1996. The rate of food processing in the oystercatcher: food intake and
 1052 energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* 10, 440–448.

1053 Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem.*
 1054 *Physiol.* 75, 1–3.

1055 Nagy, K.A., Girard, I.A., Brown, T.K., 1999. Energetics of free-ranging mammals, reptiles, and birds.
 1056 *Annu. Rev. Nutr.* 19, 247–277. doi:10.1146/annurev.nutr.19.1.247

1057 Stillman, R.A., Caldow, R.W.G., Alexander, M.J., 2000. Individual variation in intake rate : the relative
 1058 importance of foraging efficiency and dominance. *J. Anim. Ecol.* 69, 484–493.

1059 Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G., Triplet, P., 2002.
 1060 Predicting the strength of interference more quickly using behaviour-based models. *J. Anim.*
 1061 *Ecol.* 71, 532–541. doi:10.1046/j.1365-2656.2002.00621.x

1062 Stillman, R.A., West, A.D., Goss-Custard, J.D., McGrorty, S., Frost, N.J., Morrissey, D.J., Kenny, A.J.,
 1063 Drewitt, A.L., 2005. Predicting site quality for shorebird communities: A case study on the
 1064 Humber estuary, UK. *Mar. Ecol. Prog. Ser.* 305, 203–217. doi:10.3354/meps305203

1065 Triplet, P., Stillman, R.A., Goss-Custard, J.D., 1999. Prey abundance and the strength of interference
 1066 in a foraging shorebird. *J. Anim. Ecol.* 68, 254–265. doi:10.1046/j.1365-2656.1999.00280.x

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