Global sensitivity analysis of an end-to-end marine ecosystem model of the North Sea: Factors affecting the biomass of fish and benthos

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Abstract:

Comprehensive analysis of parameter and driver sensitivity is key to establishing the credibility of models representing complex systems. This is especially so for models of natural systems where experimental manipulation of the real-world to provide controlled validation data is not possible. End-to-end ecosystem models (nutrients to birds and mammals) of marine ecosystems fall into this category with applications for evaluating the effects of climate change and fishing on nutrient fluxes and the abundances of flora and fauna. Here we present results of both 'one-at-a-time' (OAT) and variance based global sensitivity analyses (GSA) of the fish and fishery aspects of StrathE2E, an end-to-end ecosystem model of the North Sea. The sensitivity of the model was examined with respect to internal biological parameters, and external drivers related to climate and human activity. The OAT Morris method was first used to screen for factors most influential on model outputs. The Sobol GSA method was then used to calculate quantitative sensitivity indices. The results indicated that the fish and shellfish components of the model (demersal and pelagic fish, filter/deposit and scavenge/carnivore feeding benthos) were influenced by different sets of factors. Harvesting rates were highly influential on demersal and pelagic fish biomasses. Suspension/deposit feeding benthos were directly sensitive to changes in temperature, while the temperature acted indirectly on pelagic fish through the connectivity between model components of the food web. Biomass conversion efficiency was the most important factor for scavenge/carnivorous feeding benthos. The results indicate the primacy of fishing as the most important process affecting total fish biomass, together with varying responses to environmental factors which may be relevant in the context of climate change. The non-linear responses and parameter interactions identified by the analysis also highlight the necessity to use global rather than local methods for the sensitivity analysis of ecosystem models.

Highlights

► Report of a global sensitivity analysis conducted on a marine end-to-end ecosystem model. ► Different fishery guilds are influenced by different profiles of parameters and drivers. ► Fishing rates are the most important factor affecting demersal and pelagic fish biomass. ► Biomass of suspension feeding benthos is directly influenced by temperature. ► Metabolic parameters relating to biomass conversion were influential for all guilds.

Keywords: Climate change ; Ocean acidification ; Global sensitivity analysis ; Morris sensitivity method ; Sobol sensitivity method ; North Sea

1. Introduction

A variety of marine ecosystem models have been developed that include both bottom-up (fluctuations in nutrient supply) and top down pressures (harvesting of apex predators), with the aim of elucidating the effects that fishing, environmental change and nutrient inputs have on fish stocks (reviewed by Plagányi, 2007). These end-to-end models achieve this by combining physicochemical and oceanographic processes with the trophic interactions between organismal groupings; from primary producers to top predators (Rose et al., 2010; Travers et al., 2007). Usage of these models has included the examination of trophic cascade effects within food webs, and explorations of climate change effects on selected fisheries (Heath et al., in press; Kaplan et al., 2010).

Many end-to-end ecosystem models require hundreds or thousands of parameters, the majority of which have values that cannot be accurately measured or are totally unknown leading to considerable uncertainty regarding the reliability of predictions (Steele, 2012). This becomes increasingly relevant in situations where a relatively minor change in a factor's value results in a major change in model output (Link et al., 2012). For such complex ecological models it is therefore vitally important to focus on accurately representing those factors that are most influential for the model outputs (Arhonditsis and Brett, 2004). This demands that a comprehensive sensitivity analysis of model parameters and drivers is conducted. Although the usage of sensitivity analysis has often been overlooked in marine ecosystem models (Arhonditsis and Brett, 2004), it is an essential procedure in conventional model development and its importance is stressed in official guidelines regarding the modelling of environmental systems (European Commission, 2009; Saltelli et al., 2009; U.S. Environmental Protection Agency, 2009).

Sensitivity analysis examines the uncertainty in the output of a model and how this relates to the uncertainties in the model input (Saltelli et al., 2008). It is used to identify which factors are

influential to the model output and which are not, and therefore can examine whether model inferences are robust regarding parameterisation or dependent on numerous unverifiable assumptions. By quantifying sensitivity measures to form indices it is also possible to gain insights into model operation, and for functional models highlight those parameters, or forcing data, that have the potential to govern a specific ecological system (e.g. Makler-Pick et al., 2011). Use of sensitivity indices is of particular pertinence in the context of end-to-end ecosystem models, as it may aid in quantitatively attributing causes to effects, the understanding of which forms a key requirement of conservation planning under climate change (Parmesan et al., 2013; Zwiers and Hegerl, 2008).

There are two main methods of sensitivity analysis; local and global (Cariboni et al., 2007). Local sensitivity analysis is usually derivative based and belongs to a class of one-at-a-time (OAT) methods. For these, single factors are perturbed with all other factors held fixed and variation in the output is measured. However, local sensitivity methods are unreliable for all but the simplest of models due to interactions between factors and non-linear relationships between input factor ranges and the model output (Saltelli and Annoni, 2010; Wang et al., 2013). In global sensitivity analysis, all factors are changed together across the full multi-dimensional input space. Where the probability distribution of a factor is unknown a uniform distribution can be used. This approach is considered model independent, and the interactions between factors may be explored.

Depending on method used, the output of a global sensitivity analysis can either be a qualitative or quantitative ranking of factors in terms of their effects on model output. The techniques required for obtaining the latter tend to have a high computational cost and therefore a qualitative screening step is recommended to rank factors and a subset of the most influential passed for quantitative analysis (Mokhtari et al., 2006).

A widely used screening tool is the Morris method (Morris, 1991). This variant on an OAT analysis allows examination at different points of the factor input space, and is therefore considered a global rather than a local sensitivity technique (Saltelli et al., 2008; Saltelli and Annoni, 2010). Factors ranked as important using the Morris method can be further analysed using a global sensitivity method such as the one developed by Sobol (1993). The Sobol method is variance based and quantifies the relative effects of factors on model output, and interactions between factors (Saltelli et al., 2008). The combination of the Morris method followed by the Sobol method is an established methodology that has been successfully implemented for sensitivity analyses across a diverse range of disciplines including environmental and biological sciences (e.g. deJonge et al., 2012; Sumner et

al. 2012).

The complexity of end-to-end ecosystem models has meant that making detailed sensitivity analyses is considered difficult and potentially unfeasible (Fulton 2010; Plagányi 2007). While the importance of global sensitivity analysis is recognised, and despite their known limitations, only local sensitivity methods have been attempted (e.g. Köhler and Wirtz, 2002; Niiranen et al., 2012). Where used, these studies have all been constrained in scope, focusing on specific sets or groupings of factors. As a result, use of this critical methodology has at best been limited, or else omitted for these types of ecosystem models (Fulton 2010; Plagányi 2007).

The end-to-end ecosystem model examined in this study is referred to as StrathE2E and was developed by Heath (2012). This model uses functional groups of taxa rather than defined species in the representation of nutrient dynamics. This allows for a degree of parameter constraint and is considered more reliable in terms of longer term analysis and prediction when compared to models based on individual species representations (Steele et al., 2013). Where data were not available, parameter values were obtained using to a two stage process of hand fitting followed by simulated annealing using maximum likelihood estimations (Heath, 2012). This calibration procedure results in optimal parameter value estimates, in contrast to the alternative approach, usually used for end-to-end ecosystem models, that relies on the manual tuning of parameters to find a best fit between computed and observed data. In addition to not ensuring optimal calibration the tuning process is also inferior for the detection of inadequacies in model structure and parameter choice (Arhonditsis and Brett, 2004; Kawamiya, 2002).

The geographical setting of StrathE2E is the North Sea; a marginal sea of the Atlantic Ocean that constitutes a significant area of the North Western European continental shelf (Gröger et al., 2013; Heath, 2012). Due to high biological productivity continental shelves support important fisheries, providing over 90% of global fisheries catches, with the North Sea representing one of the worlds most valuable fishing resources for the past several centuries (Pauly et al., 2002; Rijnsdorp et al., 1996; Worm et al., 2009). Continental shelves may also act as significant sinks for atmospheric CO_2 accounting for up to 50% of the global ocean's net annual carbon uptake; a process that leads to ocean acidification (Thomas et al., 2004). Eutrophication is also considered a key problem affecting areas of the North Sea in addition to some of the highest local rates of climate change related temperature increases recorded (Heath et al., 2012; McQuatters-Gollop et al., 2009; Raynor et al., 2003). Understanding the relative contributions that fishing and environmental change have

on North Sea fish and shellfish stocks is a priority endeavor for the European fisheries science community (Dulvy et al., 2008).

The objective of this paper is to conduct a global sensitivity analyses on the StrathE2E ecosystem model. Due to the relatively large number of parameters involved, the Morris method is used to screen for influential factors that are then examined using the Sobol method. The aim of the sensitivity analysis is to derive insights into StrathE2E function, identify those factors that are influential regarding the fishery outputs, and therefore aid toward the ultimate goal of understanding how North Sea fisheries could be affected by environmental change.

2. Materials and Methods

2.1 Model description

A detailed description, including all features, parameters, driving data and outputs of StrathE2E is presented in the paper and associated supporting material of Heath (2012).

The spatial domain represented by StrathE2E is the entire North Sea, with boundaries as defined by the International Hydrographic Organisation (International Hydrographic Organization, 1953). The model simulates fluxes of a single nutrient (Nitrogen) between mass state variables representing: detritus, dissolved nutrient, phytoplankton, benthos, zooplankton, fish and top predators. These state variables are further resolved into two water column depth layers (called deep and surface) and a sediment layer. Rates of exchange between the compartments are described in a series of 22 linked ordinary differential equations. StrathE2E is based on the food web presented in the schematic of Figure 1. The time dependant drivers were resolved to monthly values that were calculated from available datasets and included irradiance, temperature, vertical exchange rates, horizontal volume and exchange rates across open ocean boundaries of each layer, and external inputs from rivers and the atmosphere. Fishing rates were represented by the proportion of biomass of pelagic fish, demersal fish and benthic invertebrates removed per day from the North Sea also obtained from existing datasets (Heath, 2012).

StrathE2E has four outputs that relate to fishery stocks, these represent the combined biomass of all pelagic fish spp. (e.g. herring, sprats, mackerel, Norway pout); all demersal fish spp. (e.g. cod, haddock, whiting, plaice); all invertebrate benthic filter and deposit feeders (e.g. filter feeding molluscs, brittlestars, nematodes, polychaetes) and all invertebrate benthic carnivores/ scavengers (e.g. crabs, lobsters, sea urchins, starfish).

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The factors examined in the sensitivity analysis are presented in tables 1 and 2. Further information regarding driving data are given in the supplementary material, with nominal parameter values given in table 1. There follows a brief overview of the Morris and Sobol methods.

2.2. Morris sensitivity analysis

The Morris method is an OAT design as only one input factor (x_i) is altered between successive runs of the model. The input space of each factor has p levels in a uniform [0,1] probability distribution function (PDF) that is rescaled for the actual value that is used in the model. The elementary effect for the ith input factor is calculated from the successive runs using

$$EE_i(X) = \frac{y(x_1 \ldots x_{i-1}, x_i + \Delta, \ldots, x_n) - y(x_1 \ldots x_n)}{\Delta} \qquad (1)$$

where $\Delta = p/[2(p-1)]$ and p is even. Each factor is modified once resulting in $n+1$ runs of the model.

The procedure is repeated r times providing r elementary effects for each factor, (r being referred to as the trajectory of the factor sample space). The sensitivity measures, as suggested by Morris (1991), are the mean μ_i and the standard deviation σ_i of each elementary effect across all trajectories. The mean captures the impact that uncertainty in the factor input has on the model output, thus indicating important factors, while the standard deviation indicates nonlinear responses to factor values and/or interactions with other factors. An alternative to μ is $\mu^\star$ that represents the mean of the absolute values of the elementary effects (Campanolongo et al., 2007).

$$\mu_i^\star = \frac{1}{r} \sum_{j=1}^{r} \left| EE_i^j \right| \qquad (2)$$

This measure is widely used as it reduces type II errors, that can be encountered when using μ and is the one adopted in this paper.

As the runs of the model represent a trajectory within the factor sample space, it is recommended to optimise the choice of trajectories to facilitate maximising their spread in the input domain, prior to conducting the analysis (Campolongo et al., 2007; Saltelli et al., 2008). Therefore 1000 trajectories were created, each with 4 levels, and the 50 with the highest spread d, based on the

sum of geometric distances between trajectory pairs m and l were selected using

$$d_{ml} = \begin{cases} \sum_{i=1}^{n+1} \sum_{j=1}^{n+1} \sqrt{\sum_{z=1}^{n} \left[X_z^{(i)}(m) - X_z^{(j)}(l) \right]^2} \\ 0 \end{cases} \tag{3}$$

where n is the number of input factors and $X_z^{(i)}(m)$ represents the zth coordinate of the ith point of the mth trajectory. The euclidean distances D between all the possible pairs of selected trajectories were calculated and the 10 that represented the highest value of D were used in the elementary effects method (i.e. $r = 10, p = 4$).

