

This is a repository copy of Modelling the impact of tidal range energy on species communities.

White Rose Research Online URL for this paper: https://eprints.whiterose.ac.uk/163783/

Version: Accepted Version

## Article:

Baker, Amy L., Craighead, Robert M., Jarvis, Emma J. et al. (6 more authors) (2020) Modelling the impact of tidal range energy on species communities. Ocean and Coastal Management. 105221. ISSN 0964-5691

https://doi.org/10.1016/j.ocecoaman.2020.105221

## Reuse

This article is distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs (CC BY-NC-ND) licence. This licence only allows you to download this work and share it with others as long as you credit the authors, but you can't change the article in any way or use it commercially. More information and the full terms of the licence here: https://creativecommons.org/licenses/

# Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



# . Modelling the impact of tidal range energy on species communities

- 2 Amy L. Baker<sup>a</sup>, Robert M. Craighead<sup>a</sup>, Emma J. Jarvis<sup>a</sup>, Harriett C. Stenton<sup>a</sup>,
- 3 Athanasios Angeloudis<sup>b</sup>, Lucas Mackie<sup>c</sup>, Alexandros Avdis<sup>c</sup>, Matthew D. Piggott<sup>c</sup> and
- 4 Jon Hill<sup>a,\*</sup>

18

12

13

14

15 16

17

18

19

20

21

25

26

28

29

30

31

32

35

38

39

40

41

45

46

50

- <sup>a</sup>Department of Environment and Geography, University of York, UK
- bSchool of Engineering, Institute for Infrastructure & Environment, University of Edinburgh, UK
- <sup>7</sup> CDepartment of Earth Science and Engineering, Imperial College London, UK.

## ARTICLE INFO

## Keywords: tidal energy environmental impacts modelling

#### ABSTRACT

Tidal energy has the potential to form a key component of the energy production in a number of countries, including the UK. Nonetheless, the deployment of tidal energy systems is associated with potential environmental impacts as prime resource sites often coincide with unique ecosystems inhabited by sensitive organisms. Previous studies have generally focused on the hydrodynamic impact of tidal energy schemes, i.e. how schemes alter the flow dynamics and sedimentary transport processes. Whilst these efforts are key in understanding environmental impacts, there is no straightforward step for translating sediment to faunal changes. Species distribution models offer methods to quantitatively predict certain possible impacts of tidal energy extraction. The River Severn is a distinguished candidate region for tidal energy in the UK featuring sites under stringent ecological protection regulations. We examine the impact of a proposed Severn tidal barrage on 14 species via the linking of hydrodynamic modelling to species distribution models. Through a selection of species that are linked via a simple food web system we extrapolate changes in prey species to the respective predator species. We show that species at lower trophic levels would be adversely affected by the barrage, but higher trophic level organisms increase in possible habitable area. Once food web relationships are acknowledged this increase in habitat area decreases, but is still net positive. Overall, all 14 species were affected, with most gaining in distribution area, and only four losing distribution area within the Severn Estuary. We conclude that a large-scale tidal barrage may have detrimental and complex impacts on species distribution, altering food web dynamics and altering food availability in the Severn Estuary. The methodology outlined herein can be transferred to the assessment and optimisation of prospective projects globally to aide in the sustainable introduction of the technology.

# 1. Introduction

Marine renewable energy systems have been in the industry spotlight by investors and developers (Borthwick, 2016) due to incentives facilitating methods of producing carbon free energy. This is motivated by international commitments to mitigate anthropogenic climate change (Shields et al., 2011). In 2015, the United Nations Framework Convention on Climate Change (UNFCCC) adopted the Paris Agreement. As a consequence, the UK declared the country would make changes to contain global temperature increase at 2°C, whilst pursuing efforts to limit the increase to below 1.5 °C (Anderson and Peters, 2016). Tidal-based marine renewable energy systems are highly attractive in the UK as the country has one of the largest marine energy resources in the world (Neill et al., 2018) and represents approximately 50% of Europe's total tidal capacity (Greenmatch, 2017).

The use of tidal renewable energy systems can affect tidal patterns in the far-field, i.e. at relatively large distances from the site where energy is produced, and therefore a comprehensive assessment on the ecological impacts is necessary (du Feu et al., 2017). Most forms of tidal energy that include the use of marine energy technologies placed in the water will have an effect on the marine environment and by extension the surrounding ecosystem. Tidal technologies affect the currents, waves and sediment dynamics of an estuary and therefore have an impact on benthic species living in both the sediment and the water column (Frid et al., 2012). Furthermore, a multitude of hydrodynamic parameters are influenced by the introduction of a tidal energy system, such as sediment transport, salinity, and concentration of dissolved oxygen as summarised in the review of Kadiri et al. (2012).

 $ORCID(s); \ 0000-0001-5021-3643 \ (A.\ Angeloudis); \ 0000-0002-2695-3358 \ (A.\ Avdis); \ 0000-0002-7526-6853 \ (M.D.\ Piggott); \ 0000-0003-1340-4373 \ (J.\ Hill)$ 

<sup>\*</sup>Corresponding author

ion.hill@york.ac.uk(J. Hill)

The scale and lifetime of the renewable energy technology and the surrounding marine environment are controlling factors on the extent of these impacts (El-Geziry et al., 2009). Previous studies regarding tidal range energy have generally focused on hydrodynamic impacts (Neill et al., 2009; Xia et al., 2010a; Martin-Short et al., 2015) and resource interactions (Lewis et al., 2017), extending to the quantification of suspended sediment transport flux changes (Gill, 2005; Shields et al., 2011; Falconer et al., 2018). A recent study by du Feu et al. (2019) employed simplified ecological modelling coupled to an adjoint optimisation solver to explore the interplay between maximising power and reducing environmental impact, concentrating on bed shear stress as a driver of environmental impact. Nevertheless, to-date there has been little research on the impacts tidal energy systems could have on food web dynamics by accounting for the changes in trophic links within an environment, although it is know food web are sensitive to environmental changes (de Jonge et al., 2019a; de Jonge and Schückel, 2019). This is also an aspect that can be carried out via ecological modelling.

Ecological modelling is a vital tool to assess potential effects of environmental changes on organisms in an area of interest. A number of methods, including habitat suitability modelling, climate envelope modelling, and species distribution modelling (SDM) can be used (Lobo et al., 2010). SDM has been frequently used to obtain either the realised or potential distribution of a species, and has become commonplace in biogeography and biodiversity research over the last 20 years (Lobo et al., 2010; Araújo and Guisan, 2006). SDM can thus provide a way of predicting the impact tidal energy systems may have on a range of species based on environmental layers provided by hydrodynamic models. SDM explores the dynamic relationship between the geographical occurrence rate of species and corresponding environmental variables (Naimi and Araújo, 2016) and offers a means to numerically predict the future distribution of a species. The two prominent approaches to SDM are either modelling species individually or modelling community information (Hallstan et al., 2012). Studies have shown that modelling species individually generally gives higher predictive accuracy (Hallstan, 2011). In the marine realm SDM are less well used as there are particular issues with accounting for feeding and ontological changes (Robinson et al., 2011). We attempt to address the first of these in this work.

The Bristol Channel and the Severn Estuary have been the focus of a number of tidal energy proposals, with a recent one being a pilot (or pathfinder) scale tidal lagoon in the Swansea Bay area (TLP, 2017). Due to the unique and sensitive nature of the Severn Estuary, construction of a tidal energy system would need to be carefully designed and constructed to minimise impact on these unique habitats (Angeloudis and Falconer, 2017). The scale of the impact depends on the habitat from which the tidal energy is extracted and hence ecological impact assessments have to be site-specific. Here, we configure hydrodynamic models of the Severn Estuary and assess the impact of a Severn Barrage design. We then demonstrate a methodology for assessing the potential ecological impacts of such marine infrastructure. We initially employ the hydrodynamic model outputs to construct a set of environment layers which are fed into an SDM model of the Bristol Channel and Severn Estuary. We sequentially examine changes in the distribution of 14 species which can be linked in a simple food web and examine if accounting for trophic links exacerbates or lessens the predicted impacts.

#### 1.1. The Severn Estuary

The Severn Estuary represents a unique environment across England and Wales, featuring one of the largest coastal plains in the country (Potts and Swaby, 1993; Kirby and Parker, 1983). The inner Severn Estuary hosts the second highest tidal range in the world (~14m) (Bird, 2008), amplified by tidal resonance effects attributed to the estuarine geometry. This tidal range encompasses a substantial amount of marine energy in the transition between low and high tides. The estuary has a wide variety of environments which include littoral mudflats, sublittoral sand banks, and gravel/muddy areas. Due to the vast assortment of conditions the estuary has been designated a Ramsar site (wetland site of international importance), Special Protected Area (SPA) and Special Areas of Conservation (SAC) site, to securely protect the environment for key species (Natural England & the Countryside Council for Wales, 2009). The wide array of habitats provide vital nurseries, feeding and breeding grounds for adult and juveniles of the 111 listed fish species inhabiting the estuary, which makes it one of the most diverse ecosystems in the UK (Henderson and Bird, 2010).

The potential of tidal energy technologies in the Severn can be demonstrated by the multiple high profile projects under investigation Neill et al. (2018), including designs for a Severn Barrage that could individually deliver 5-10% of the country's electricity needs Baker (1987). Consecutive proposals for barrage variants in the Severn Estuary were dismissed and denied planning permission, due in part to environmental concerns and economic challenges as with similar schemes worldwide. The latest breakthrough in the industry was delivered through the tidal lagoon concept and

in particular the 320 MW Swansea Bay tidal lagoon proposal TLP (2017), which aimed to balance project economics and environmental concerns by proposing an artificial lagoon pilot scheme in the Swansea Bay area within the Bristol Channel. The most recent UK Government review by Hendry (2017) was supportive of the tidal lagoon technology highlighting how a Swansea Bay based pathfinder project would be followed by a series of complementary larger projects in the Severn Estuary and the Irish Sea. Contrary to the findings of the technical review, the UK Government proceeded in 2018 to dismiss the Swansea Bay tidal lagoon proposal questioning its value, citing nuclear and offshore wind options as more competitive TLP (2018).

