An overview of the marine food web in Icelandic waters using Ecopath with Ecosim

Joana P.C. Ribeiro,∗ Bjarki Þ. Elvarsson, Erla Sturludóttir, Gunnar Stefansson

Science Institute, University of Iceland, Dunhagi 7, 107 Reykjavík, Iceland
Marine and Freshwater Research Institute, Skúlagata 4, 101 Reykjavík, Iceland

Abstract
Fishing activities have broad impacts that affect, although not exclusively, the targeted stocks. These impacts affect predators and prey of the harvested species, as well as the whole ecosystem it inhabits. Ecosystem models can be used to study the interactions that occur within a system, including those between different organisms and those between fisheries and targeted species. Trophic web models like Ecopath with Ecosim (EwE) can handle fishing fleets as a top predator, with top-down impact on harvested organisms. The aim of this study was to better understand the Icelandic marine ecosystem and the interactions within. This was done by constructing an EwE model of Icelandic waters. The model was run from 1984 to 2013 and was fitted to time series of biomass estimates, landings data and mean annual temperature. The final model was chosen by selecting the model with the lowest Akaike information criterion. A skill assessment was performed using the Pearson’s correlation coefficient, the coefficient of determination, the modelling efficiency and the reliability index to evaluate the model performance. The model performed satisfactorily when simulating previously estimated biomass and known landings. Most of the groups with time series were estimated to have top-down control over their prey. These are harvested species with direct and/or indirect links to lower trophic levels and future fishing policies should take this into account. This model could be used as a tool to investigate how such policies could impact the marine ecosystem in Icelandic waters.

Keywords: Ecosystem dynamics, Trophic web, Ecopath with Ecosim, Icelandic waters

1. Introduction
Fisheries affect targeted stocks, as well as the whole ecosystem. Fisheries can have negative effects due to maximizing stock profitability. These include

∗Corresponding author
Email address: pcrjoana@gmail.com (Joana P.C. Ribeiro)
damage to the habitat and impacts to predators and prey of the fished species (Pikitch et al., 2004). The need for fisheries management arose from overexploitation of fish stocks. Since they were first developed, different measures of fisheries management have been employed across systems and their effectiveness has been previously studied (Stefansson and Rosenberg, 2005). Fishing policies, or lack thereof, have not always prevented overexploitation (Cook et al., 1997).

Fisheries management strategies have had a tendency to focus on a single species and not on wider, more realistic multi species scenarios (Hanna, 1999; Pikitch et al., 2004). Ecosystems harbour different species within them, which interact with each other and with their environment. The species in a given system are connected through trophic links and other types of ecological interactions. Ecosystem models can be used to gain better understanding of the underlying dynamics within a system. Trophic links in particular can be studied using food web models, also referred to as trophic models. When a system is harvested, the interaction between the targeted species and the fishing fleet is introduced in the system. In this case, fishing fleets can be handled by food web models as a top predator which interact with targeted stocks through top-down trophic control.

A widely used food web model is Ecopath with Ecosim (EwE; Christensen and Pauly, 1992; Walters et al., 1997; Pauly et al., 2000; Walters et al., 2000). Typical uses of EwE include answering ecological questions, quantifying trophic flows and studying the food-web structure and investigating potential impacts of fisheries on ecosystems. EwE has also been used as a fisheries management scenarios evaluation tool (for a complete overview on EwE capacities and limitations see Christensen and Walters, 2004).

Two EwE models for Icelandic waters had previously been published (Buchary, E.A.; Mendy, A.N. and Buchary, E.A., in Guénette et al., 2001; Mendy, 1998). The earlier model (Buchary, E.A. and Mendy, A.N. in Guénette et al., 2001; Mendy, 1998) modelled the trophic web in Icelandic waters in the year 1997 and did not include Ecosim. The latter model (Buchary E.A. in Guénette et al., 2001) was a reconstruction of the food web in Icelandic waters in 1950 and included a dynamic component that simulated the trophic dynamics between 1950 and 1997. These models did not cover more recent dynamics nor were they evaluated using a skill assessment. Other work on trophic interactions in Icelandic waters include specific predator-prey interactions (Stefansson et al., 1998), isotope analyses of organisms in the Icelandic sea (Petursdottir et al., 2012) and end to end modelling of the marine ecosystem (Sturhudottir et al., 2018).