2.3. Sobol sensitivity analysis

The method used was initially developed by Sobol (1993) with further refinements by Saltelli (2002) as reviewed by Saltelli et al. (2008), and is based on the decomposition of the output variance of the model in question, which can be represented by

$$Y = f(X) = f(X_1, \ldots, X_n) \tag{4}$$

where Y is the model output, and $X = (X_1 \ldots X_n)$ is the set of factors. The variance decomposition of f being

$$V(Y) = \sum_{i=1}^{n} V_i + \sum_{i=1}^{n} \sum_{j=i+1}^{n} V_{ij} \ldots + V_{1\ldots,n} \tag{5}$$

where X has been scaled between 0 and 1, to form a n-dimensional unit hyperspace Ω^n; $V(Y)$ is the total variance; V_i is the partial variance, of X_i on Y and is given by $V_i = V[E(Y \mid X_i)]$, also known as 'main effect', while V_{ij} is the impact of X_i and X_j on the total variance minus their first order effects. Using this variance decomposition, the first order sensitivity S_i, and the total effect sensitivity index S_{ti} are given by Saltelli et al. (2008) as

$$S_i = \frac{V[E(Y \mid X_i)]}{V(Y)} \tag{6}$$

$$S_{ti} = 1 - \frac{V[E(Y \mid X_{\sim i})]}{V(Y)} \tag{7}$$

The Monte Carlo based procedure proposed by Saltelli et al. (2008), using quasi-random sampling of model factors, was used to obtain the first order and total effects indices for each factor.

2.4. Implementation of Sensitivity Analyses

The sensitivity analysis was coded in R 2.15.01 (R core Team, 2012). All computations were conducted on a desktop PC. The implementation of StrathE2E in the sensitivity analysis, was identical to the one previously detailed in Heath (2012), representing the same fisheries and spatial domain, with identical nominal values for parameter data (table 1), driving data and fishing rates (table 2).

As probability distributions were not known for the parameters (s1-s122), uniform distributions with bounds varying 10% either side of the nominal values were chosen. For the driving data and fishing rates (d1,d6-d24), the datasets in the original model description (Heath, 2012) were used (see supplementary data). For driver d1 (Sea surface irradiance), additional data was obtained from the Weybourne data archive (Weybourne Atmospheric Observatory, 2006). For the benthic invertebrate fishing rate drivers (d25 & d26), the original model only used fishing data from a single timepoint. Therefore the demersal fishing rate distribution was chosen to represent the benthic invertebrate fishing rates. Inverse cumulative distribution functions were calculated for the monthly data of each of these drivers. For drivers (d2-d5), originally calculated from simulation and limited sampling, uniform distributions with bounds varying 10% either side of the nominal values were chosen using transformations where appropriate. These distributions were used to derive the input values to both the Morris and Sobol methods for a specified probability. For the Sobol method the entire range of the distribution was used, while for the Morris method the distribution was split into p+1 (i.e. 5) equal intervals and the values at the center of the bins used (Saltelli et al., 2008).

For all of the analyses, the model was run for 40 years to approximate a stationary annual cycle, and the final year data used. The model outputs examined were the biomasses of pelagic fish adults, pelagic fish larvae, demersal fish adults, demersal fish larvae, suspension feeding benthos and carnivorous/ scavenging benthos.

The StathE2E model produces time-dependant outputs, that can be analysed by calculating the sensitivity indices at each time point, resulting in a time-varying sensitivity analysis. While this approach can be useful for identifying which factors are influential at particular times, for this study a single measure was preferred, so that influential factors could be identified across the whole of the model output. Two complimentary methods were used independently to reduce the dimensionality of the model outputs immediately prior to the calculation of the sensitivity indices: integration and functional principal component analysis (fPCA) (Sumner et al., 2012). While integration allows

sensitivity indices relating to absolute biomasses to be calculated, the results of the fPCA can indicate when other features of the model output have been affected by a factor.

The $\mu^\star$ statistic was used to rank the results of the Morris method. The 10 factors with the highest value of $\mu^\star$ for each of the fisheries outputs, were collated from the analysis, and re-analysed using the Sobol method. To ensure convergence of the sensitivity indices, a sample size of 15,000 was used, leading to 540,000 model evaluations.

3. Results

3.1 Morris sensitivity analysis

The results of the Morris sensitivity analysis are presented in figures 2-7, as plots of the values of $\mu^\star$ against the corresponding standard deviation. The collation of the 10 highest ranked factors based on $\mu^\star$ values from all outputs of interest, resulted in 6 drivers and 28 parameters being included in the subsequent Sobol analysis (Tables 3-5). The rankings obtained by fPCA and integration were identical.

3.2 Sobol sensitivity analysis

The resulting indices for the 34 factors are presented in figures 8-13. Comparison of the Sobol analysis using fPCA and integration indicated no notable differences between the results obtained by the two techniques, implying that total biomass was the main feature of the output runs altered during the analyses. For all outputs the sum of the first order sensitivity indices were less than one, indicating that the model was non-additive.

3.3 Comparison of method outputs

The top ten rankings from each of the six outputs from the Sobol analysis are compared to the rankings obtained from the results of the Morris method (tables 4-6). The two methods produced marginally different results. This difference is to be expected as the Morris method has a limited exploration of the input factor space when compared to the Sobol method and is indicative of non-linearities in the response of the model to changes in factor values. The rankings however, concurred regarding those factors that could be regarded as highly influential, with the exception of demersal fishing in the pelagic fish outputs. This parameter was influential in the Sobol analysis but was not so highly ranked using the Morris method. The following results consider the Sobol sensitivity analysis only.

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3.3.1. Suspension/deposit feeding benthos

Three factors (i.e. Deep temperature (d9), Deep nitrate (d14) and Deep layer thickness(s2)) were highly influential with sensitivity indices over two times larger than the other factors (Figure 8). Deep temperature (d9) was the most influential factor regarding the biomass of the suspension/ deposit feeding benthos. The first order sensitivity index was almost identical to the total sensitivity of this factor indicating that it has a direct effect on the biomass of this benthic guild. The differences in first order and total sensitivity indices of deep nitrate and the thickness of the deep layer indicates that these factors interact with additional factor(s) in the model. The other factors with total sensitivity indices >0.05, had relatively marginal influence and were irradiance (d1), deep detritus (d18), irradiance of maximum phytoplankton nutrient uptake (s6), nitrate upgtake rate by phytoplankton (s14), biomass conversion of suspension feeding benthos (s78) and biomass excretion by suspension feeding benthos (s87).

3.3.2. Carnivorous/ scavenging benthos

Three factors (i.e. Uptake rate of scavenging benthos (s64), uptake converted to biomass of scavenging benthos (s79) and biomass excreted by scavenging benthos (s88)) were highly influential regarding the biomass of carnivorous/scavenging benthos (Figure 9). The sensitivity indices of these factors were over three times larger than other factors regarding this guild. While there were differences between the first order and total sensitivity indices, indicating factor interactions, the relative size of the three main factor indices suggest that they are primarily responsible for determining the biomass of the carnivorous/ scavenging benthos guild.

3.3.3. Pelagic fish

The sensitivity indices for pelagic fish adults and pelagic fish larvae were comparable, demonstrating similar profiles regarding the influence of factors (Figures 10 & 11). For both, the impact of pelagic fishing (d24) and demersal fishing (d23) were the two most influential factors on the resultant biomasses. However, the relative magnitude of the these indices was different for the two outputs with the fishing factors having less influence on pelagic fish larvae than for the pelagic fish adults. For the remaining factors, the sensitivity indices were all slightly higher for the pelagic fish larvae compared to the pelagic fish adults, however the overall profile remained the same.

Excluding demersal fishing, the sensitivity indices for pelagic fishing were over two times larger than other factors for the pelagic fish larvae and over three times larger for the pelagic fish adults.

Demersal fishing sensitivity indices were 50% larger than the other non fishing factors for pelagic fish larvae, and two times larger than the other non-fishing factors for pelagic adult fish. For the pelagic fish larvae, biomass conversion by pelagic fish larvae (s80), uptake of herbivorous zooplankton by pelagic larvae (s28) and the half saturation constant of herbivorous zooplankton uptake by pelagic larvae (s29) were factors of marginal influence (sensitivity indices >0.05). The indices of these factors had slightly lower indices for pelagic adult fish, but again they were considered to have an influence (sensitivity indices >0.05). Comparison of the first order sensitivity indices with the total sensitivity indices suggested that while influential factors were directly affecting the output, interactions with other factors were also occurring.

3.3.4. Demersal fish

Demersal fishing was the influential factor on demersal fish larvae and demersal fish adult biomass (Figures 12 & 13). Its influence was greater on the demersal adult fish guild as compared to the demersal larval guild with indices over 5 times and 3 times greater respectively than the other factors. The total sensitivity indices of most of the other factors had relatively low first order indices when compared to the total sensitivity index suggesting that while most of the factors seemed to exert an influence (total sensitivity indices >0.05), this was due to interactions within the model. An exception to this was biomass conversion by demersal fish larvae (s81) for which the two indices were comparable, suggesting that this factor had a direct effect on the demersal fish outputs.

4. Discussion

Ecosystem models that combine environmental, biological and fishing data are recognised as important in understanding the effects of climate change and ocean acidification on fisheries (Le Quense and Pinnegar, 2012; Mackinson et al., 2009; Travers et al., 2007). We report on the results of a global sensitivity analysis conducted on one of these end-to-end ecosystem models that incorporates the impact of fishing and environmental drivers on a marine food web.

The advantages of global sensitivity analysis over local one-at-a-time methods are well documented, however, it is the latter that have dominated the modelling literature (Saltelli and Annoni, 2010). An assumption of substantially increased computational cost may in part have contributed to this. The methodology where the results of the Morris method are used to screen factors for inclusion into the more computationally intensive Sobol method has been successfully used across

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modelling disciplines to reduce computational times (e.g. Ciric et al., 2012; Salacinska et al., 2010; Saltelli and Annoni 2010). For StrathE2E, this approach was also considered successful. For other end-to-end ecosystem models, the model run-times may make the Sobol variance method computationally expensive, even with a pre-screening step. In these cases the Morris method alone could be used to identify sets of influential and non-influential factors to comprise a qualitative assessment of factor influence as has already been used for some lower trophic aquatic food web models (Ciric et al., 2012; Zheng et al., 2012). Continued refinements to the methodology mean that this is increasingly being used as a stand alone method for the sensitivity analysis of complex models (Campolongo et al., 2011; Zheng et al., 2012). For those end-to-end models that are computationally very expensive to run, the use of emulators may be appropriate (Saltelli et al., 2008; Saltelli and Annoni, 2010; Scott et al., 2011).

The results of the Sobol analysis on StrathE2E, suggests that as a functional model, the structure of which reflects the interactions between main ecosystem components, insights may be obtained regarding the relative contributions that individual factors have on the fishery guilds. It is notable that the four fishery guilds represented are sensitive to different groups of factors. As StrathE2E does not model individual species, changes in influential factor values for example those associated with environmental change, would be realised in the North Sea ecosystem as alterations in total guild biomass based on extant species composition.

For the suspension feeding benthos guild, deep temperature (d9) was the most influential factor. If StrathE2E is accepted as an accurate representation of the North Sea, changes in deep temperature will have a direct impact on the resultant biomass of suspension feeding benthos. This is obviously of pertinence in the context of climate change, as increases of 0.2 to 0.6^{o}C per decade have been recorded in the seas around the UK and Ireland (Rayner et al., 2003). The influence of this factor also concurs with experimental studies that show temperature as a major environmental factor affecting benthic filter feeders development, distribution and recruitment (reviewed by Byrne, 2011) and other North Sea ecosystem modelling efforts that have also reported temperature related changes to this guilds biomass (van der Molen et al., 2013). Deep nitrate (d15) and the thickness of the deep layer (s2) were also identified as influential environmental parameters in StrathE2E, as were factors associated with primary production. In the model, mechanisms for the transfer of nitrogen to the benthic filter feeding guild exist through the deep layer detritus, deep phytoplankton, and secondary producers (figure 1). The parameters identified therefore reflect the importance

of primary production over secondary production for the transfer of biomass to the filter feeding guild.