The environmental factors at play in the Severn Estuary, such as the large tidal range and the wide variety of species, make it an ideal research site for examining the potential effect of a tidal range structures on the distribution of native species. To do this we employ the classical case study of the Severn Tidal Power Group (STPG) scheme for a Cardiff-Weston barrage, which is one of the largest tidal power proposals ever considered (Neill et al., 2018). The proposed tidal barrage spans ~16 km from Lavernock Point to Brean Down and encloses an area of ~573 km². More information on the particular scheme has been extensively reported in the literature, particularly with regards to the assessment of the potential energy output (Xia et al., 2012), hydrodynamic impacts (Xia et al., 2010b; Zhou et al., 2014; Bray et al., 2016; Falconer et al., 2018) and the development of numerical models that are tailored to the particular application, e.g. Angeloudis et al. (2016a).

# 2. Methodology

In quantifying the potential ecological impact of the proposed tidal barrage on species in the Severn Estuary, the spatial distribution of 14 indicative species were selected on the basis of a range of habitat types and modes of life, but are interconnected via a relatively simple food web. Changes in hydrodynamics induced by the introduction of a barrage were calculated using a nonlinear shallow water equation based tidal model, *Thetis*, and were processed to form several environmental layers for the Severn Estuary. SDM was used to predict the present day and future distribution of species in the presence of a tidal barrage. Statistical analysis further assessed the change in species distribution before and after the installation of the tidal barrage, thus quantifying the ecological impact.

## 2.1. Modelled Species

The species modelled are summarised in Table 1, and are linked together through the food web system shown in Fig. 1, which illustrates their inter-dependencies as food sources. This research analysed 14 species that comprise a complex food web which shows different tiered relationships, but yet remains manageable to model and analyse. Thus the approach ensures that the potential effect marine renewable energy systems may inflict on a food web system is highlighted. The species data used in this study were derived from an online database, the National Biodiversity Network (https://NBNatlas.org), that collects location data for multiple species across the UK. All species were chosen to have a minimum of 50 data entries within the area of interest.

## 2.2. Coastal ocean modelling

Numerical models that simulate coastal ocean processes can be used to predict the altered hydrodynamics caused by the introduction of marine infrastructure. In this case we employ *Thetis* (Kärnä et al., 2018), a (2-D and 3-D) flow solver for simulating coastal and estuarine flows (Angeloudis et al., 2018; Pan et al., 2019; Vouriot et al., 2019), implemented using the *Firedrake* finite element Partial Differential Equation (PDE) solver framework (Rathgeber et al., 2016). For this work *Thetis* is configured to solve the nonlinear shallow water equations in non-conservative form:

$$\frac{\partial \eta}{\partial t} + \nabla \cdot (H_d \mathbf{u}) = 0, \tag{1}$$

$$\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} - \nu \nabla^2 \mathbf{u} + f \mathbf{u}^{\perp} + g \nabla \eta = -\frac{\tau_b}{\rho H_d},\tag{2}$$

where  $\eta$  is the water elevation relative to a fixed datum,  $H_d$  is the total water depth,  $\nu$  is the kinematic viscosity of the fluid, and  $\mathbf{u}$  is the depth-averaged velocity vector. The Coriolis term is represented as  $f\mathbf{u}^{\perp}$ , where  $\mathbf{u}^{\perp}$  the velocity vector rotated counter-clockwise over  $90^{\circ}$ . In turn,  $f = 2\Omega \sin \zeta$  with  $\Omega$  corresponding to the angular frequency of the

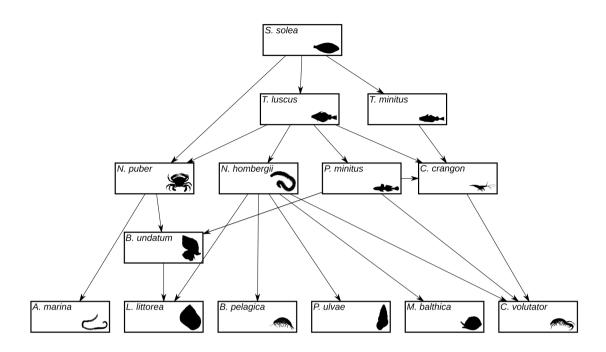


Figure 1: Food web of the 14 species modelled, which shows the tiered relationships that are assessed.

Earth's rotation, and  $\zeta$  the latitude. Bed shear stress  $(\tau_b)$  effects are represented through the Manning's n formulation as:

$$\frac{\tau_b}{\rho} = gn^2 \frac{|\mathbf{u}|\mathbf{u}}{H_d^{\frac{1}{3}}}.$$
(3)

where n is the Manning's friction coefficient. Intertidal wetting and drying processes are represented according to the formulation of Kärnä et al. (2011). The model is implemented using a discontinuous Galerkin finite element discretisation (DG-FEM), using the  $P_{1DG}-P_{1DG}$  velocity-pressure finite element pair. A semi-implicit Crank-Nicolson timestepping approach is applied for temporal discretisation with a constant timestep of  $\Delta t = 100$  s. Finally, the discretised equations are solved using a Newton nonlinear solver algorithm via the PETSc library (Balay et al., 2016).

The *Thetis* setup stems from preceding research on tidal power plant assessments (Angeloudis et al., 2018; Harcourt et al., 2019). The computational domain was extended from the confines of the Bristol channel that are normally used for the assessment of more smaller tidal lagoon schemes. This expansion was deemed essential given the scale and expected impacts of a Severn Barrage. Notably, earlier studies have extended the domain even further, and up to the continental shelf (Zhou et al., 2014) with room for more sensitivity analyses to be performed in resolving the open boundary problem for varying designs. The computational mesh was generated following an unstructured meshing methodology using *qmesh* and *Gmsh* (Geuzaine and Remacle, 2009) as described in Avdis et al. (2018). The domain's extent and discretisation are illustrated in Fig. 2 for completeness.

The simulated periods spanned a month (6/5/2003 to 6/6/2003) following a preliminary 5-day spin-up period that ensured independence of the predictions from the model's initial equilibrium conditions. Hydrodynamics were forced at the seaward boundaries through weakly imposed elevation boundaries based on the leading eight constituents from the TPXO tidal harmonic database (Egbert and Erofeeva, 2002), together with average flux boundaries at inland bound-

149

150

152

154

155

156

157

161

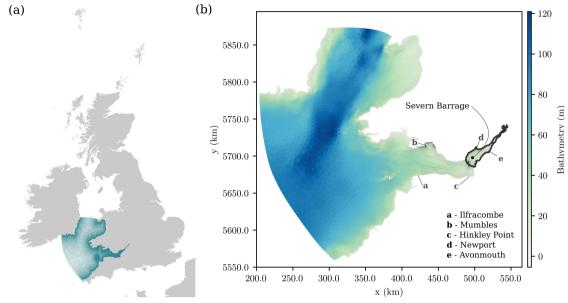


Figure 2: (a) Superimposed coastal model domain relative to the UK and (b) coastal model bathymetry interpolated from the dataset of (Edina Digimap Service, 2014) featuring an 1 arc-second resolution (~30 m). The coordinates above are based on a UTM zone 30N projection (spatial reference EPSG:32630). Adapted from Angeloudis (2019). Numbers indicate locations mentioned in the main text: 1. Swansea Bay, 2. Carmarthen Bay, 3. Devon coastline.

aries representing significant river inflows as per the UK National River Flow Archive. A Manning's number of n = 0.018 s/m<sup>1/3</sup> was imposed across the domain with more details on the validation of the extended domain reported in Angeloudis (2019) and omitted here for brevity.

## 2.3. Tidal power plant modelling

Tidal range energy refers to the potential energy contained in the transition of the water height between low and high tides. A tidal power plant regulates the operation of turbines and sluice gates to facilitate a head difference H across its two sides, defined as the difference between the inner ( $\eta_i$ ) and the outer water ( $\eta_o$ ) levels at the location of the turbines. There are varying strategies for the operation of tidal power plants (Bernshtein, 1961; Burrows et al., 2009), with a bidirectional operation with/without pumping intervals being the preferred options for most current proposals. This is due to advantages relating to the enhanced power output, wider distribution of power and reduced environmental impacts (Waters and Aggidis, 2016). Here, no pumping is performed in the hydrodynamic model for simplicity, but energy is generated on both the ebb and flood cycles. Fig. 3 summarises the operation for the Severn Barrage modelled in this study, that featured a capacity of 8640 MW and a cross-sectional surface area of 35000  $m^2$  consistent with previous modelling studies Xia et al. (2010a); Falconer et al. (2009). The representation of the tidal power plant within the *Thetis* hydrodynamics solver was implemented through a domain decomposition methodology detailed in Angeloudis et al. (2016b, 2018).

# 2.4. Species Distribution Modelling

Species Distribution Modelling can be carried using a number of algorithms. Here, we use Maximum Entropy (hereby MaxEnt), a geospatial machine learning method, to predict the distribution of species using environmental indicators and species occurrence points (Phillips and Dudik, 2008). MaxEnt operates by assessing the probability of the distribution of a species, based on data input into the model via environmental layers/variables (Merow et al., 2013). The modelled distribution is produced as a raster, with model predictions based on the probability of a species occurring in a particular grid cell, which is dependent on the environmental variables used as input to the MaxEnt model. MaxEnt is an accessible and reliable method of modelling the distribution of multiple species while using presence-only data (Yackulic et al., 2013). It has been used across a range of previous studies covering a range of taxa, including: least killifish (Bagley et al., 2013), desert mistletoe (Lira-Noriega et al., 2013), and seaweed meadows

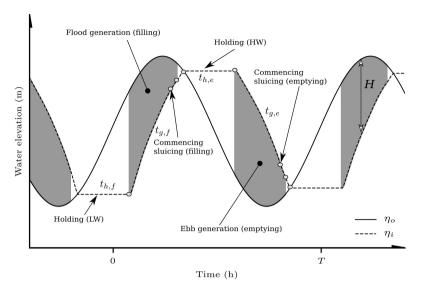


Figure 3: Two-way operation schematic for a conventional tidal power plant over an M2 tidal period T=12.42h, illustrating typical modes of operation. The grey shaded areas indicate periods when power is generated.  $t_{h,e}, t_{h,f}, t_{g,e}, t_{g_f}$  comprise operational controls used in the algorithm presented in Angeloudis et al. (2018) for a two-way operation sequence. For the generic "fixed-control" (Harcourt et al., 2019) operation these were set to  $t_{h,e}=t_{h,f}=3.25$ h  $t_{g,e}=t_{g_f}=3.0$ h respectively.

(Jueterbock et al., 2013). MaxEnt was employed via the dismo R package (Hijmans et al., 2017) to create all SDMs. Two analyses were carried out: one considering the Severn Estuary without the barrage and one which included the proposed barrage. Each script loads the obtained presence data and relating environmental layers (see next section) for each species. The model then analyses these presence points against 20,000 (3% of all data cells) randomly selected pseudo-absence points. We also ran with 2,000 randomly selected background points to assess sensitivity to pseudoabsence points. There was no significance difference in these results and data from these simulations are contained in the supplementary information. In order to validate each SDM, we performed a 5-way k-fold test, and an assessment of the Area Under Curve value (AUC) for both the individual k-fold tests as well as the complete model. The 5-way k-fold test randomly removes 20% of the presence and absence points to run a model. This is repeated five times to check the model output is not sensitive to particular presence/absence points. We also examined the Spatial Sorting Bias (SSB) to check the coverage of our presence point data. All AUC tests produced a value of over 0.75 and all SSB tests gave a value close to 1.0, which are considered adequate for producing a useful SDM result (Araujo et al., 2005; Hijmans, 2012), though we note that AUC is an imperfect measure of model performance and hence we ensured each species had at least 25 data points after filtering (van Proosdij et al., 2016). The output of MaxEnt modelling is a prediction showing the expected probability of the species being present. The modelling process was repeated for both analyses using the appropriate environmental layers and again accounting for the presence of prey species according to the food web shown in Fig. 1.

In order to create a MaxEnt model for each species, we first need to create a number of environment layers. These were created by extracting data from the hydrodynamic models and interpolating these data from the unstructured mesh onto a regular raster grid (100 m resolution, 1,717,725 grid cells in total with 675,941 containing data) as required by MaxEnt. Layers are either trivially derived from the model (e.g. bathymetric depth) or require averaging or other calculations over the simulation duration (e.g. average speed). The layers and descriptions are summarised in Table 2. For each species used in this study, preliminary work ascertained which environmental layers produced strong response functions by systematically removing the environmental layers for which the response function was constant. These response functions are calculated by the MaxEnt algorithm and are used to calculate the probability of a species occurring in a location as a function of the values in the environment layer; in essence they are the probable effect of an environmental layer on habitat suitability probability for an individual species. The combination of layers for each species are outlined in Table 3. Presence predictions for primary consumers have also been used as environmental layers for secondary and tertiary consumers to incorporate the impact of prey species on predators as per the food web

189

190

191

192

193

196

197

198

199

201

202

203

204

205

207

208

209

210

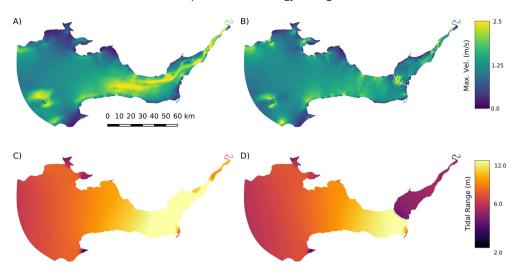
211

213

214

215

#### Impacts of tidal energy barrages



**Figure 4:** Examples of the changes in the hydrodynamic layers used as input to the SDMs. The maximum velocity is shown in A. (without barrage) and B. (with barrage) where there is a large decrease across the whole estuary, with only some coastal areas not showing a decrease. Tidal range (C – without barrage and D – without barrage) shows a distinct decrease landward of the barrage.

in Fig. 1. Results for this analysis are reported separately.

## 3. Results

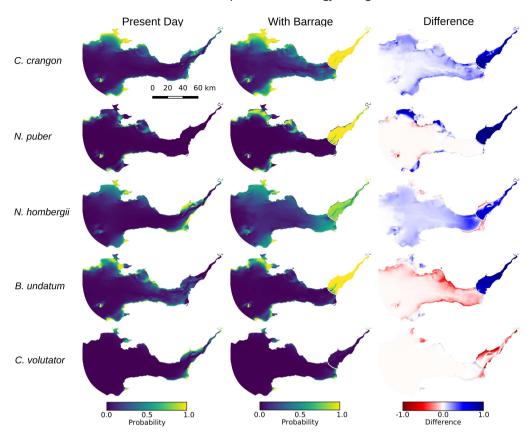
The introduction of a Severn barrage would have a significant effect on the hydrodynamics of the region (Fig. 4). There are major changes landward of the barrage with a decrease in tidal range, as well as the maximum and average velocities. Consequently there is a shift in areas that are classified as inter- and sub-tidal. Tidal range changes are not immediately evident seaward of the barrage, though some bays do see a small increase in tidal range, such as in the Swansea Bay area. Combined, these hydrodynamic changes affect the entire region of interest.

Overall the impact of the barrage is to increase the habitat availability *landward* of the barrage for most species. Only a few species (described below) show a reduction in suitable habitat in this region. Coastal regions show a mixed picture with some species showing an increase in species suitability and some a decrease. Overall, most species increase in habitat suitability area, with only a few showing a decrease. Analysis of area changes highlight a range of responses across the 14 modelled species (Table 4). Some species have a maximum loss of 252.1 km² (40.8% loss) (*C. crangon*), whereas other species have a maximum area gain of 1233.1 km² (113.1% gain) (*L. littorea*). This variation in increase/decrease for all 14 species (Table 4) suggests the barrage will have a wide range of impacts on species distribution and prevalence. Overall, there is a net gain of 5315.81 km² (39.87%) in species area cover across the estuary after barrage installation.

The barrage has clear implications on distributions of benthic species such as *C. volutator* and *C. crangon*. For *C. volutator*, a decrease in species distributions is generally observed across the estuary, with very few areas where species distributions is predicted to increase (Fig. 5). Whereas, for *C. crangon* a significant increase in species distributions is shown across the whole estuary, with only minor decreases along the Welsh coast, for example in Swansea Bay (Fig. 5). It is noticeable that the barrage creates a large habitat area landward of the barrage for *C. crangon* and *N. puber* where these organisms see a large increase in habitable area. Spatially, there are some areas which experience a decrease in habitat suitability. Swansea Bay, for example, shows a decrease for all benthic organisms, except *N. puber*.

Out of the ten benthic species modelled in this research, four had prey species applied as environmental layers (*C. cragnon*, *N. hombergii*, *B. undatum*, and *N. puber*). When accounting for prey species in modelling, benthic species distributions continue to increase in area, but the increase is smaller (Fig. 6). When modelling without the use of prey species as environmental layers, an increase in species distributions was noted behind the barrage.

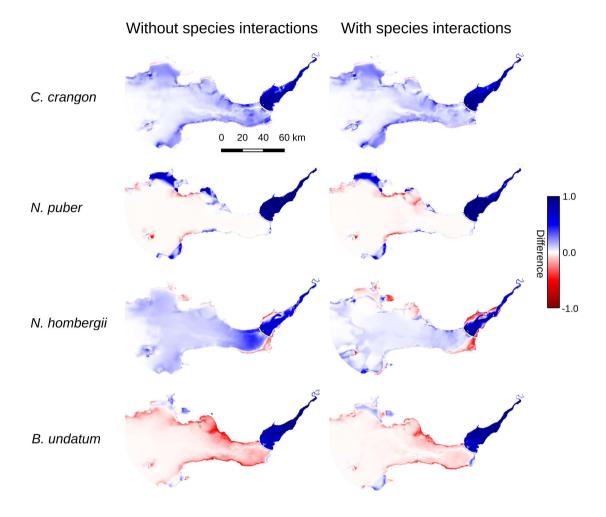
#### Impacts of tidal energy barrages



**Figure 5:** SDM predictions for five of the 11 benthic species (one per row) with the present day prediction shown in the first column, the prediction with the Severn barrage in place in column 2. Column 3 shows the difference between the two predictions (blue indicates an increase in probability, red a decrease).

Pelagic species are known to be problematic in SDMs (Robinson et al., 2011). However, two (*S. solea* and *T. luscus*) of the four pelagic species are demersal. *T. lucus* and *P. minitus* show similar patterns of change with a large increase of suitable habitat landward of the barrage and a general decrease within the estuary (Fig. 7). The most striking change occurs in *S. solea* with a large drop in suitability behind the barrage and in the outer estuary, but with a modest increase within the central regions and Carmarthen Bay. Conversely *T. minitus* show an increase across the whole estuary after barrage installation. All four pelagic species were modelled with prey species as environmental layers. Once the prey species were added, distributions show similarities with the SDM without prey species, but also some important differences. First *S. solea* shows a similar pattern of a loss of area landward of the barrage, but with a large increase within the estuary. However, additional habitat losses are predicted along the outer edge of Carmarthen Bay and along the Devon coast. *T. luscus* now shows increase in habitat in Swansea and Carmarthen Bay as opposed to minor decrease and *T. minitus* has a lower increase landward of the barrage, but higher increases in Carmarthen Bay. *P. minitus* shows a complex change when prey species are added as environmental layers with areas that were previously an increase in habitat suitability after barrage installation now showing decreases and vice-versa. However, the area landward of the barrage still shows a strong increase.