The two parameters, proportion of uptake converted to suspension feeder biomass (s78), and the uptake rate of nitrate by phytoplankton (s14), are of particular interest in relation to modelling the impacts of environmental change on the filter feeder guild. Two meta-analyses have suggested that ocean acidification will negatively affect the growth of benthic filter feeding invertebrates and this will be acerbated by increased temperatures (Harvey et al., 2013; Kroeker et al., 2013). In contrast, phytoplankton growth will be positively affected by ocean acidification and temperature (Harvey et al., 2013; Kroeker et al., 2013). Recent experimental and field studies have suggested that for the suspension feeder *Mytilus edulis*, increased food availability counteracts the negative effects of ocean acidification (Thomsen et al., 2013). However, while the amount of North Sea phytoplankton biomass is increasing there has been a significant regime shift to species of lower nitrogen content (McQuatters-Gollop et al., 2007). There is therefore obvious potential for the StrathE2E model to further examine the sensitivity of the filter feeding guild to the complex interplay of these parameters.

The three parameters that have a dominant influence on the carnivorous/scavenging benthos guild are related to food acquisition and biomass conversion/excretion rates. This suggests that members of this guild are not overly affected by the environmental drivers and other external parameters included in the model, but are largely governed by their ability to obtain food and metabolise it. This is in contrast with the results of the sensitivity analysis on the suspension feeding benthic guild, where multiple factors are of influence. Experimental studies have suggested that these two guilds will be affected differently by CO_2 induced environmental changes, (Harvey et al., 2013; Kroeker et al., 2013) and to an extent this appears to be reflected in the model.

Heath (2012) examined the effect of fishing on the benthic productivity, conducting a preliminary OAT analysis using StrathE2E. This suggested that demersal fishing rates affected the benthic food web. Although fishing rates do exert an influence on the benthic guilds, this is insignificant compared to the factors already identified.

By far the most important factor for both demersal and pelagic fish guilds was their respective fishing rates. This is unsurprising, as it is well documented that fishing can have a direct effect on fish numbers. Using StrathE2E, Heath (2012) reported that demersal and pelagic fishing affected the resultant biomass of both the demersal and pelagic fish guilds, thus highlighting linkages between

them. The sensitivity analysis concurs with this observation, but further indicated that demersal fishing is far more influential to pelagic fish biomass than pelagic fishing is to demersal fish biomass. Previous examination of marine ecosystem models has indicated that while fishing is an important influence on fish biomass, it is not a deterministic response, as complex food web interactions between species, and trophic levels make species responses difficult to predict (Mackinson et al., 2009; Speirs et al., 2010). The differences observed between the total and first order sensitivity indices of the fishing rates concurred with this, indicating that within the model, fishing was very influential but interactions with other factors did occur to produce the resultant outputs. Previous studies have highlighted the difficulties inherent in identifying possible impacts of environmental change on North Sea fisheries due to the effects that commercial fishing has on demersal and pelagic fish numbers (Pitois et al., 2012). By fixing fishing rates in the StrathE2E model, the impacts of factors associated with environmental change could be further explored to identify their relative importance assessed for the fish stocks.

A notable difference between the pelagic and demersal guilds was that significant interactions occurred between many of the factors to influence the demersal guild biomass, while the pelagic guild was influenced by fewer factors, with less interactions between them. This is likely to be a reflection of the extensive linkages of the demersal species to both the benthic, demersal and pelagic food webs, while the pelagic fish species were limited to the pelagic web (Heath, 2012). Because of interactions, multiple factors may therefore need to be varied to cause substantial changes in the output biomass of the demersal fishery making this guild relatively robust to single factor change, in comparison to the pelagic guild.

For both fish guilds, changes in parameter value are more influential on larval fish stages than their adult counterparts. For the larval stages, uptake rates and half saturation constants of herbivorous zooplankton uptake by fish larvae (s28, s29, s38, s39), together with the proportion of this uptake converted to fish biomass (s80, s81) were identified as influential. Although the direct effects of temperature on fish are well documented, North Sea larval fish populations are probably influenced by climate indirectly through bottom-up effects impacting on plankton availability (Alvarez-Fernandez et al., 2012; Pitois et al., 2012). Therefore the model appears to reflect this distinction through the influence of factors relating to the uptake and conversion of herbivorous zooplankton rather than temperature. Studies on ocean acidification have indicated that larval stages will be affected most through changes in their growth and mortality rates (Baumann et al.,

2012; Frommel et al., 2012). Varying mortality rates of larvae and eggs by $\pm 8\%$ was not identified as influential in the Morris method analysis and therefore it would appear that only large scale mortalities on this life stage would affect recruitment. In contrast, those parameters associated with growth (s80, s81) were identified as influential. The similarity between the first order sensitivity indices and their respective total sensitivity indices suggests that any changes in these parameters will be directly reflected in the biomass of the demersal and pelagic fish guilds.

In conclusion, a global sensitivity analysis was conducted on StrathE2E, an end-to-end marine ecosystem model that was parameterised using fisheries and environmental data of the North Sea. The analysis identified that each of the fishery guilds of the model were influenced by different drivers and parameters. Carnivorous/ scavenging invertebrate benthos appeared to be the most resilient guild to potential environmental influence, provided their rate of biomass conversion was not affected. This parameter was found to be influential for all of the other guilds examined and suggests that representing environmental stressors such as ocean acidification in the model as changes to metabolic parameters, could lead to wide ranging impacts on fisheries productivity. Future work should aim to extend the sensitivity analysis to specifically explore the response of the guilds to predicted future temperature profiles and changes of factors in response to the environmental pressures highlighted. For filter feeding benthic invertebrates, examination of second order interactions should also be conducted to try an elucidate the relationships between temperature and uptake rates.

5. Acknowledgements

6. References

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Table 1: Static parameters of StrathE2E model

Reference	Parameter	Value	Unit	Definition
s1	thik_s	28	m	Thickness of surface layer bounded by sea surface and 30m
s2	thik_d	42	m	Thickness of deep layer bounded by 30m and seabed
s3	thik_x	0.1	m	Thickness of sediment layer
s4	porosity	0.45	m^3m^{-3}	Proportion of water in seabed sediment
s5	thik_r	10	m	Thickness of bottom boundary layer (for benthos feeding)
s6	Lmaxup	5	$E.m^2.d^{-1}$	Irradiance at maximum nutrient uptake by phytoplankton
s7	sed_wat_dif	$1x10^{-6}$	m^2d^{-1}	Coefficient of vertical flux between sediment pore water and deep layer
s8	qtena	2		Q_{10} uptake value for autotrophs
s9	qtenh	2.2		Q_{10} uptake value for heterotrophs
s10	qtenm	2.4		Q_{10} uptake and metabolic value for bacteria
s11	qtenr	10		Q_{10} reference value
s12	p_pref	0.95748		Preference of zooplankton for plankton
s13	d_pref	0.04251		Preference of zooplankton for detritus
s14	uNIT_phytt	1.03476	$mMN.m^{-2}.d^{-1}$	Uptake rate of nitrate by phytoplankton
s15	hsNIT_phytt	16.57074	$mMN.m^{-3}$	Half saturation constant of nitrate uptake by phytoplankton
s16	uAMM_phytt	2.15309	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of ammonia by phytoplankton
s17	hsAMM_phytt	16.57074	$mMN.m^{-3}$	Half saturation constant of ammonia uptake by phytoplankton
s18	uphyt_herbt	1.14055	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of phytoplankton by herbivorous zooplankton
s19	hsphyt_herb	4.84752	$mMN.m^{-3}$	Half saturation constant of phytoplankton uptake by herbivorous zooplankton
s20	udet_herbt	0.050643	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of detritus by herbivorous zooplankton
s21	hsdet_herb	4.84752	$mMN.m^{-3}$	Half saturation constant of detritus uptake by herbivorous zooplankton
s22	uherb_carnt	0.27134	$mMN.m^{-2}.d^{-1}$	Maximum uptake of herbivorous zooplankton by carnivorous zooplankton
s23	hsherb_carn	1.82208	$mMN.m^{-3}$	Half saturation constant of herbivorous zooplankton uptake by carnivorous zooplankton
s24	ufishplar_carn	0.030827	$mMN.m^{-2}.d^{-1}$	Maximum uptake of pelagic fish larvae by carnivorous zooplankton
s25	hsfishplar_carn	1.82208	$mMN.m^{-3}$	Half saturation constant of pelagic fish larvae uptake by carnivorous zooplankton
s26	ufishdlar_carn	0.0118	$mMN.m^{-2}.d^{-1}$	Maximum uptake of demersal fish larvae by carnivorous zooplankton
s27	hsfishdlar_carn	1.82208	$mMN.m^{-3}$	Half saturation constant of demersal fish larvae uptake by carnivorous zooplankton
s28	uherb_fishplart	0.51189	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of herbivorous zooplankton by pelagic fish larvae
s29	hsherb_fishplar	6.43283	$mMN.m^{-3}$	Half saturation constant of herbivorous zooplankton by pelagic fish larvae
s30	uherb_fishpt	0.04884	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of herbivorous zooplankton by pelagic fish
s31	hsherb_fishp	1.29974	$mMN.m^{-3}$	Half saturation constant of herbivorous zooplankton by pelagic fish
s32	ucarn_fishpt	0.01272	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of carnivorous zooplankton by pelagic fish
s33	hscarn_fishpt	1.29974	$mMN.m^{-3}$	Half saturation constant of carnivorous zooplankton by pelagic fish
s34	ufishdlar_fishpt	0.00093	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of demersal fish larvae by pelagic fish
s35	hsfishdlar_fishpt	1.29974	$mMN.m^{-3}$	Half saturation constant of demersal fish uptake by pelagic fish
s36	ufishplar_fishpt	0.00307	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of pelagic fish larvae by pelagic fish
s37	hsfishplar_fishp	1.29974	$mMN.m^{-3}$	Half saturation constant of pelagic fish larvae uptake by pelagic fish
s38	uherb_fishdlart	0.22005	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of herbivorous zooplankton by demersal fish larvae
s39	hsherb_fishdlar	2.49093	$mMN.m^{-3}$	Half saturation constant of herbivorous zooplankton by demersal fish larvae
s40	ucarn_fishdt	0.0003	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of carnivorous zooplankton by demersal fish
s41	hscarn_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of carnivorous zooplankton by demersal fish
s42	ubenths_fishdt	0.00524	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of benthic suspension feeders by demersal fish
s43	hsbenths_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of benthic suspension feeders rate by demersal fish
s44	ubenthc_fishdt	0.00045	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of benthic carnivores by demersal fish
s45	hsbenthc_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of benthic carnivore uptake by demersal fish
s46	ufishplar_fishdt	0.00182	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of pelagic fish larvae by demersal fish
s47	hsfishplar_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of pelagic fish larvae uptake by demersal fish
s48	ufishdlar_fishdt	0.00092	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of demersal fish larvae by demersal fish