The interpretation of the shifts in probability when prey species are added can be complex. *N. pubar*, for example, has two prey species (*A. marine* and *B. undatum*, the latter of which preys on *L. littorea*). The differences in habitat shift when including these prey species is highlighted in the Swansea Bay area. Prior to including prey species *N. puber* showed a small increase in habitat suitability, which then shifted to a decrease once prey were added. This difference is due to the decrease both prey species show in those areas and for *B. undatum* in turn is possibly driven by the shift in *L. littorea* (Fig. 8). The shift in *L. littorea* is largely driven by changes in the maximum velocity (see supplementary



**Figure 6:** SDM predictions for five of the four benthic species (one per row) where they have dependencies on other species, with the present day prediction shown in the first column, the prediction with the Severn barrage in place in column 2. Column 3 shows the difference between the two predictions (blue indicates an increase in probability, red a decrease).

material). The alteration in area is seen across all 10 realisations of the SDM model (Fig. 8) shows a wider spread of areas when prey species are included (right hand plots in Fig. 8), but there is substantial overlap between the two. Prior to barrage installation the two density functions (yellow in Fig. 8) show substantial overlap again, but the mean area calculated increases slightly.

For the area calculations when accounting for prey species in the modelling process, the impacts of the barrage on area cover are more constrained with most species showing smaller gains in area than without prey species included (Table 5). The exception is *T. minitus* which shows a 125% gain compared to a 113% without prey species (Table 4). The changes in area for *S. solea* is not significant. The inclusion of prey species has remarkably little effect on the bulk statistics with the percentage change of area calculated as 37.17% (when the six lower trophic level species are also included), but as shown in Fig. 8 it does have an impact spatially.

265

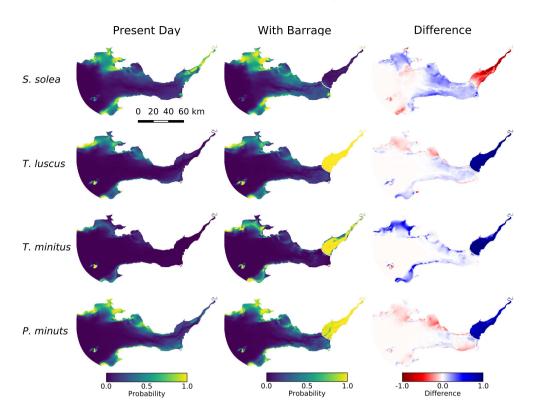
266

267

270

271

272



**Figure 7:** SDM predictions for the four pelagic species (one per row) with the present day prediction shown in the first column, the prediction with the Severn barrage in place in column 2. Column 3 shows the difference between the two predictions (blue indicates an increase in probability, red a decrease).

## 4. Discussion

Velocity of a water body is known to impact sedimentary processes due to alterations to transportation and accumulation patterns (Widdows et al., 1998; Neill et al., 2009). The Severn Estuary features high current velocities, attributed to the driving tidal dynamics; these are further increased on flood tides due to exposure to waves from the Atlantic (Binnie, 2016) in combination with the tidal velocities. The barrage will substantially reduce the tidal velocities across the estuary. Previous research has shown that benthic organisms can be affected through installing a barrage by changes to sedimentation (Shields et al., 2011) especially in regions with higher tidal asymmetry such as the Severn Estuary (Neill et al., 2009; Uncles, 1981). Reduced velocity following barrage installation would slow natural sediment transportation that occurs through the estuary via ebb and flood tides which arrange habitats (Kadiri et al., 2012). This will result in sediment accumulation in regions with bed shear stress convergence, while erosion would increase in regions with bed shear stress divergence (Neill et al., 2009). Increase in sediment accumulation, alongside higher erosion across different regions will alter the current sedimentology of the estuary, which has further impacts on species prevalence and species distributions due to lack of habitat availability. Therefore, a tidal barrage is thought to detrimentally impact ecology and species distributions through changing maximum velocity, altering sedimentation processes and consequently species habitats.

The model predictions presented here highlighted an overall decrease in only the lowermost trophic level benthic species distributions and an overall shift in predominance of suitable habitat landward of the barrage. This shift is generated by the reduction in velocities and a more consistent water level. Although there is a large shift in habitat location within the estuary the overall area of suitable habitat increases for most species (Fig. 9), with only 4 of the fourteen species showing a reduction in suitable area. This is contrary to previous research where it was thought that

there would be a significant loss in benthic habitat availability (Frid et al., 2012). When including an estimation of the predator-prey relationships the increase is less substantial, but there is still an increase in suitable habitat (Fig. 1).

Species distributions models have a number of uncertainties associated with them, especially as measures of ecological impact. Primarily they calculate the probability of a suitable habitat. However, a 2D SDM cannot accurately model 3D interactions (Duffy and Chown, 2017). Some of the species modelled here, such as T. lucus, are true pelagic species that reside in the water column (a 3D environment), which may explain some of the large increases in suitable habitat in the pelagic species. However, some benthic species also show increases of a similar magnitude. In order to mitigate this probable deficiency we also included prey species as environmental layers as feeding is a key process for both benthic and pelagic predators Robinson et al. (2011). Moreover, 2D modelling becomes increasingly inappropriate when modelling 3D consumer relationships. As food webs are examples of dynamic interplay between 3D trophic interactions at different levels, a 2D model cannot project accurate changes and can consequently predict communities as overly vulnerable (Pawar et al., 2012). The inadequacy of 2D modelling pelagic species is exemplified in this research through the analysis of T. lucus, however the addition of prey species as environmental layers partially mitigates against the lack of 3D relationships. In the case of T. lucus the area change post barrage installation increased further when taking feeding into account. Including SDM outputs of prey species as layers of further SDMs is unconventional but this method allows our predictions to include some measure of the complex trophic relationships that occur and not to relay solely on shifts in environmental factors. Whilst this is ideal for modelling benthic species that have limited movement through the water column, it lacks accuracy when modelling pelagic species which rely on 3D aspects of the environment. To enhance further research into marine environments it would be recommended to model prey species where appropriate and use 3D hydrodynamic modelling (Duffy and Chown, 2017), however, this would introduce a significant number of possible environmental layers that could be used, possibly creating even more complex outcomes, although there are currently no three-dimensional SDMs available (Duffy and Chown, 2017). We therefore must conclude that the installation of a tidal barrage will have complex impacts on species distribution for pelagic species as they occupy the water column and the true impact cannot be fully modelled using a 2D hydrodynamics model. Nonetheless it is evident that a barrage will alter species distribution, ecology and predatory relationships which constricts the food web and diminishes food availability.

The overall impact of installing a barrage on the Severn Estuary is a 38% net gain in area cover (Table 4). Through analysis of response functions of environmental layers (not shown), there is a noticeable relationship between species distributions and tidal range (influencing 11 species), and maximum velocity (impacting 10 species). Thus, the net gain in area cover is heavily influenced by alterations to tidal regime and the associated sedimentation processes by extension (Widdows et al., 1998; Neill et al., 2009) and these primarily occur landward of the barrage. However, the impact a barrage inflicts on species distribution and modelled trophic relationships are complex and cannot be fully captured by SDMs. Despite the overall net gain across all 14 species, most of the primary benthic producers (*B. pelagica*, *P. ulvae*, *M. balthica*, and *C. volutator*) show a reduction in suitable area cover, especially in Swansea or Carmarthen Bays, highlighting the complexities of modelling whole ecosystems. These are regions where sedimentation seems to change through alterations to velocity and tidal regime (Neill et al., 2009; Kadiri et al., 2012). This implies a strong spatial bias in impacts on biodiversity. Overall, whilst there is a net increase in suitable habitat, the distribution of normalised suitable area shows a distinct wider distribution, highlighting the species that show both negative and positive area changes (Fig. 10). When including the prey species as environment layers the post-barrage area distribution shows a positive shift compared to not including the prey species (Fig. 10).

A polynomial model, such as that incorporated in the MaxEnt model, is a useful tool for determining the input factors which drive a response, and allow for non-linear responses to be estimated (Elith et al., 2011). However, while using a polynomial function is ideal for modelling changes in location, MaxEnt can be prone to over-fitting features. Therefore, the model becomes over reliant on one function or layer which might not significantly change (Elith et al., 2011; Morales et al., 2017). As a result, when accounting for prey species in modelling, the prediction can become over constrained which consequently produces an unrealistic representation of the expected species distributions change. An optimised regularisation multiplier parameter in MaxEnt can be used to reduce the extent to which the constrains are added (Morales et al., 2017). Furthermore, other SDM algorithms such as Bioclim and GLM (Generalised Linear Model) can be used to overcome the problems observed when using MaxEnt, but these methods have different drawbacks (Elith et al., 2006).

Whilst this study is limited to 14 species in the Severn Estuary, the techniques used and results can be applicable to any proposed tidal energy installation globally, especially if the completeness of the food web is increased (de Jonge et al., 2019b). Internationally the need to generate carbon free energy to mitigate the impacts of climate change is

207

208

299

300

301

302

303

304

305

306

307

309

310

311

312

314

315

316

317

318

319

320

321

322

323

324

326

327

328

329

332

333

334

335

336

338

339

340

341

345

increasing. However, while policies such as the Kyoto Protocol 1997 and the Paris Agreement 2015 call for change, they do not enforce the need to minimise damages to ecosystems and ecological functioning. The UK has high potential for tidal energy and increased investment in this energy sector (Greenmatch, 2017). This has increased the need for ecological assessments to examine the potential for ecological impact caused by industrial activities (Calow, 1998) and analyse the balance between ecological harm and the need for carbon free energy production. The methods presented here could be used within an optimisation framework as in (du Feu et al., 2019) to optimise barrier or tidal lagoon operation as part of methods to minimise environmental and ecological shifts.

For locations with a high tidal range (such as the Severn Estuary), a tidal based energy system seems favourable as the source is stable and reliable. However, this research suggests that installing a static tidal barrage has overall impacts on ecological distributions and food web dynamics including wide spatial shifts. Garrett and Cummins (2005) state too small a tidal installation result in a minimum energy generation, yet too large interrupts tidal stream patterns and consequently could be an ecologically damaging methods of generating clean energy (O Rourke et al., 2010). In addition, it has been shown that impacts from a tidal barrage are not limited to the immediate region surrounding the barrage (Kadiri et al., 2012). Therefore, a climate-ecology balance is thought to be difficult to achieve with tidal based energy. Here, we show that an overall positive impact might be possible, but there might be areas that lose biodiversity. However, SDMs cannot account for species having to shift location; it shows only suitable habitat.

In this study, we have outlined the ecological impacts that can occur on the distribution of certain sensitive species in the vicinity of tidal energy schemes. However, it must be remarked that there will be additional ecological impacts to migratory fish which could be impeded by the presence of the barrage (Wolf et al., 2009) and may experience injury. The form of injury can vary and is typically attributed to hydrodynamic effects from pressure and turbulence changes, shear effects and even direct collision with the operation of the turbines (Davies, 1988). It is expected that further research on the development of fish-friendly turbine designs could serve to mitigate some of these effects (Hogan et al., 2014), with reports (Retiere, 1994) that the impact of the turbines on fish populations can be partially contained within tolerable levels subject to operational constraints in the regulation of the power plant. Furthermore, the SDM methodology discussed herein does not consider effects above water, such as potential reductions in intertidal areas that could reduce the feeding grounds of wading birds (Goss-Custard et al., 1991).

## 5. Conclusion

350

351

352

353

355

356

357

358

350

362

363

365

367

368

369

370

371

372

373

374

375

376

377

378

381

382

383

384

385

387

388

389

390

303

394

395

396

The UK's bid to hold rises in average global temperatures to below 1.5°C emphasises the need for more renewable energy sources, such as tidal power (Anderson and Peters, 2016; Greenmatch, 2017). The Severn Estuary is ideal for harnessing tidal power to produce energy for a significant proportion of the UK due to its vast tidal range. We modelled energy generation from a barrage on both ebb and flood cycles to calculate the impact on the hydrodynamics. We then modelled 14 species linked via a food web system, this study has shown that installing a tidal barrage on the Severn Estuary could impact on the surrounding ecosystem in complex ways. By comparing predicted habitat areas before and after barrage installation it was noted that 10 species were significantly impacted by the proposed tidal barrage. As well as this, assessment of species distributions showed that all 14 species have a significant change in probable presence, with a mix of decreased and increase predicted habitat. Therefore, it can be concluded that installing a barrage in the Severn Estuary may damage the surrounding ecosystem, especially at the lower trophic levels. To further enhance this ecological assessment, secondary and tertiary consumers were modelled with the addition of prey species as environmental layers, to account for the changes in food web dynamics and food availability. The results from SDM predictions using prey species as environmental layers and analysis of area change show a more constrained increase in suitable habitat area. Analysis of response functions and literature supports these findings and suggests that the impacts of the barrage are predominantly through changes to sedimentation processes (transportation, accumulation and erosion patterns), and tidal regime (impounding water for a period of the water cycle). While these impacts have been shown to detrimentally affect the benthos of the Severn Estuary, alterations to sedimentation and tidal regime are complex to establish when modelling pelagic species due to the lack of interaction with the bed of the estuary. Therefore, changes to tidal regime and sedimentation are predicted to directly and indirectly impact benthopelagic species (S. solea), yet the relationship is complex to fully model through 2D SDM of true pelagic species (e.g. T. lucus). It is challenging to reliably predict the ecological impacts of tidal energy but the combination of SDM and hydrodynamic modelling represents a useful methodology to quantify potential scenarios to assess impact. The methods outlined here form the basis for further study into the ecological impacts of tidal energy schemes and could be applied to any site globally.

# 398 Acknowledgements

300

400

401

402

404

407

408

409

410

449

All code used in this work is available https://github.com/EnvModellingGroup/baker\_etal\_2020 under a GPL v3.0 licence. Data used and produced in this work is available under DOI:10.6084/m9.figshare.11297480 under a CC BY 4.0 licence

This work forms part of the BSc dissertations of Baker, Craighead, Jarvis, and Stenton supervised by Hill. Angeloudis acknowledges the support of NERC through the fellowship grant NE/R013209/2.

# CRediT authorship contribution statement

Amy L. Baker: Conceptualisation of this study, running SDMs, initial draft of text. Robert M. Craighead: Running SDMs, contributions to text. Emma J. Jarvis: Running SDMs, contributions to text. Harriett C. Stenton: Running SDMs, contributions to text. Athanasios Angeloudis: Running and design of hydrodynamic models, contributions to text. Lucas Mackie: Running hydrodynamic models, contributions to text. Alexandros Avdis: Design of hydrodynamic models, contributions to text. Matthew D. Piggott: Design of hydrodynamic models, contributions to text. Jon Hill: Conceptualisation of this study, running SDMs, draft of text.

#### 411 References

- Anderson, K., Peters, G., 2016. The trouble with negative emissions. Science 354, 182-183. doi:10.1126/science.aah4567.
- Angeloudis, A., 2019. Tidal range structure operation assessment and optimisation. Dams and Reservoirs 29, 45–54. doi:https://doi.org/10.1680/jdare.18.00042.
- Angeloudis, A., Ahmadian, R., Falconer, R.A., Bockelmann-Evans, B., 2016a. Numerical model simulations for optimisation of tidal lagoon schemes. Applied Energy 165, 522–536. doi:10.1016/j.apenergy.2015.12.079.
- Angeloudis, A., Falconer, R., Bray, S., Ahmadian, R., 2016b. Representation and operation of tidal energy impoundments in a coastal hydrodynamic model. Renewable Energy 99, 1103–1115. doi:10.1016/j.renene.2016.08.004.
- Angeloudis, A., Falconer, R.A., 2017. Sensitivity of tidal lagoon and barrage hydrodynamic impacts and energy outputs to operational characteristics.

  Ren. Energy 114(A), 337–351. doi:10.1016/j.renene.2016.08.033.
- Angeloudis, A., Kramer, S.C., Avdis, A., Piggott, M.D., 2018. Optimising tidal range power plant operation. Applied energy 212, 680–690. doi:10.1016/j.apenergy.2017.12.052.
- Araújo, C.V.M., Moreira-Santos, M., Patrício, J., Martins, I., Moreno-Garrido, I., Blasco, J., Marques, J.C., Ribeiro, R., 2015. Feeding niche preference of the mudsnail Peringia ulvae. Marine and Freshwater Research 66, 573–581. doi:10.1071/MF14021.
- Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. Journal of biogeography 33, 1677–1688.
- 426 Araujo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Global change biology 11, 1504–1513. doi:10.1111/j.1365-2486.2005.01000.x.
- Avdis, A., Candy, A.S., Hill, J., Kramer, S.C., Piggott, M.D., 2018. Efficient unstructured mesh generation for marine renewable energy applications.

  Renewable Energy 116, 842–856. doi:10.1016/j.renene.2017.09.058.
  - Bagley, J.C., Sandel, M., J., T., de Lourdes Lozano-Vilano, M., Johnson, J.B., 2013. Paleoclimatic modelling and phylogeography of least killifish,
     Heterandria Formosa: insights into Pleistocene expansion-contraction dynamics and evolutionary history of North American Coastal Plain freshwater biota. BMC evolutionary biology 13, 223.
- Baker, A., 1987. Tidal power. IEE Proceedings A Physical Science, Measurement and Instrumentation, Management and Education, Reviews 134, 392. URL: http://digital-library.theiet.org/content/journals/10.1049/ip-a-1.1987.0060, doi:10.1049/ip-a-1.1987.0060.
- Balay, S., Abhyankar, S., Adams, M.F., Brown, J., Brune, P., Buschelman, K., Dalcin, L., Eijkhout, V., Gropp, W.D., Kaushik, D., Knepley, M.G., McInnes, L.C., Rupp, K., Smith, B.F., Zampini, S., Zhang, H., Zhang, H., 2016. PETSc Users Manual. Technical Report ANL-95/11 Revision 3.7. Argonne National Laboratory. URL: http://www.mcs.anl.gov/petsc.
  - Bernshtein, L.B., 1961. Tidal energy for electric power plants. Israel Program for Scientific Translations, Jerusalem, Israel.
- Binnie, C., 2016. Tidal energy from the Severn estuary, UK, in: Proceedings of the institution of civil engineers, Energy. pp. 3–17.
- Bird, D.J., 2008. The biology and conservation of the fish assemblage of the Severn Estuary (cSAC). Report Number CCW/SEW/08/1, 1–79.
- Borthwick, A.G., 2016. Marine renewable energy seascape. Engineering 2, 69 78. URL: http://www.sciencedirect.com/science/article/pii/S2095809916301503, doi:https://doi.org/10.1016/J.ENG.2016.01.011.
- Bray, S., Ahmadian, R., Falconer, R.A., 2016. Impact of representation of hydraulic structures in modelling a severn barrage. Computers & Geosciences 89, 96 106. URL: http://www.sciencedirect.com/science/article/pii/S0098300416300206, doi:https://doi.org/10.1016/j.cageo.2016.01.010.
  - Burrows, R., Yates, N.C., Hedges, T.S., Li, M., Zhou, J.G., Chen, D.Y., 2009. Tidal energy potential in UK waters. Proceedings of the institution of civil engineers. Proceedings of the Institution of Civil Engineers: Maritime Engineering 161, 155–164.
  - Calow, P., 1998. Ecological risk assessment: risk for what? How do we decide? Ecotoxicology and environmental safety 40, 15–18.
- Cattrijsse, A., Dankwa, H.R., Mees, J., 1997. Nursery function of an estuarine tidal marsh for the brown shrimp Crangon crangon. Journal of sea
   research 38, 109–121. doi:10.1016/S1385-1101(97)00036-1.
- 452 Davies, J.K., 1988. A review of information relating to fish passage through turbines: implications to tidal power schemes. Journal of Fish