Table 1: Static parameters of StrathE2E model

Reference	Parameter	Value	Unit	Definition
s49	hsfishdlar_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of demersal fish larvae uptake by demersal fish
s50	ufishp_fishdt	0.00204	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of pelagic fish by demersal fish
s51	hsfishp_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of pelagic fish uptake by demersal fish
s52	ufishd_fishdt	0.0018	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of demersal fish larvae by demersal fish
s53	hsfishd_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of demersal fish larvae uptake by demersal fish
s54	udisc_fishdt	0.00141	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of discards by demersal fish
s55	hsdisc_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of discards uptake rate by demersal fish
s56	ucorp_fishdt	0.00034	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of corpses by demersal fish
s57	hscorp_fishd	0.34059	$mMN.m^{-3}$	Half saturation constant of corpses uptake by demersal fish
s58	uphyt_benthst	1.12143	$mMN.m^{-2}$	Maximum uptake rate of phytoplankton by benthic suspension feeders
s59	hsphyt_benths	145.6142	$mMN.m^{-2}$	Half saturation constant of phytoplankton uptake by benthic suspension feeders
s60	udet_benthst	2.23109	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of suspended detritus by benthic suspension feeders
s61	hsdet_benths	145.6142	$mMN.m^{-2}$	Half saturation constant of suspended detritus uptake by benthic suspension feeders
s62	used_benths	0.05326	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of sediment detritus by suspension feeding benthos
s63	hssed_benths	145.6142	$mMN.m^{-2}$	Half saturation constant of sediment detritus uptake by suspension feeding benthos
s64	ubenths_benthct	0.02817	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of suspension feeding benthos by scavenging benthos
s65	hsbenths_benthc	6.64709	$mMN.m^{-2}$	Half saturation constant of suspension feeding benthos uptake by scavenging benthos
s66	ucorp_benthct	0.03088	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of corpses by scavenging benthos
s67	hscorp_benthc	6.64709	$mMN.m^{-2}$	Half saturation constant of corpse uptake by scavenging benthos
s68	ufishp_bird	0.00881	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of pelagic fish by birds and mammals
s69	hsfishp_bird	1.57222	$mMN.m^{-3}$	Half saturation constant of pelagic fish uptake by birds and mammals
s70	ufishd_bird	0.03239	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of demersal fish by birds and mammals
s71	hsfishd_bird	1.57222	$mMN.m^{-3}$	Half saturation constant of demersal fish uptake by birds and mammals
s72	udisc_bird	0.07565	$mMN.m^{-2}.d^{-1}$	Maximum uptake of discards by birds and mammals
s73	hsdisc_bird	1.57222	$mMN.m^{-3}$	Half saturation constant of discard rate of birds and mammals
s74	ucorp_bird	0.02003	$mMN.m^{-2}.d^{-1}$	Maximum uptake rate of corpses by birds and mammals
s75	hscorp_bird	1.57222	$mMN.m^{-3}$	Half saturation constant of corpse uptake by birds and mammals
s76	aH	0.34		Proportion of uptake converted to biomass by herbivorous zooplankton
s77	aC	0.34		Proportion of uptake converted to biomass by carnivorous zooplankton
s78	aBs	0.34		Proportion of uptake converted to biomass by suspension feeding benthos
s79	aBc	0.34		Proportion of uptake converted to biomass by scavenging benthos
s80	aFplar	0.34		Proportion of uptake converted to biomass by pelagic fish larvae
s81	aFdlar	0.34		Proportion of uptake converted to biomass by demersal fish larvae
s82	aFp	0.275		Proportion of uptake converted to biomass by pelagic fish adults
s83	aFd	0.25		Proportion of uptake converted to biomass by demersal fish adults
s84	abird	0.15		Proportion of uptake converted to biomass by birds and mammals
s85	eHt	0.01	d^{-1}	Rate of biomass excreted by herbivorous zooplankton
s86	eCt	0.005	d^{-1}	Rate of biomass excreted by carnivorous zooplankton
s87	eBst	0.01	d^{-1}	Rate of biomass excreted by suspension feeding benthos
s88	eBct	0.0075	d^{-1}	Rate of biomass excreted by scavenging benthos
s89	eFplart	0.00005	d^{-1}	Rate of biomass excreted by pelagic fish larvae
s90	eFdlart	0.00005	d^{-1}	Rate of biomass excreted by demersal fish larvae
s91	eFpt	0.001	d^{-1}	Rate of biomass excreted by pelagic fish adults
s92	eFdt	0.001	d^{-1}	Rate of biomass excreted by demersal fish adults
s93	ebird	0.00014	d^{-1}	Rate of biomass excreted by birds and mammals
s94	mt	0.00831	d^{-1}	Rate of mineralisation at reference temperature
s95	nst	0.00391	d^{-1}	Rate of nitrification in surface layer at reference temperature

Table 1: Static parameters of StrathE2E model

Reference	Parameter	Value	Unit	Definition
s96	dst	0.00004	d^{-1}	Rate of denitrification in deep layer at reference temperature
s97	ndt	0.04577	d^{-1}	Rate of nitrification in deep layer at reference temperature
s98	ddt	0.00006	d^{-1}	Rate of denitrification in deep layer at reference temperature
s99	msedt	0.00799	d^{-1}	Rate of mineralisation in sediment at reference temperature
s100	nsedt	0.03203	d^{-1}	Rate of nitrification in sediment at reference temperature
s101	dsedt	0.32545	d^{-1}	Rate of denitrification in sediment at reference temperature
s102	xst	0.0308	d^{-1}	Death rate of surface phytoplankton
s103	xdt	0.05362	d^{-1}	Death rate of deep phytoplankton
s104	xcarn	0.00058		Coefficient of density dependant mortality for carnivorous zooplankton
s105	xbenthc	0.00047		Coefficient of density dependant mortality for benthic carnivores
s106	xpfishlar	1.9×10^{-6}		Coefficient of density dependant mortality for pelagic fish larvae
s107	xdfishlar	1.2×10^{-6}		Coefficient of density dependant mortality for demersal fish larvae
s108	xpfish	0.00004		Coefficient of density dependant mortality for pelagic fish
s109	xdfish	0.00005		Coefficient of density dependant mortality for demersal fish
s110	xbird	0.055		Coefficient of density dependant mortality for birds/mammals
s111	dsink_s	0.14588	d^{-1}	Sinking rate of detritus in surface layer
s112	dsinkd_klow	0.22159	d^{-1}	Sinking rate of detritus in deep layer
s113	dsink_dkhi	0.0463	d^{-1}	Mixing rate of detritus between layers
s114	Pdiscard	0.1		Fraction of pelagic fish catch discarded
s115	Sdiscard	0.12		Fraction of shellfish catch discarded
s116	dfdp	0.09041		Coefficient for biomass dependency for demersal catch discards
s117	bendamage	0.001		Proportion of demersal fishing as mortality on suspension feeding benthos
s118	demdamage	0		Proportion of demersal fishing as mortality on carnivorous benthos
s119	disc_corp	0.42938	d^{-1}	Rate of discards sinking to become seabed corpses
s120	xcorp_det	0.09064	d^{-1}	Conversion rate of corpse mass to detritus at reference temperature
s121	DF_fecundity	0.4	g.g^{-1}	Demersal fish fecundity
s122	PF_fecundity	0.25	g.g^{-1}	Pelagic fish fecundity

Table 2: Time dependant drivers and fishing rates

Reference	Parameter	Unit	Description
d1	slight	$Em^{-2}d^{-1}$	Sea surface irradiance
d2	logespm	$mg\ m^{-3}$	Suspended particulate matter
d3	logkvert	m^{-1}	Vertical attenuation coefficient of irradiance
d4	mixlscale	m^2s^{-1}	Vertical diffusion coefficient
d5	sinflow	d^{-1}	Flushing rate of surface layer by open ocean boundaries
d6	dinflow	d^{-1}	Flushing rate of deep layer by open ocean boundaries
d7	rivervol	d^{-1}	Flushing rate of surface layer by river inputs
d8	stemp	^{o}C	Temperature of surface layer
d9	dtemp	^{o}C	Temperature of deep layer
d10	s_nitrate	$mMNm^{-3}$	Boundary concentration of surface layer nitrate
d11	s_ammonia	$mMNm^{-3}$	Boundary concentration of surface layer ammonia
d12	s_phyt	$mMNm^{-3}$	Boundary concentration of surface layer phytoplankton
d13	s_uzoo	$mMNm^{-3}$	Boundary concentration of surface layer zooplankton
d14	d_nitrate	$mMNm^{-3}$	Boundary concentration of deep layer nitrate
d15	d_ammonia	$mMNm^{-3}$	Boundary concentration of deep layer ammonia
d16	d_phyt	$mMNm^{-3}$	Boundary concentration of deep layer phytoplankton
d17	d_uzoo	$mMNm^{-3}$	Boundary concentration of deep layer zooplankton
d18	d_detritus	$mMNm^{-3}$	Boundary concentration of deep layer detritus
d19	riv_nitrate	$mMNm^{-3}$	Volume weighted river nitrate concentrations
d20	riv_ammonia	$mMNm^{-3}$	Volume weighted river ammonia concentrations
d21	atmnitrate	$mMNm^{-2}d^{-1}$	Deposition rate of nitrate from atmosphere into surface layer
d22	atmammonia	$mMNm^{-2}d^{-1}$	Deposition rate of ammonia from atmosphere into surface layer
d23	DF	d^{-1}	Demersal fishery harvest rate
d24	PF	d^{-1}	Pelagic fishery harvest rate
d25	BC	d^{-1}	Benthic carnivore harvest rate
d26	BS	d^{-1}	Benthic suspension feeders harvest rate

Table 3: Factor rankings for pelagic fish

Rank	Pelagic fish larvae		Pelagic fish adults	
	Morris	Sobol	Morris	Sobol
1	Pelagic fishing (d26)	Pelagic fishing(d26)	Pelagic fishing (d26)	Pelagic fishing (d26)
2	aFplar (s80)	Demersal fishing (d25)	aFplar (s80)	Demersal fishing (d25)
3	hsherb_fishplar (s29)	aFplar (s80)	uherb_carnt (s22)	aFp (s82)
4	uherb_carnt (s22)	uherb_fishplart (s28)	Demersal fishing (d25)	aFplar (s80)
5	uherb_fishplart (s28)	hsherb_fishplar (s29)	hsherb_fishplar (s29)	uherb_fishplart (s28)
6	thik_d (s2)	uherb_carnt (s22)	aFp (s82)	uherb_fishpt (s30)
7	aC (s77)	aC (s77)	uherb_fishplart (s28)	Deep temperature (d9)
8	Demersal fishing (d25)	aFp (s82)	aC (s77)	hsherb_fishplar (s29)
9	hsherb_carn (s23)	Deep temperature (d9)	hsherb_fishp (s31)	aFdlar (s81)
10	aFp (s82)	aFdlar (s81)	uherb_fishpt (s30)	uherb_carnt (s22)

Table 4: Factor rankings for demersal fish

Rank	Demersal fish larvae		Demersal fish adults	
	Morris	**Sobol**	**Morris**	**Sobol**
1	Demersal fishing (d25)	Demersal fishing (d25)	Demersal fishing (d25)	Demersal fishing (d25)
2	aH (s76)	uherb_fishdlart (s38)	aH (s76)	uherb_fishdlart (s38)
3	aFdlar (s81)	aH (s76)	aFdlar (s81)	aH (s76)
4	DF_fecundity (s121)	Deep nitrate (d15)	uherb_fishdlart (s38)	Deep nitrate (d15)
5	hsherb_fishdlar (s39)	uphyt_herbt (s18)	aFd (s83)	aFd (s83)
6	uphyt_herbt (s18)	hsherb_fishdlar (s39)	hsherb_fishdlar (s39)	uphyt_herbt (s18)
7	uherb_fishdlart (s38)	DF_fecundity (s121)	Deep nitrate (d15)	hsherb_fishdlar (s39)
8	aFd (s83)	Pelagic fishing (d26)	uphyt_herbt (s18)	thik_d (s2)
9	Pelagic fishing (d26)	aFd (s83)	eFdt (s92)	aFdlar (s81)
10	Deep nitrate (d15)	thik_d (s2)	DF_fecundity	Pelagic fishing (d26)