- Biology 33, 111-126. URL: https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1095-8649.1988.tb05565.x, doi:10.1111/j.1095-8649.1988.tb05565.x, arXiv:https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1095-8649.1988.tb05565.x.
- de Deckere, E.M.G.T., van de Koppel, J., Heip, C.H.R., 2000. The influence of Corophium volutator abundance on resuspension, in: Life at Interfaces and Under Extreme Conditions, Springer Netherlands. pp. 37–42. doi:10.1007/978-94-011-4148-2\\_3.
- Duffy, G.A., Chown, S.L., 2017. Explicitly integrating a third dimension in marine species distribution modelling. Marine ecology progress series
   564, 1–8.
- Edina Digimap Service, 2014. Hydrospatial one, gridded bathymetry. http://digimap.edina.ac.uk/marine/., SeaZone Solutions Ltd,
  Online: accessed 2017.
- Egbert, G.D., Erofeeva, S.Y., 2002. Efficient inverse modeling of barotropic ocean tides. Journal of Atmospheric and Oceanic Technology 19, 183–204. URL: http://dx.doi.org/10.1175/1520-0426(2002)019<0183:EIM0B0>2.0.C0;2, doi:10.1175/1520-0426(2002)019<0183:EIM0B0>2.0.C0;2, arXiv:http://dx.doi.org/10.1175/1520-0426(2002)019<0183:EIM0B0>2.0.C0;2.
- El-Geziry, T.M., Bryden, I.G., Couch, S.J., 2009. Environmental impact assessment for tidal energy schemes: an exemplar case study of the Strait of Messina. Proceedings of the Institute of Marine Engineering, Science and Technology Part A: Journal of Marine Engineering & Technology 8, 39–48. doi:10.1080/20464177.2009.11020217.
- Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J.,
   G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., J. Phillips,
   S., Richardson, K., Scachetti-Pereira, R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M., E. Zimmermann, N., 2006. Novel methods
   improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. doi:10.1111/j.2006.0906-7590.04596.x.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., others, 2011. A statistical explanation of MaxEnt for ecologists. Diversity 17, 43–57.
- Falconer, R.A., Angeloudis, A., Ahmadian, R., 2018. Modeling Hydro-environmental Impacts of Tidal Range Renewable Energy Projects in Coastal Waters. WORLD SCIENTIFIC. chapter Chapter 55. pp. 1553–1574. doi:10.1142/9789813204027\_0055.
- Falconer, R.A., Xia, J., Lin, B., Ahmadian, R., 2009. The Severn Barrage and other tidal energy options: Hydrodynamic and power output modeling.

  Science in China Series E: Technological Sciences 52, 3413–3424. URL: http://link.springer.com/10.1007/s11431-009-0366-z,

  doi:10.1007/s11431-009-0366-z.
- du Feu, R.J., Funke, S.W., Kramer, S.C., Culley, D.M., Hill, J., Halpern, B.S., Piggott, M.D., 2017. The trade-off between tidal-turbine array yield and impact on flow: A multi-objective optimisation problem. Renewable Energy 114, 1247–1257. doi:10.1016/j.renene.2017.07.081.
  - du Feu, R.J., Funke, S.W., Kramer, S.C., Hill, J., Piggott, 2019. The trade-off between tidal-turbine array yield and environmental impact: A habitat suitability modelling approach. Renewable Energy 143, 390–403. doi:10.1016/j.renene.2019.04.141.
  - Fish, J.D., Fish, S., 1978. Observations on an annual migration of Bathyporeia pelagica (Amphipoda, Haustoriidae). Crustaceana.
- Frid, C., Andonegi, E., Depestele, J., Judd, A., Rihan, D., Rogers, S.I., Kenchington, E., 2012. The environmental interactions of tidal and wave energy generation devices. Environmental Impact Assessment Review 32, 133–139. doi:10.1016/j.eiar.2011.06.002.
  - Garrett, C., Cummins, P., 2005. The power potential of tidal currents in channels. Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences 461, 2563–2572. URL: https://royalsocietypublishing.org/doi/abs/10.1098/rspa.2005.1494, doi:10.1098/rspa.2005.1494, arXiv:https://royalsocietypublishing.org/doi/pdf/10.1098/rspa.2005.1494.
  - Gendron, R.P., 1977. Habitat selection and migratory behaviour of the intertidal gastropod Littorina littorea (L.). The Journal of animal ecology.
  - Geuzaine, C., Remacle, J.F., 2009. Gmsh: A 3-D finite element mesh generator with built-in pre- and post-processing facilities. International journal for numerical methods in engineering 79, 1309–1331. doi:10.1002/nme.2579.
- Gill, A.B., 2005. Offshore renewable energy: ecological implications of generating electricity in the coastal zone. The Journal of applied ecology
   42, 605–615.
- Goss-Custard, J.D., Warwick, R.M., Kirby, R., McGrorty, S., Clarke, R.T., Pearson, B., Rispin, W.E., Durell, S.E.A.L.V.D., Rose, R.J., 1991.
   Towards predicting wading bird densities from predicted prey densities in a post-barrage severn estuary. Journal of Applied Ecology 28, 1004–1026. URL: http://www.jstor.org/stable/2404222.
- Greenmatch, 2017. Enormous potential of tidal energy and wind power in the UK. Greenmatch. 27 July 2017. [Online]. Available at: [Accessed 20 November 2018]. https://www.greenmatch.co.uk/blog/2016/10/tidal-and-wind-energy-in-the-uk.
- Hallstan, S., 2011. Species distribution models, ecological applications for management of biodiversity. Swedish University of Agricultural sciences.
   [Online]. Available at: [Accessed 23, 2018.
- Hallstan, S., Johnson, R.K., Willén, E., Grandin, U., 2012. Comparison of classification-then-modelling and species-by-species modelling for
   predicting lake phytoplankton assemblages. Ecological modelling 231, 11–19. doi:10.1016/j.ecolmodel.2012.01.018.
- Harcourt, F., Angeloudis, A., Piggott, M.D., 2019. Utilising the flexible generation potential of tidal range power plants to optimise economic value.

  Applied Energy 237, 873 884. URL: http://www.sciencedirect.com/science/article/pii/S0306261918319093, doi:https://doi.org/10.1016/j.apenergy.2018.12.091.
- Henderson, P.A., Bird, D.J., 2010. Fish and macro-crustacean communities and their dynamics in the Severn Estuary. Marine pollution bulletin 61,
   100–114. doi:10.1016/j.marpolbul.2009.12.017.
- Hendry, C., 2017. The role of tidal lagoons. Technical Report. UK Government. URL: https://hendryreview.com/.
- Hijmans, R.J., 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null model. Ecology 93,
   679–688.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2017. dismo: Species Distribution Modeling.
- Hogan, T.W., Cada, G.F., Amaral, S.V., 2014. The status of environmentally enhanced hydropower turbines. Fisheries 39, 164–172. URL: https://doi.org/10.1080/03632415.2014.897195, doi:10.1080/03632415.2014.897195.
   arXiv:https://doi.org/10.1080/03632415.2014.897195.
- Imrie, D.W., McCrohan, C.R., Hawkins, S.J., 1990. Feeding behaviour in Littorina littorea: a study of the effects of ingestive conditioning and previous dietary history on food preference and rates of consumption. Hydrobiologia 193, 191–198. doi:10.1007/BF00028076.
- de Jonge, V.N., Schückel, U., 2019. Exploring effects of dredging and organic waste on the functioning and the quantitative biomass structure of

479

- the Ems estuary food web by applying Input Method balancing in Ecological Network Analysis. Ocean & coastal management 174, 38–55. doi:10.1016/j.ocecoaman.2019.03.013.
- de Jonge, V.N., Schückel, U., Baird, D., 2019a. Effects of spatial scale, species aggregation and balancing on carbon flows and ecological network analysis indicators of food webs. Marine ecology progress series 613, 15–47. doi:10.3354/meps12825.
- de Jonge, V.N., Schückel, U., Baird, D., 2019b. Subsets of food webs cannot be used as a substitute to assess the functioning of entire ecosystems.

  Marine ecology progress series 613, 49–66. doi:10.3354/meps12863.
- Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L., Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. Ecology and evolution 3, 1356–1373. doi:10.1002/ece3.541.
- Kadiri, M., Ahmadian, R., Bockelmann-Evans, B., Rauen, W., Falconer, R., 2012. A review of the potential water quality impacts of tidal renewable energy systems. Renewable and Sustainable Energy Reviews 16, 329–341. doi:10.1016/j.rser.2011.07.160.
- Kärnä, T., de Brye, B., Gourgue, O., Lambrechts, J., Comblen, R., Legat, V., Deleersnijder, E., 2011. A fully implicit wettingâĂŞdrying method
   for DG-FEM shallow water models, with an application to the Scheldt Estuary. Computer Methods in Applied Mechanics and Engineering 200,
   509–524. doi:10.1016/j.cma.2010.07.001.
- Kärnä, T., Kramer, S.C., Mitchell, L., Ham, D.A., Piggott, M.D., Baptista, A.M., 2018. Thetis coastal ocean model: discontinuous Galerkin discretization for the three-dimensional hydrostatic equations. Geoscientific Model Development 11, 4359–4382. URL: https://www.geosci-model-dev.net/11/4359/2018/, doi:10.5194/gmd-11-4359-2018.
- Kirby, R., Parker, W., 1983. Distribution and behavior of fine sediment in the severn estuary and inner bristol channel, uk. Canadian Journal of Fisheries and Aquatic Sciences 40, s83–s95.
- Lewis, M.J., Angeloudis, A., Robins, P.E., Evans, P.S., Neill, S.P., 2017. Influence of storm surge on tidal range energy. Energy 122, 25–36. doi:10.1016/j.energy.2017.01.068.
- Lira-Noriega, A., Soberón, J., Miller, C.P., 2013. Process-based and correlative modelling of desert mistletoe distribution: a multiscalar approach.
   Ecological applications: a publication of the Ecological Society of America 4, 8.
- Lobo, J.M., Jimenez-Valderde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography 33, 103–114.
- Martin-Short, R., Hill, J., Kramer, S.C., Avdis, A., Allison, P.A., Piggott, M.D., 2015. Tidal resource extraction in the Pentland Firth, UK: Potential impacts on flow regime and sediment transport in the Inner Sound of Stroma. Renewable Energy 76, 596–607. doi:10.1016/j.renene.2014.
   11.079.
- Meißner, K., Darr, A., Rachor, E., 2008. Development of habitat models for Nephtys species (Polychaeta: Nephtyidae) in the German Bight (North Sea). Journal of sea research 60, 276–291. doi:10.1016/j.seares.2008.08.001.
- Merow, C., Smith, M.J., Silander, Jr, J.A., 2013. A practical guide to MaxEnt for modelling species' distribution: what it does, and why inputs and settings matter. Ecography 36, 1058–1069.
- Morales, N.S., Fernández, I.C., Baca-González, V., 2017. MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. PeerJ 5, e3093. doi:10.7717/peerj.3093.
- Naimi, B., Araújo, M.B., 2016. SDM: a reproducible and extensible R platform for species distribution modelling. Ecography 39, 368–375.
- Natural England & the Countryside Council for Wales, 2009. The Severn Estuary / Môr Hafren. Technical Report. Natural England.
- Neill, S.P., Angeloudis, A., Robins, P.E., Walkington, I., Ward, S.L., Masters, I., Lewis, M.J., Piano, M., Avdis, A., Piggott, M.D., Aggidis, G., Evans, P., Adcock, T.A., Zidonis, A., Ahmadian, R., Falconer, R., 2018. Tidal range energy resource and optimization âĂŞ past perspectives and future challenges. Renewable Energy 127, 763–778. URL: https://www.sciencedirect.com/science/article/pii/S0960148118305263, doi:https://doi.org/10.1016/j.renene.2018.05.007.
- Neill, S.P., Litt, E.J., Couch, S.J., Davies, A.G., 2009. The impact of tidal stream turbines on large-scale sediment dynamics. Renewable Energy 34, 2803–2812. doi:10.1016/j.renene.2009.06.015.
- Norman, C.P., Jones, M.B., 1992. Influence of depth, season and moult stage on the diet of the velvet swimming crab Necora puber (brachyura, portunidae). Estuarine, coastal and shelf science 34, 71–83. doi:10.1016/S0272-7714(05)80127-1.
- O Rourke, F., Boyle, F., Reynolds, A., 2010. Tidal energy update 2009. Applied energy 87, 398–409. doi:10.1016/j.apenergy.2009.08.014.
- Olafsson, E.B., 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve Macoma balthica: a field experiment. The Journal of animal ecology .
- Pan, W., Kramer, S.C., Piggott, M.D., 2019. Multi-layer non-hydrostatic free surface modelling using the discontinuous Galerkin method. Ocean
   Modelling 134, 68–83.
- Pawar, S., Dell, A.I., Savage, V.M., 2012. Dimensionality of consumer search space drives trophic interaction strengths. Nature 486, 485–489. doi:10.1038/nature11131.
- Phillips, S.J., Dudik, M., 2008. Modelling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. Ecography 31, 161–175.
- Pihl, L., Rosenberg, R., 1984. Food selection and consumption of the shrimp Crangon crangon in some shallow marine areas in western Sweden.
   Marine ecology progress series. Oldendorf 15, 159–168.
- 570 Potts, G.W., Swaby, S.E., 1993. The fishes of the Severn Estuary. [Online]. Available at: publications 18, 2018.
- van Proosdij, A.S.J., Sosef, M.S.M., Wieringa, J.J., Raes, N., 2016. Minimum required number of specimen records to develop accurate species distribution models. Ecography 39, 542–552. doi:10.1111/ecog.01509.
- Rathgeber, F., Ham, D.A., Mitchell, L., Lange, M., Luporini, F., Mcrae, A.T.T., Bercea, G.T., Markall, G.R., Kelly, P.H.J., 2016. Firedrake:

  Automating the finite element method by composing abstractions. ACM Trans. Math. Softw. 43, 24:1–24:27. URL: http://doi.acm.org/

  10.1145/2998441, doi:10.1145/2998441.
- 876 Retiere, C., 1994. Tidal power and the aquatic environment of La Rance. Biological Journal of the Linnean Society 51, 25-36. URL: https://doi.org/10.1111/j.1095-8312.1994.tb00941.x, doi:10.1111/j.1095-8312.1994.tb00941.x, arXiv:http://oup.prod.sis.lan/biolinnean/article-pdf/51/1-2/25/14072394/j.1095-8312.1994.tb00941.x.pdf.

#### Impacts of tidal energy barrages

- Riisgård, H.U., Banta, G.T., 1998. Irrigation and deposit feeding by the lugworm Arenicola marina, characteristics and secondary effects on the environment: a review of current knowledge. Vie et milieu 48, 243–257.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global ecology and biogeography: a journal of macroecology 20, 789–802. doi:10.1111/j.1466-8238.2010.00636.x.
- Schubert, A., Reise, K., 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. Marine ecology progress series 34, 117–124.
- Shields, M.A., Woolf, D.K., Grist, E.P.M., Kerr, S.A., Jackson, A.C., Harris, R.E., Bell, M.C., Beharie, R., Want, A., Osalusi, E., Gibb, S.W., Side,
   J., 2011. Marine renewable energy: The ecological implications of altering the hydrodynamics of the marine environment. Ocean & coastal management 54, 2–9. doi:10.1016/j.ocecoaman.2010.10.036.
- TLP, 2017. Tidal Lagoon Power Development Consent Application. http://www.tidallagoonpower.com/
  application-for-development-consent/. Accessed: 15-10-2017.
- TLP, 2018. TLP Tidal Lagoon Programme: Summary value for money assessment. Technical Report. Department for Buisness, Energy and Industrial Strategy, UK Government. URL: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/s
- Uncles, R.J., 1981. A note on tidal asymmetry in the severn estuary. Estuarine, coastal and shelf science 13, 419–432. doi:10.1016/
   50302-3524(81)80038-2.
- Valentinsson, D., Sjödin, F., Jonsson, P.R., Nilsson, P., Wheatley, C., 1999. Appraisal of the potential for a future fishery on whelks (Buccinum undatum) in Swedish waters: CPUE and biological aspects. Fisheries research 42, 215–227. doi:10.1016/S0165-7836(99)00050-8.
- Vouriot, C.V.M., Angeloudis, A., Kramer, S.C., Piggott, M.D., 2019. Fate of large-scale vortices in idealized tidal lagoons. Environmental Fluid
   Mechanics 19, 329–348.
- Waters, S., Aggidis, G., 2016. Tidal range technologies and state of the art in review. Renewable and Sustainable Energy Reviews 59, 514–529.
   doi:10.1016/j.rser.2015.12.347.
- Wheeler, A., 1969. The fishes of the British Isles and North-West Europe. 1st ed. W&J Mackay & co, Chatham.
- Widdows, J., Brinsley, M.D., Salkeld, P.N., 1998. Use of annular flumes to determine the influence of current velocities and bivalves on material
   flux at the sediment-water interface. Estuaries 21, 552–559.
- Wolf, J., Walkington, I.A., Holt, J., Burrows, R., 2009. Environmental impacts of tidal power schemes, in: Proceedings of the Institution of Civil
   Engineers-Maritime Engineering, Maritime Engineering. pp. 165–177.
  - Xia, J., Falconer, R.A., Lin, B., 2010a. Hydrodynamic impact of a tidal barrage in the Severn Estuary, UK. Renewable Energy 35, 1455–1468. doi:10.1016/j.renene.2009.12.009.
- Xia, J., Falconer, R.a., Lin, B., 2010b. Impact of different operating modes for a Severn Barrage on the tidal power and flood inundation in the
   Severn Estuary, UK. Applied Energy 87, 2374–2391. URL: http://linkinghub.elsevier.com/retrieve/pii/S030626190900511X,
   doi:10.1016/j.apenergy.2009.11.024.
- Xia, J., Falconer, R.A., Lin, B., Tan, G., 2012. Estimation of annual energy output from a tidal barrage using two different methods. Applied Energy 93, 327-336. URL: http://linkinghub.elsevier.com/retrieve/pii/S0306261911008452, doi:10.1016/j.apenergy.2011.12.
- Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, A., Nichols, J.D., Campbell-Grant, E.H., Veran, S., 2013. Presence-only modelling using MAXENT: when can we trust the inferences? Methods in ecology and evolution / British Ecological Society 4, 236–243.
- Zhou, J., Pan, S., Falconer, R.a., 2014. Effects of open boundary location on the far-field hydrodynamics of a Severn Barrage. Ocean Modelling 73, 19-29. URL: http://linkinghub.elsevier.com/retrieve/pii/S146350031300187X, doi:10.1016/j.ocemod.2013.10.006.

Table 1 The habitat preferences and food source of each species modelled, showing how species link together as shown in Fig. 1.