Table 5: Factor rankings for benthic invertebrates

Rank	Suspension feeding benthos		Carnivorous/ scavenging benthos	
	Morris	**Sobol**	**Morris**	**Sobol**
1	thik_d (s2)	Deep temperature (d9)	aBc (s79)	aBc (s79)
2	Deep temperature (d9)	Deep nitrate (d15)	ubenths_benthct (s64)	ubenths_benthct (s64)
3	Deep nitrate (d15)	thik_d	eBct (s88)	eBct (s88)
4	eBst (s87)	Irradiance (d1)	Pelagic fishing (d26)	xbenthc (s105)
5	Lmaxup (s6)	eBst (s87)	xbenthc (s105)	Pelagic fishing (d26)
6	uNIT_phytt (s14)	Lmaxup (s6)	aC (s77)	Deep nitrate (d15)
7	aBs (s78)	Deep detritus (d20)	Deep temperature (d9)	thik_d (s2)
8	Deep detritus (d20)	uNIT_phytt (s14)	uherb_carnt (s22)	Demersal fishing (d25)
9	Irradiance (d1)	aBs (s78)	qtenh (s9)	aC (s77)
10	hsNIT_phytt (s15)	uphyt_herbt (s18)	thik_d (s2)	uherb_carnt (s22)
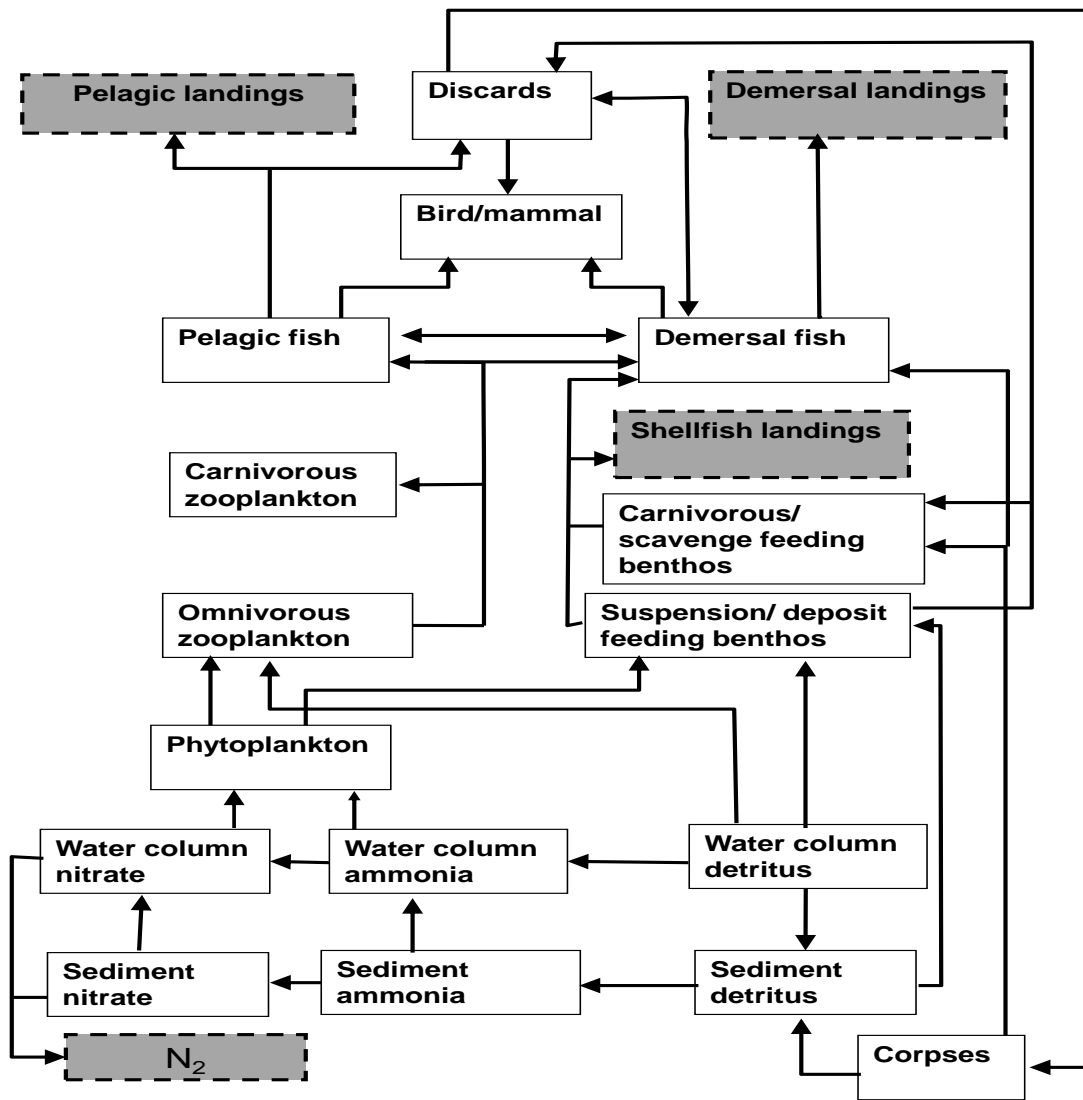
Figure 1: Schematic showing the StrathE2E North Sea food web model components and fluxes. Grey boxes represent exports from the food web due to biochemistry and fishing; white boxes represent state variables and arrows show biogeochemical and feeding fluxes. Not shown are the subdivisions by depth layer or sediment; transport and mixing fluxes; excretion fluxes to ammonia or the density dependant mortality fluxes to corpses (after Heath 2012)