Name	Common Name	Habitat description	Food source
Solea solea	Dover sole	Reside in the soft, fine sands and estuarine muds (Wheeler, 1969; Bird, 2008).	Feed on smaller species, including amphipods, crustaceans, worms, and smaller fish e.g. poor cod (Wheeler, 1969; Bird, 2008).
Trisopterus luscus	Bib	Found mainly over sandy regions surrounding the coast as they favour a mixed rocky/sand habitat (Wheeler, 1969; Bird, 2008).	Feed on pink and brown shrimp, as well as some shore crabs (Wheeler, 1969; Bird, 2008).
Trisopterus minitus	Poor cod	Found in muddy and sandy beds up to depths of 15-200m (Wheeler, 1969; Bird, 2008).	Unspecified bottom feeders and typically feed on planktonic crustaceans and polychaete worms (Wheeler, 1969; Bird, 2008).
Pomatoschistus minitus	Sand goby	Abundant in inshore waters over muddy and sandy beds (Wheeler, 1969; Bird, 2008).	Feed on polychaete worms, molluscs, and amphipods (Wheeler, 1969; Bird, 2008).
Crangon crangon	Brown shrimp	Populate areas of sandy, muddy beds in the intertidal zone, with a preferred grain size of 125-710 μm (Pihl and Rosenberg, 1984).	Specific diet of smaller crustaceans and rely heavily on <i>C. volutator</i> (Cattrijsse et al., 1997).
Necora puber	Velvet swim- ming crab	Inhabit the stony, rocky surfaces of the intertidal zone (Norman and Jones, 1992).	Feed on benthic species, algae and small crustaceans (Norman and Jones, 1992).
Nephtys hombergii	Catworm	Intertidal to sublittoral shallows, in muddy sand with preferred grain sizes of less than 50 μm (Meißner et al., 2008).	General diet that consists of small benthic organisms including other polychaetes (Schubert and Reise, 1986).
Buccinum undatum	Whelk	Found from low depths up to 1200m, in muddy, sand, gravel and rock of the subtidal zone (Valentinsson et al., 1999).	Feed on carrion, including other molluscs (Valentinsson et al., 1999).
Corophium volutator	Mud shrimp	Occupy burrows in fine sediments, but can also be found in mudflats, saltmarshes, and brackish ditches (de Deckere et al., 2000).	Diatoms and other microorganisms in sediment (de Deckere et al., 2000).
Littorina littorea	Periwinkle	Inhabit rocky shores, tidal pools, sandy environments and mudflats (Gendron, 1977).	Filter feeding on phytoplankton and zooplankton (Imrie et al., 1990).
Arenicola marina	Lugworm	Preferred habitat of mid to low shore, sandy and muddy tidal flats, and settle in organic rich muds (Riisgård and Banta, 1998).	Subsurface deposit feeder (Riisgård and Banta, 1998).
Macoma balthica	Pink clam	Populate the upper regions of the intertidal to sublittoral zone, just a few centimetres below the surface in fine sands and mud (Olafsson, 1986).	Filter feeding on phytoplankton and zooplankton (Olafsson, 1986).
Peringia ulvae	Mud snail	Have been recorded in lagoons and muddy sands and in areas with relatively low salinity (Araújo et al., 2015).	Macro- and micro-algae (Araújo et al., 2015).
Bathyporeia pelagica	Sand digger shrimp	Occupy wet, fine to medium sand (Fish and Fish, 1978).	Epistrate feeder (Fish and Fish, 1978).

 Table 2

 Environmental layers derived from the hydrodynamic model

Environmental Layer	Description	
Always dry (categorical)	Locations with height above highest tidal height.	
Average speed (m/s)	The mean current over the 30 day run time.	
Maximum speed (m/s)	The maximum current over the 30 day run time.	
Depth (m)	Water depth (negative above mean tide height).	
Maximum water elevation (m)	Highest surface elevation over the 30 day simulation.	
Minimum water elevation (m)	Lowest surface elevation over the 30 day simulation.	
Subtidal (categorical)	Locations that are below the lowest tidal height.	
Intertidal (categorical)	Locations that are between highest and lowest tidal height.	
Tidal range (m)	Difference between minimum and maximum tidal height.	

**Table 3**Species and the environmental layer used for each. Where prey species were used as environmental layer these are also listed.

Species Name	Environmental Layers	Prey species used
S. solea	Bathymetry, Average velocity, Maximum elevation, Tidal range, Intertidal, Minimum elevation, Maximum velocity	T. lucus, T. minitus, N. puber
T. lucus	Bathymetry, Average velocity, Maximum elevation	N. puber, C. crangon, P. minitus, N. hombergii
T. minutus	Bathymetry, Average velocity, Maximum velocity, Maximum elevation	N. hombergii, C. crangon
P. minitus	Bathymetry, Tidal range, Average velocity, Maximum elevation	C. crangon, C. volutator, B. undatum
C. crangon	Bathymetry, Tidal range, Average velocity, Minimum elevation, Maximum velocity	C. volutator
N. puber N. hombergii	Bathymetry, Tidal range, Average velocity, Maximum elevation, Maximum velocity, Minimum elevation Bathymetry, Minimum elevation, Maximum velocity, Average velocity, Tidal range	A. marina, B. undatum L. littorea, M. balthica,
		C. volutator, P. ulvae, B. pelagica
B. undatum	Bathymetry, Minimum elevation, Maximum velocity, Maximum elevation	L. littorea
C. volutator	Bathymetry, Tidal range, Maximum elevation, Maximum velocity	N/A
L. littorea	Bathymetry, Tidal range, Maximum elevation, Minimum elevation, Maximum velocity	N/A
A. marina	Average velocity, Bathymetry, Tidal range, Intertidal	N/A
M. balthica	Bathymetry, Minimum elevation, Tidal range	N/A
P. ulvae	Bathymetry, Tidal range	N/A
B. pelagica	Bathymetry, Maximum velocity, Maximum elevation, Subtidal, Tidal range	N/A

**Table 4**Area difference calculated from habitat suitability maps before and after barrage installation for all 14 species considered. Negative percentage difference indicate a loss of area. Statistical significance (*p* values) are shown by \* symbols.

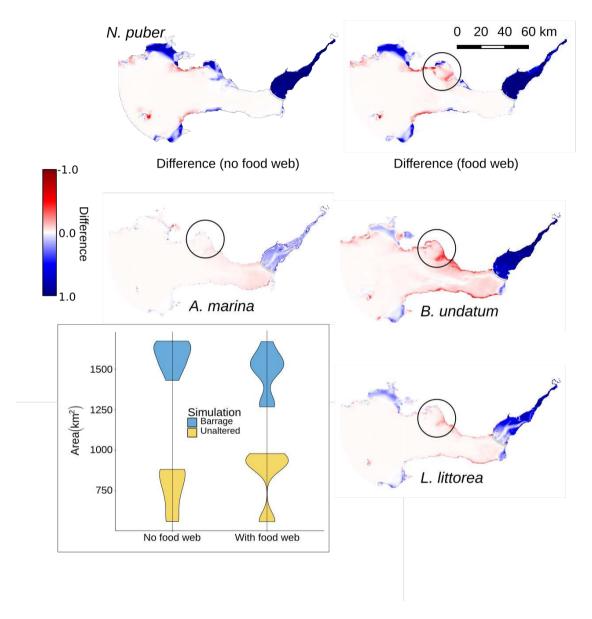
Taxon	Area (km²)	Area with barrage (km²)	Percent increase
S. solea	1030.17	1183.52	14.9%***
T. luscus	924.68	1527.13	65.2%***
T. minitus	1090.66	2323.79	113.1%***
P. minitus	1198.32	1520.85	26.9%***
C. crangon	1488.78	2745.74	84.4%***
N. puber	761.85	1581.14	107.5%***
N. hombergii	1238.18	2124.35	71.5%***
B. undatum	831.04	1073.34	29.2%***
C. volutator	618.12	365.71	-40.8%***
L. littorea	864.85	1128.47	30.5%***
A. marina	1164.83	1234.20	6.0%***
M. balthica	632.58	568.33	-10.2%***
P. ulvae	605.38	558.71	-7.7%***
B. pelagica	883.86	713.83	-19.2%***

<sup>\*\*\*</sup> $p \le 0.01$ , \*\* $p \le 0.05$ , \* $p \le 0.1$ 

**Table 5**Area difference before and after barrage installation for the eight species that had dependencies on other species when the food web in Fig. 1 is accounted for. Negative percentage difference indicate a loss of area. Statistical significance (*p* values) are shown by \* symbols.

Taxon	Area (km²)	Area with barrage (km²)	Percent increase
S. solea	707.84	666.134	$-5.9\%^{ns}$
T. lucus	889.19	1471.72	65.5%***
T. minitus	958.44	2159.54	125.3%***
P. minitus	1410.54	2074.19	47.0%***
C. crangon	1227.33	2241.64	82.6%***
N. puber	843.85	1485.84	76.1%***
N. hombergii	868.51	1353.94	55.9%***
B. undatum	847.48	1285.32	51.7%***

<sup>\*\*\*</sup> $p \le 0.01$ , \*\* $p \le 0.05$ , \* $p \le 0.1$ , \*\*not significant



**Figure 8:** Difference of including prey relationships in the SDM using *N. puber* as an example. Top maps show the probability difference before and after barrage emplacement not using prey species (left) and using prey species (right). The area around Swansea Bay is highlighted where a major difference is observed. The difference maps for the prey species for *N. puber* are shown below with arrows denoting the prey relationships. The same area is highlighted with a large (negative) difference shown for *B. undatum* in particular which is driving this change. This is confirmed via the MaxEnt response functions (not shown). The bottom left panel shows the output of the 10 SDM models for *N. puber* for the four scenarios (with and without barrage, and with and without prey species). There is a notable reduction in the area increase when prey species are added in the "with barrage" simulation.

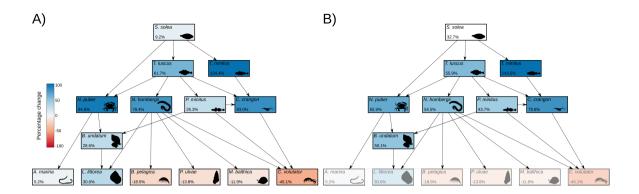
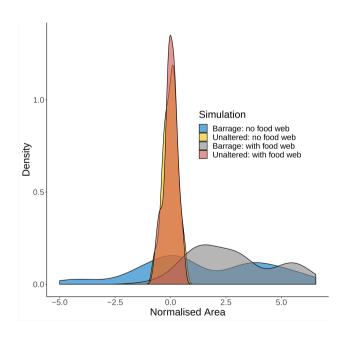


Figure 9: Area loss across the food web in the Severn. A) without consideration of prey species in the SDM and B) with prey species in the SDM. Red indicates loss of area, blue indicates increase in area. The bottom row of the food web in B has been made partially transparent to indicate that these were not recalculated from A). S. Solea is also left white in B) as the reported area change is not statistically significant.



**Figure 10:** Normalised area across 10 SDM realisations for all 14 species for four sets of scenarios. Area is normalised to the unaltered species area (hence their mean is zero)