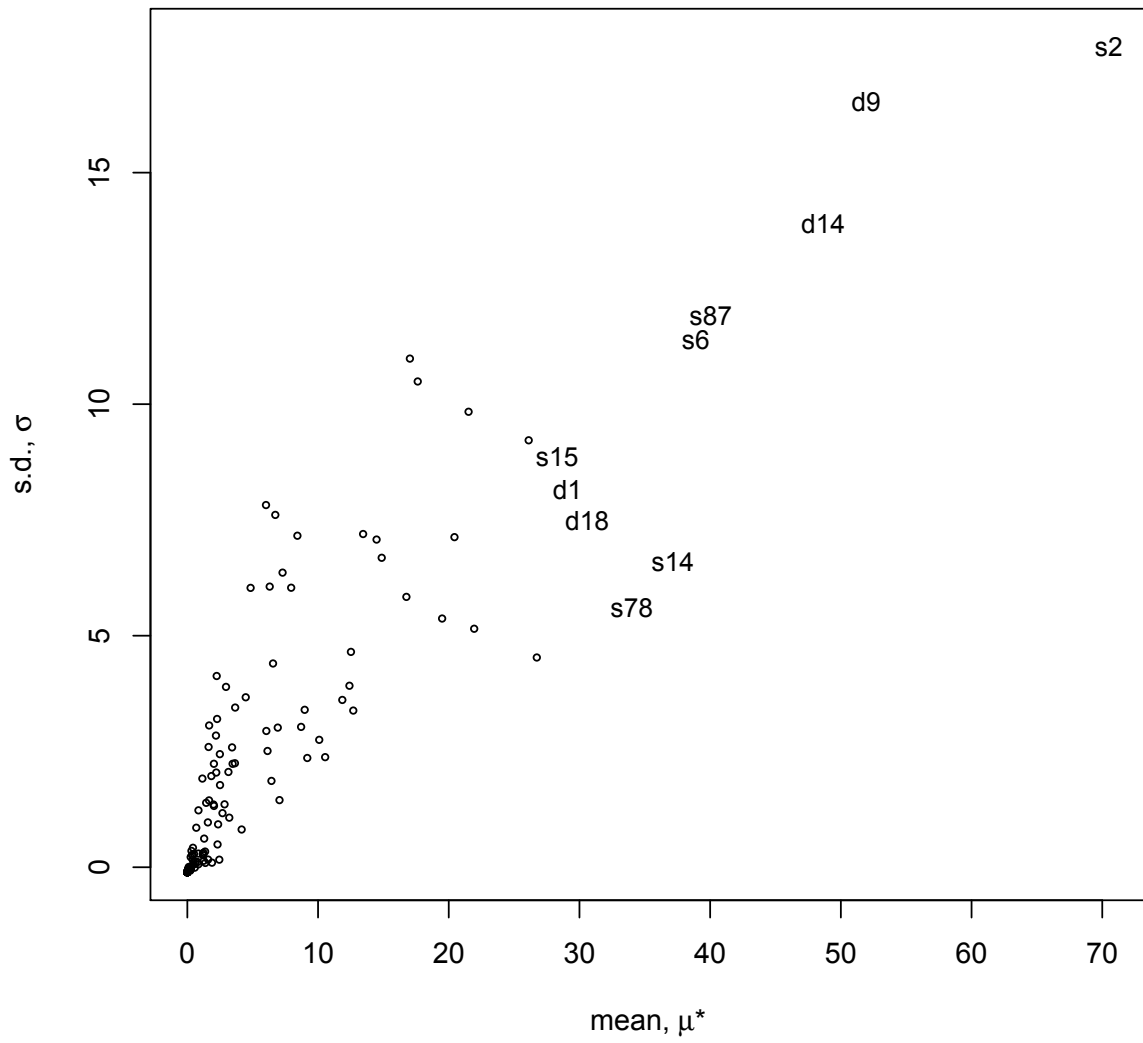
Figure 2: Results of Morris sensitivity analysis for suspension feeding benthos. Labels for the ten most influential factors are shown.
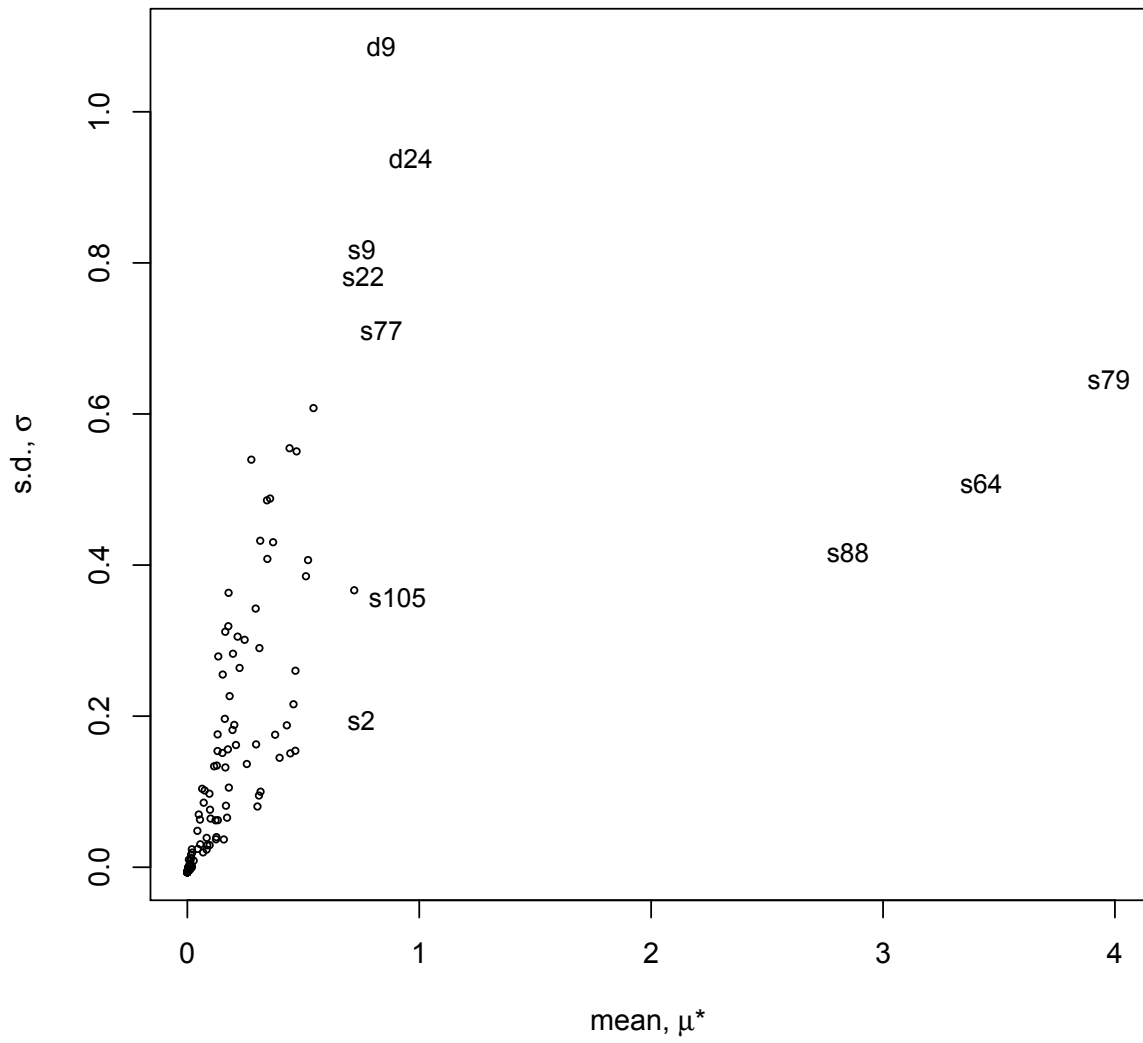
Figure 3: Results of Morris sensitivity analysis for carnivorous/scavenging benthos. Labels for the ten most influential factors are shown.
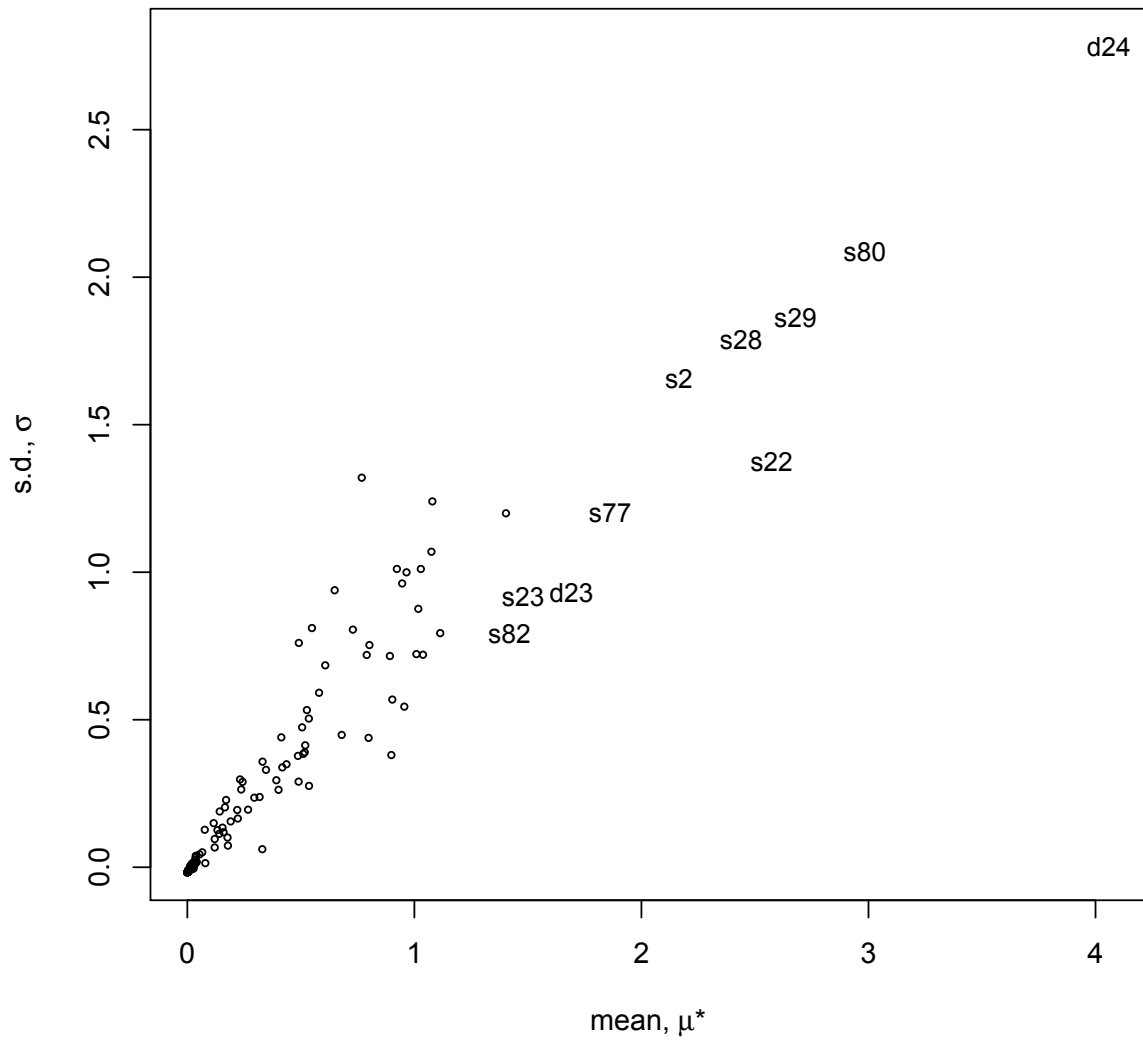
Figure 4: Results of Morris sensitivity analysis for pelagic fish larvae. Labels for the ten most influential factors are shown.
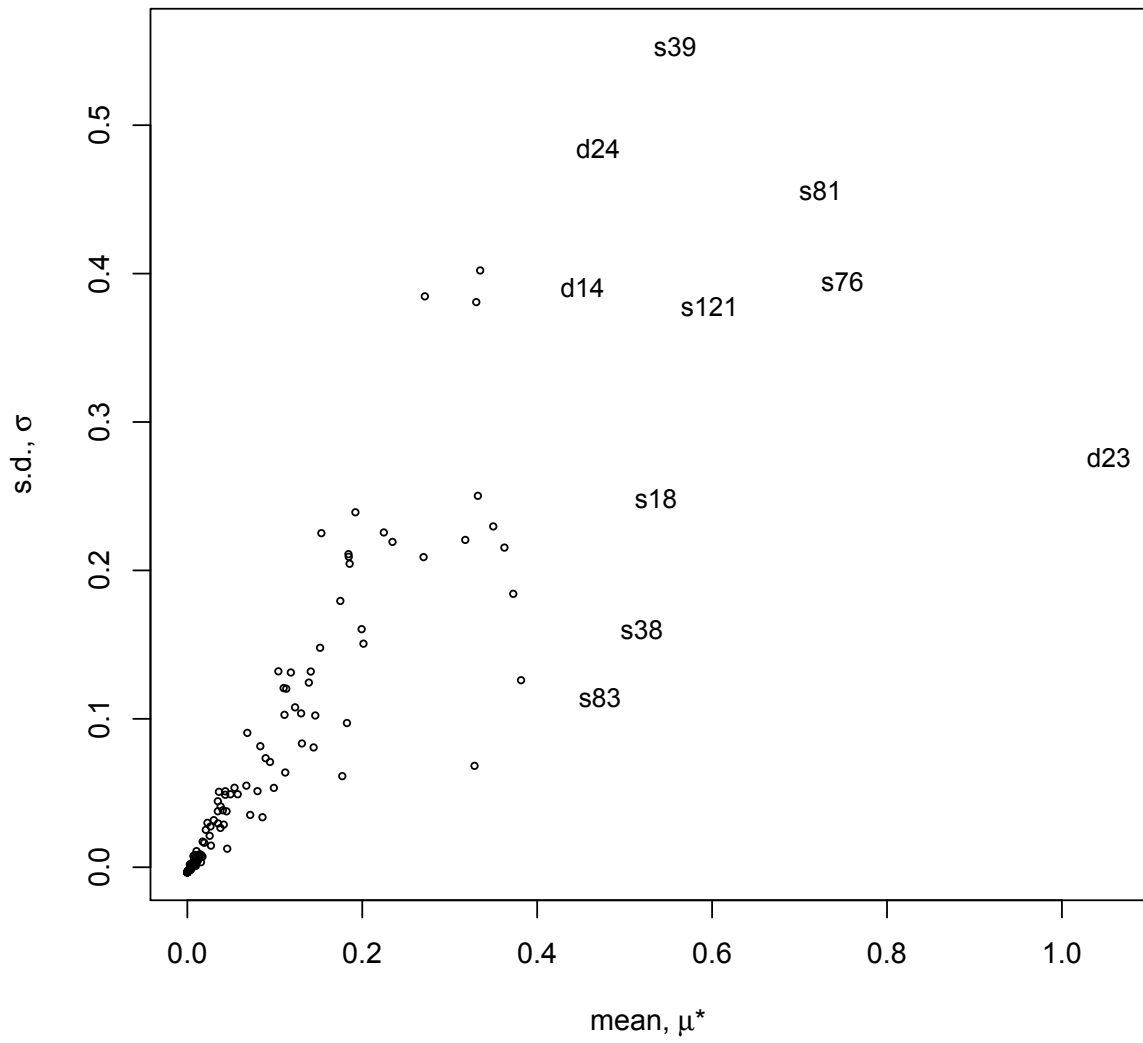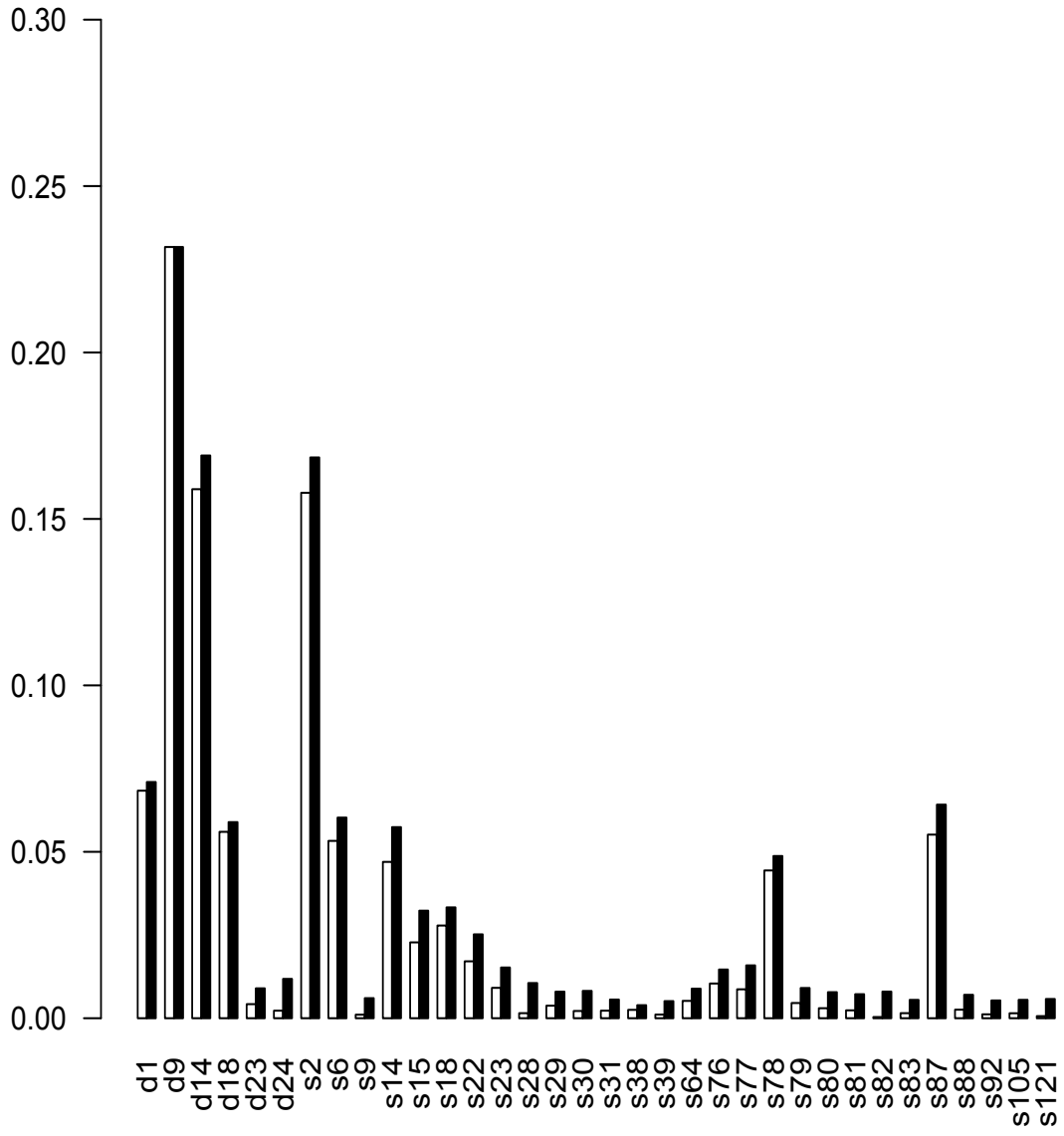
Figure 5: Results of Morris sensitivity analysis for adult pelagic fish. Labels for the ten most influential factors are shown.
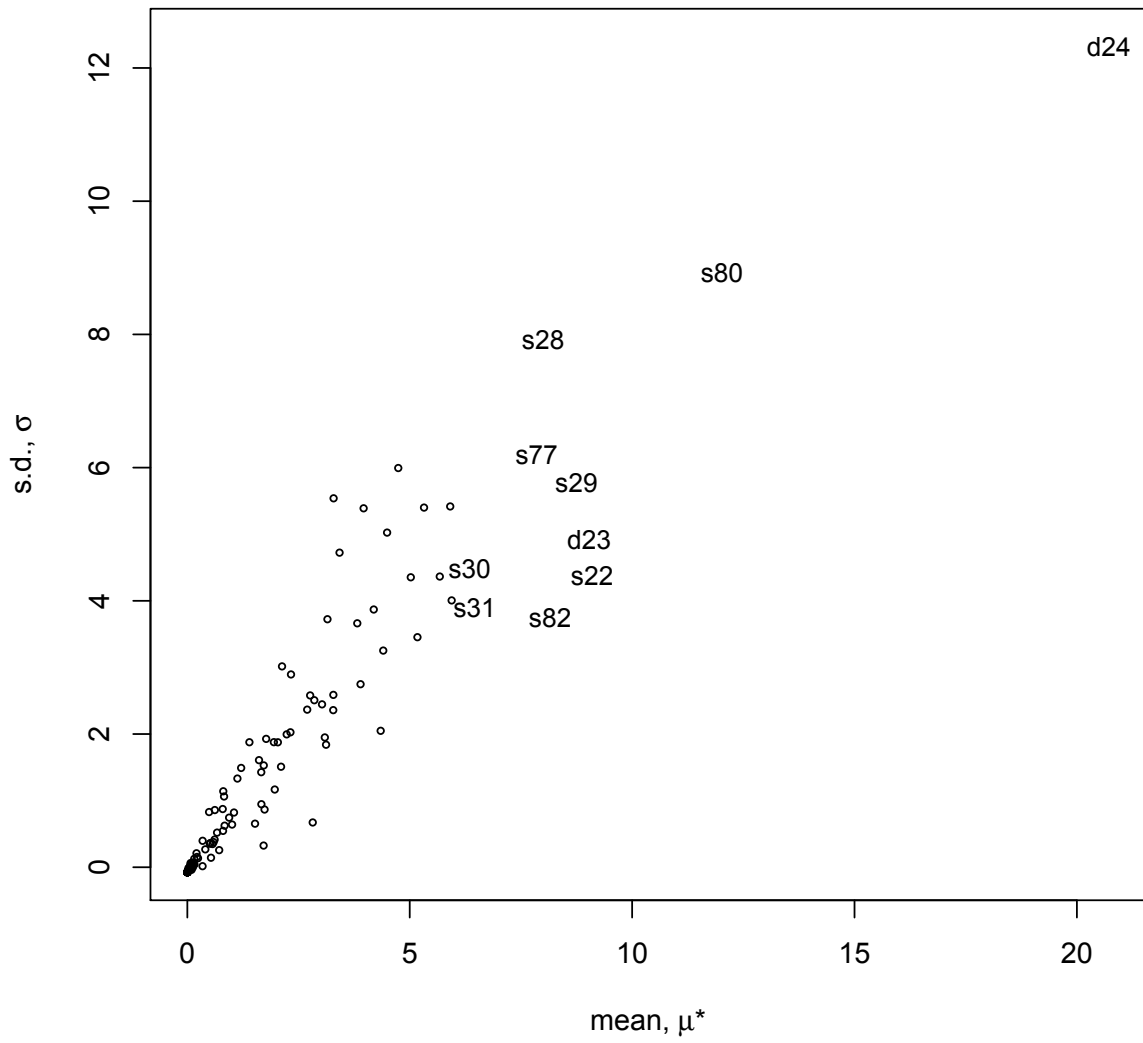
Figure 6: Results of Morris sensitivity analysis for demersal fish larvae. Labels for the ten most influential factors are shown.
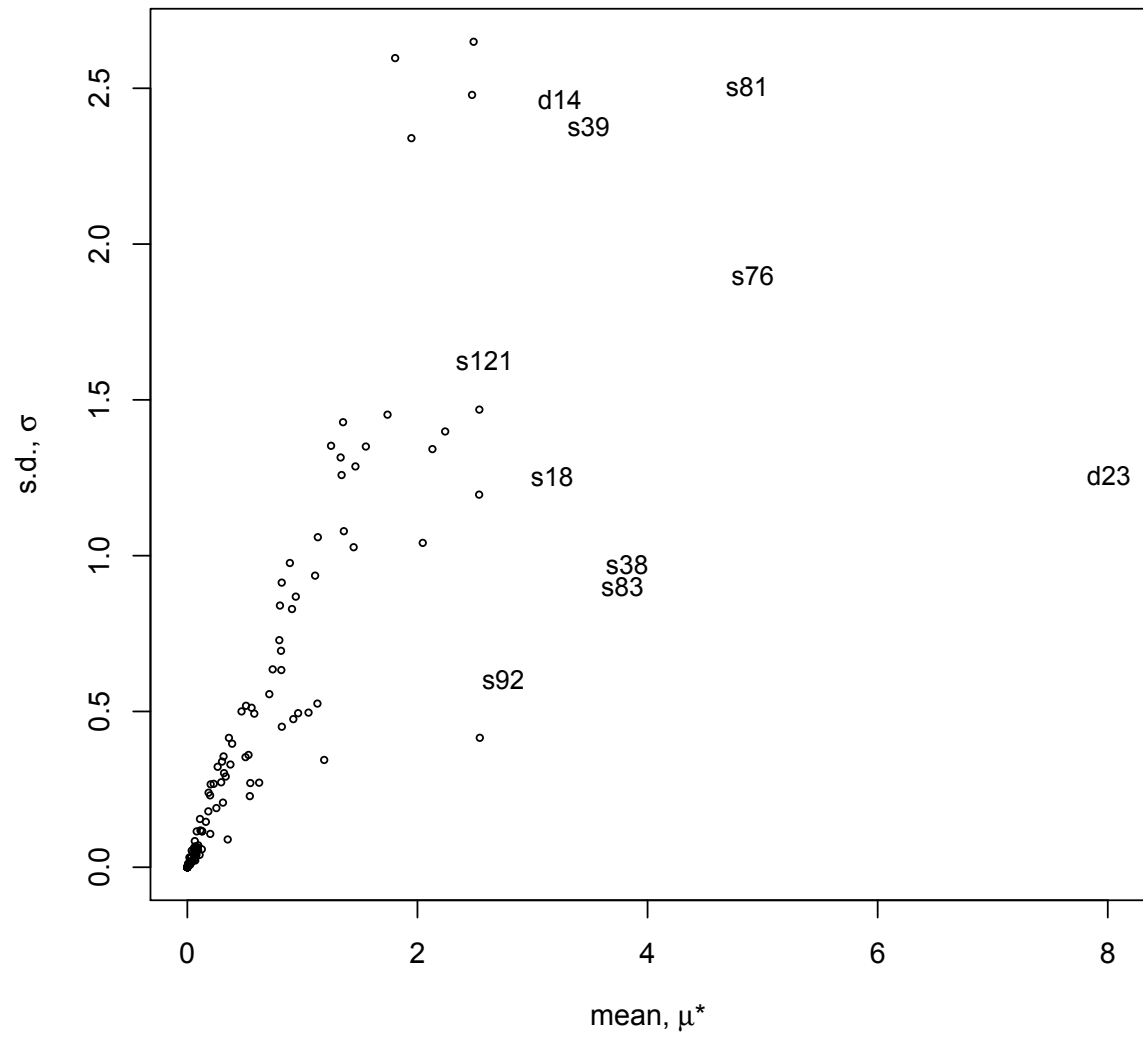
Figure 7: Results of Morris sensitivity analysis for adult demersal fish. Labels for the ten most influential factors are shown.

Figure 8: Results of Sobol sensitivity analysis for suspension feeding benthos. Filled columns represent total effects, open columns represent first order effects.
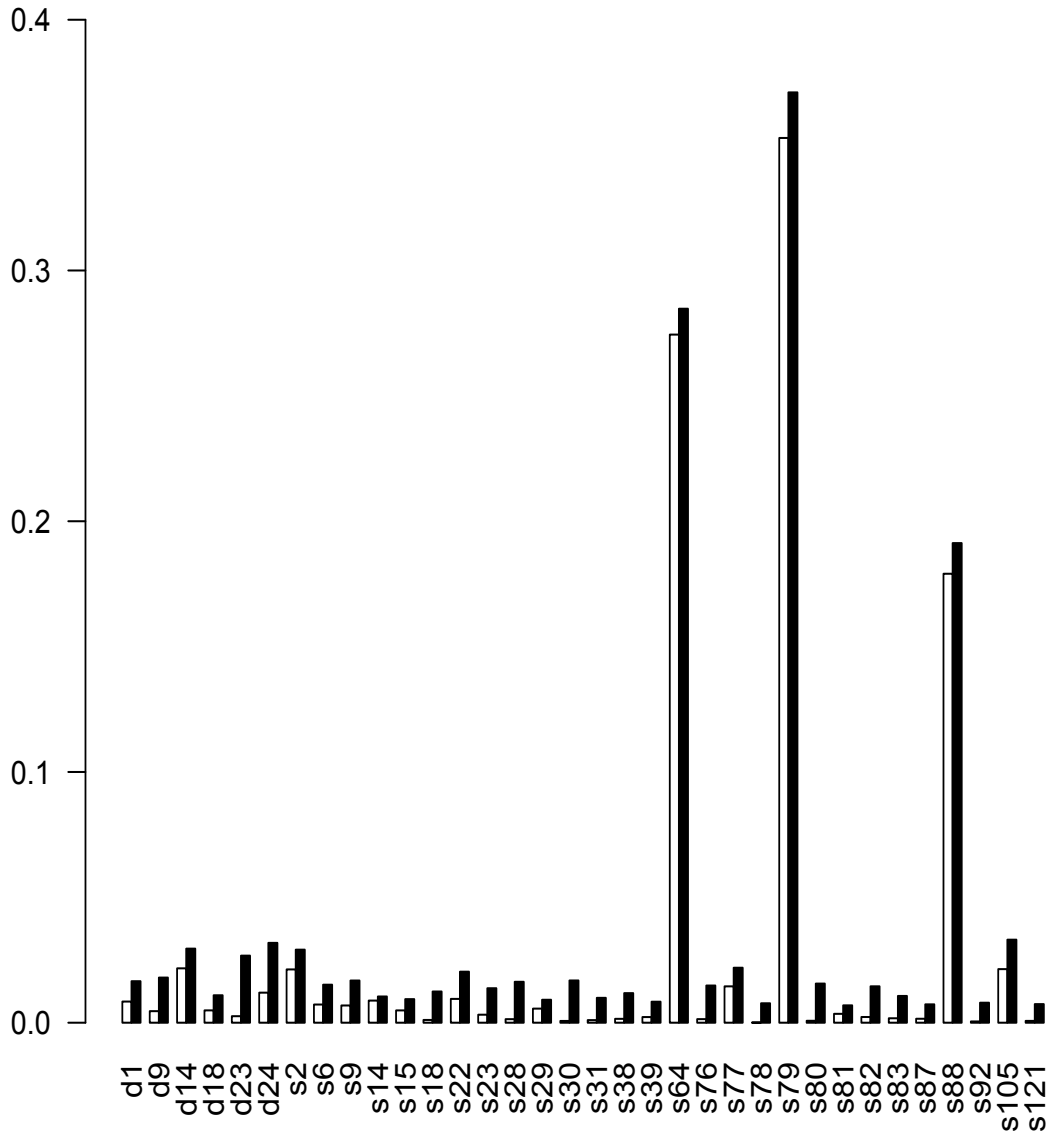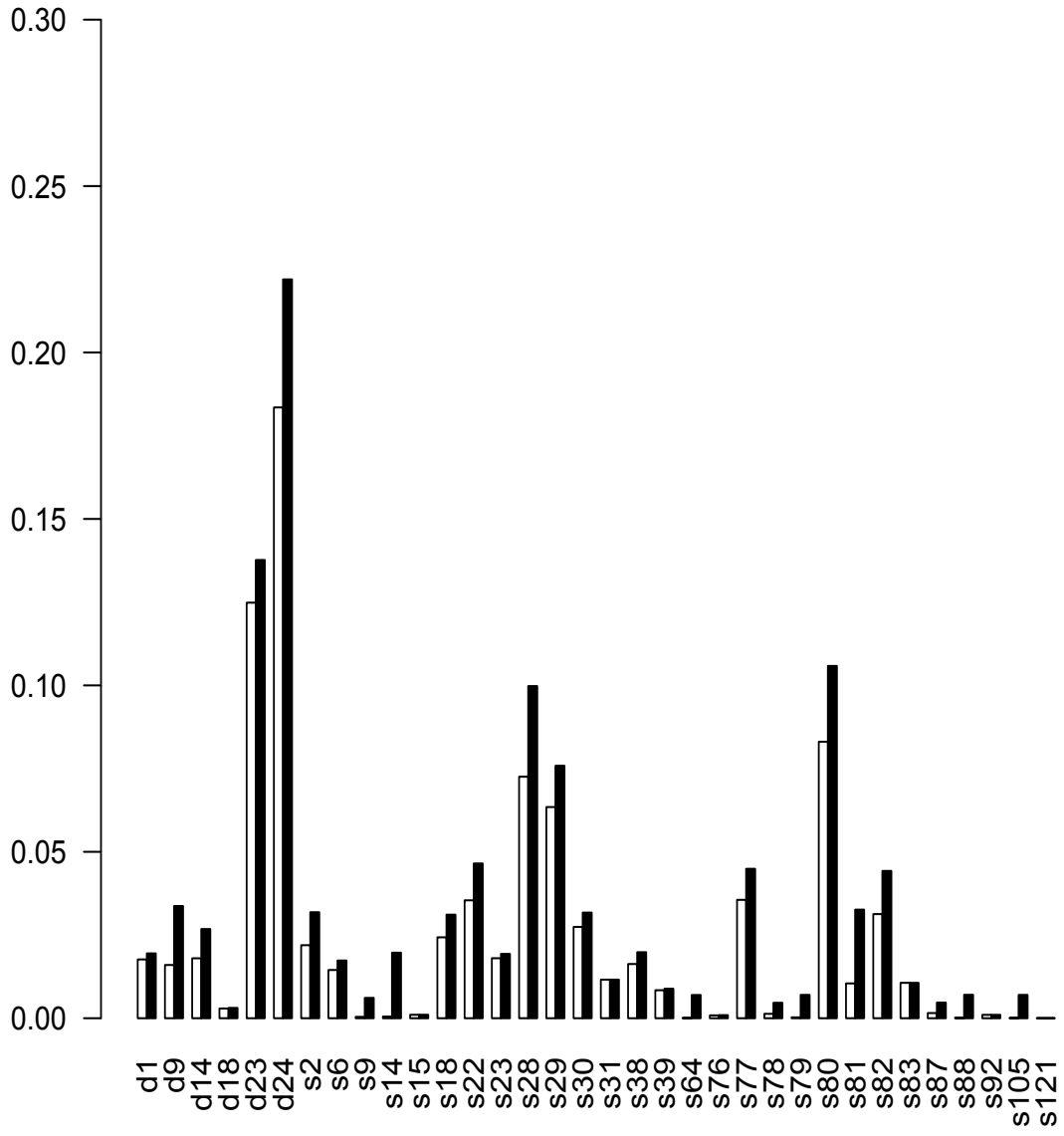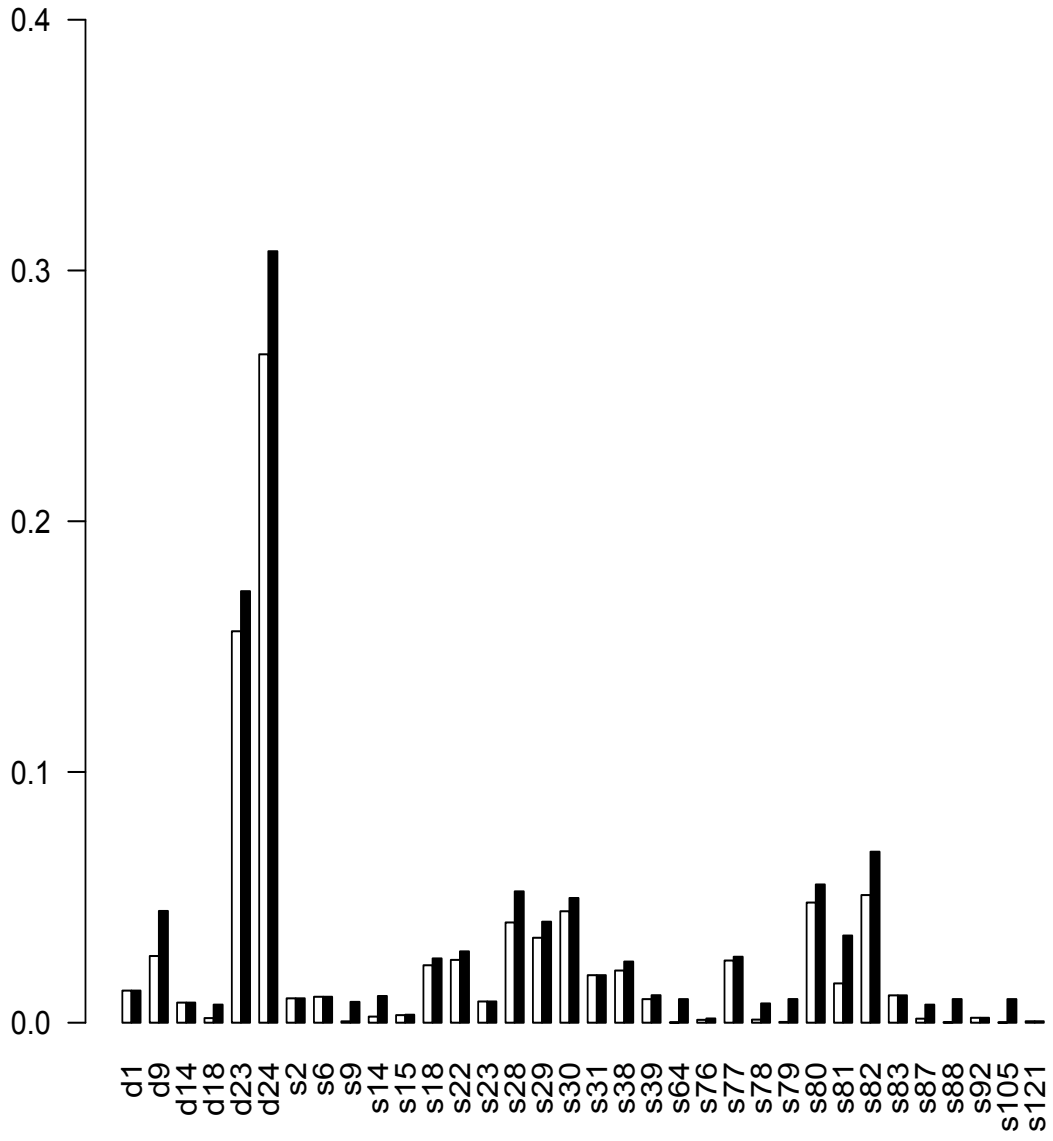
Figure 9: Results of Sobol sensitivity analysis for carnivorous/scavenging benthos. Filled columns represent total effects, open columns represent first order effects.

Figure 10: Results of Sobol sensitivity analysis for pelagic fish larvae. Filled columns represent total effects, open columns represent first order effects.

Figure 11: Results of Sobol sensitivity analysis for adult pelagic fish. Filled columns represent total effects, open columns represent first order effects.
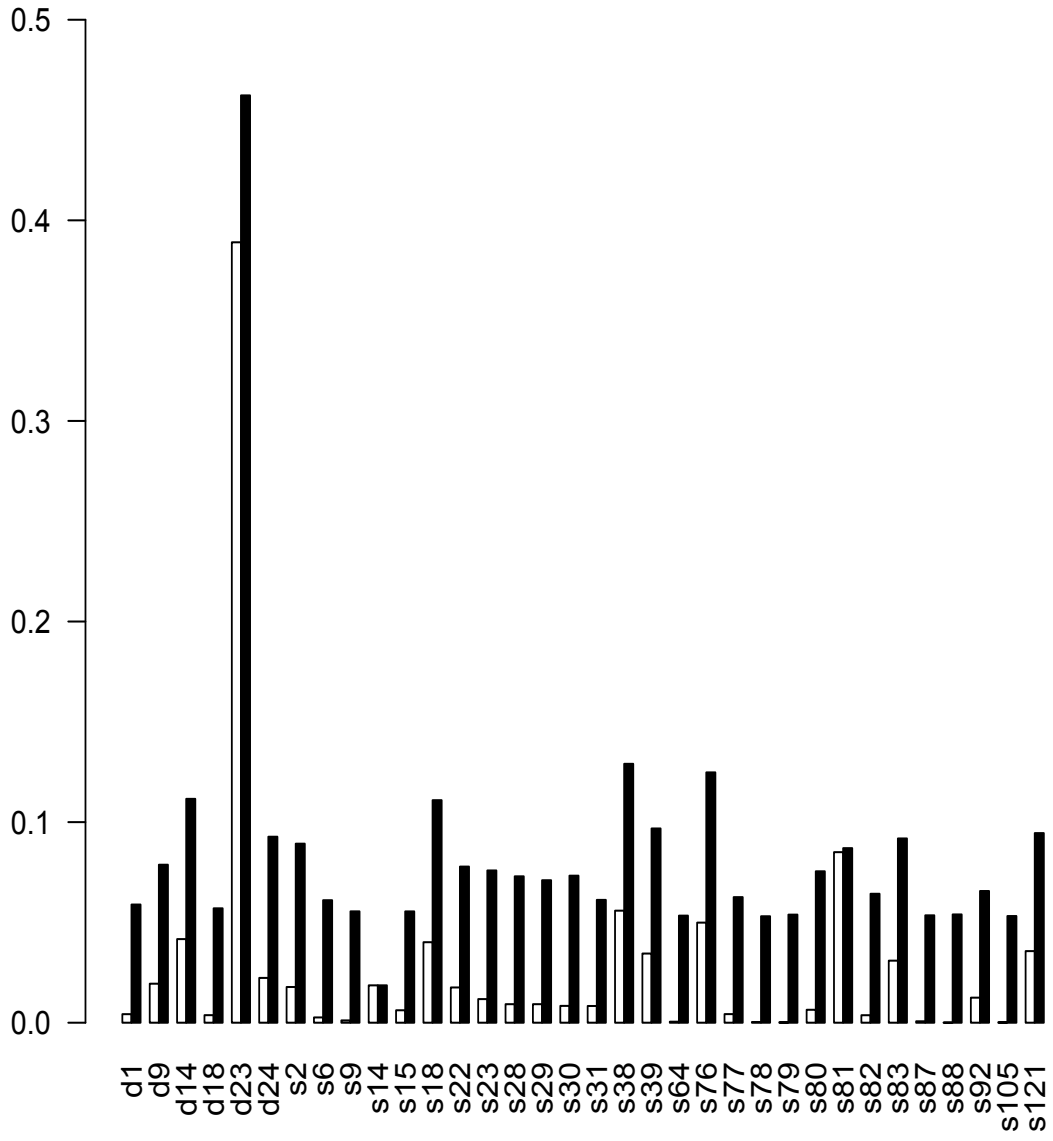
Figure 12: Results of Sobol sensitivity analysis for demersal fish larvae. Filled columns represent total effects, open columns represent first order effects.
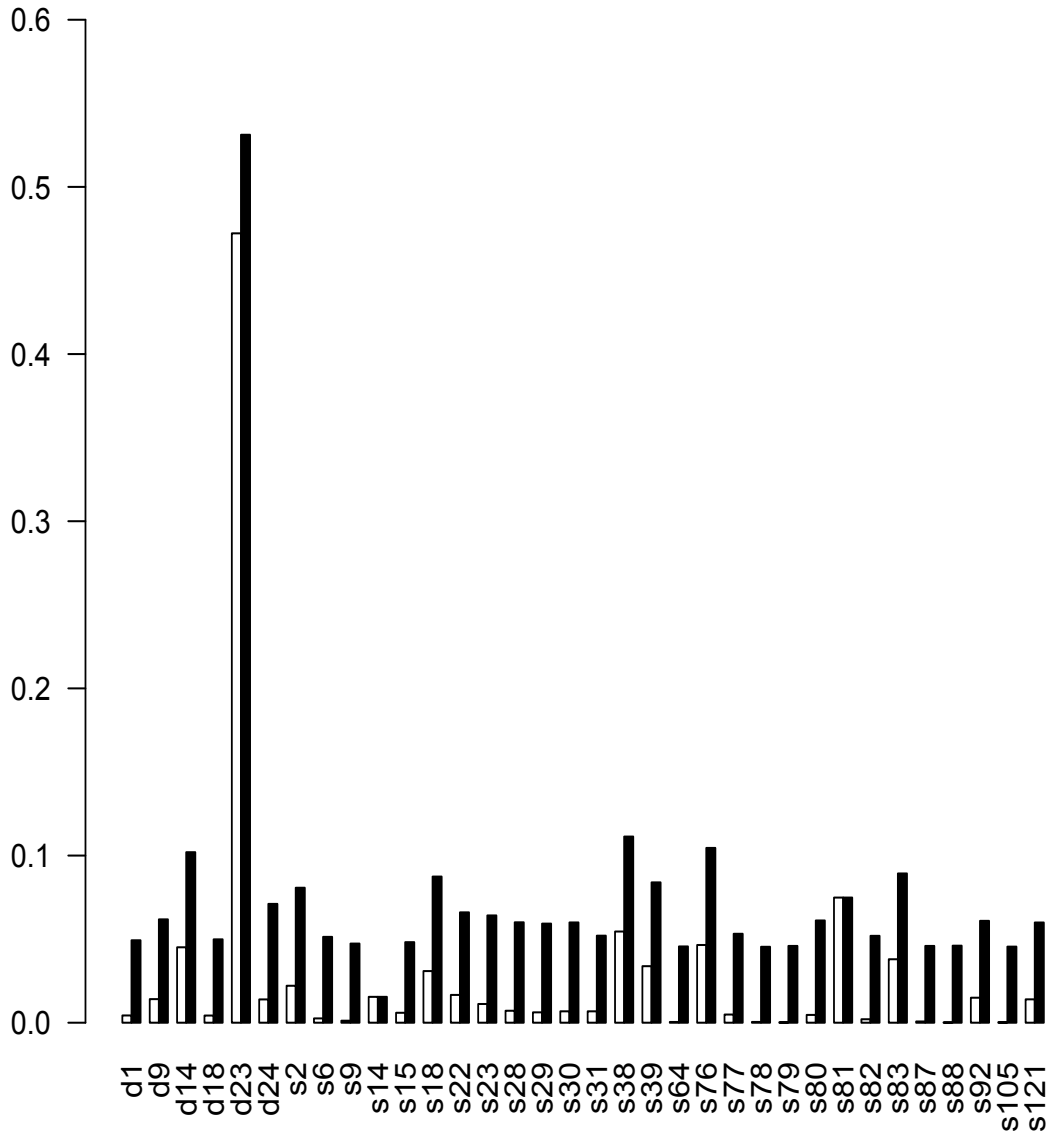
Figure 13: Results of Sobol sensitivity analysis for adult demersal fish. Filled columns represent total effects, open columns represent first order effects.