The marine environment around Iceland has been exploited for centuries. In the 20th century, fisheries were the main source of income in Iceland (Popescu and Poulsen, 2012). Economically important species include demersal fish such as cod (Gadus morhua), saithe (Pollachius virens), haddock (Melanogrammus aeglefinus), redfish (Sebastes spp.) and Greenland halibut (Rinhardtiuhipoglossoides), as well as pelagic species such as herring (Clupea harengus), capelin (Mallotus villosus) and, in later years, blue whiting (Micromesistius poutassou; Astthorsson et al., 2007).
The aim of this study was to gain better understanding of the ecosystem in Icelandic waters by using EwE to model the trophic interactions between species in the ecosystem, as well as the interactions between fisheries and targeted species. The aim was also to evaluate the performance of the model with a skill assessment.

2. Methods

2.1. Study area

Iceland is an island located in the North Atlantic ocean, at the junction of the Middle Atlantic Ridge and the Greenland-Scotland ridge (Astthorsson et al., 2007). Its exclusive economic zone (EEZ) spans an area of 758 000 km² (Popescu and Poulsen, 2012) (Figure 1). This area includes the continental shelf around Iceland.

Figure 1: Icelandic EEZ with Iceland marked in black and highlighted continental shelf.

The Icelandic waters harbour organisms ranging from phytoplankton to marine mammals, as well as sea birds. Some of these are differently distributed along the ecosystem in Icelandic waters, due to different water salinity and temperature between the southern and western areas and the northern and eastern parts (Astthorsson et al., 2007). The southern and western areas have warm and saline Atlantic water, while the water in northern and eastern areas is a mix of Atlantic, Arctic and Polar water (Malmberg and Jonsson, 1997; Jonsson and
Valdimarsson 2005; Astthorsson et al. 2007). The different habitats resulting from this difference in water composition is exploited by some species, including commercially important fish stocks. These spawn in southern and western waters and feed off northern and western waters (Astthorsson et al. 1994, 2007).

2.2. Mass-balance model

To study the marine ecosystem of Icelandic waters, EwE (Christensen and Pauly 1992; Walters et al. 1997; Pauly et al. 2000; Walters et al. 2000) was chosen as a tool to give a simple overview of the entire system. EwE is composed of two modelling stages, Ecopath and Ecosim. Ecopath is the mass-balance part of EwE and its master equation is as follows:

\[ B_i \left( \frac{PB}{i} \right) = \sum_j B_j \left( \frac{QB}{j} \right) DC_{ij} + Y_i + E_i + BA_i + B_i \left( \frac{P}{B} \right) \left( 1 - EE_i \right) \] (1)

Here, \( B_i \) is the biomass of functional group \( i \), \( (P/B)_i \) is the production to biomass ratio, equivalent to total mortality \( (Z) \) in closed systems and corresponding to the sum of natural mortality \( (M) \) and fishing mortality \( (F) \), \( B_j \) is the biomass of predator \( j \), \( (Q/B)_j \) is the consumption to biomass ratio of \( j \), \( DC_{ij} \) is the proportion of \( i \) found in the stomach of \( j \), \( Y_i \) is the yield, \( E_i \) is the net migration, \( BA_i \) is the biomass accumulation and \( EE_i \) is the ecotrophic efficiency, which corresponds to the production of \( i \) explained by the model. \( F \) is calculated in Ecopath as the ratio \( Y/B \).

2.2.1. Functional groups

The Icelandic Ecopath model was comprised of 35 functional groups, of which six contained two stanzas each. The most relevant species of phytoplankton, zooplankton, invertebrates, fish, marine mammals and sea birds were included in the 35 functional groups used in the EwE model here presented (Table 1). Species were chosen as multi-stanza and/or individual functional groups depending on their economical importance and/or their role on the ecosystem and available biomass estimates and/or landings data. The aggregation of different species in a single functional group was based on species type and habitat use (Table A.1).

Commercial species were targeted by a single fishing fleet, without discrimination regarding fishing gear.
Table 1: List of the functional groups for the Icelandic waters EwE model.

| Functional groups    | Seabirds | Herring* (0-3) | Commercial demersal |
|----------------------|----------|---------------|---------------------|
| Minke whale          |          | Herring* (4+) | Other demersal      |
| Baleen whales        |          | Redfish* (0-7)| Cephalopod          |
| Tooth whales         |          | Redfish* (8+) | Mollusc             |
| Pinniped             |          | Greenland halibut* (0-5) | Lobster |
| Greenland shark      |          | Greenland halibut* (6+) | Shrimp |
| Dogshark             |          | Capelin       | Benthos             |
| Skate rays           |          | Blue whiting  | Jellyfish           |
| Cod* (0-3)           |          | Mackerel      | Krill               |
| Cod* (4+)            |          | Sandeel       | Crustacean zooplankton |
| Saithe* (0-3)        |          | Large pelagic | Small zooplankton  |
| Saithe* (4+)         |          | Small pelagic | Phytoplankton       |
| Haddock* (0-2)       |          | Flatfish      | Detritus            |
| Haddock* (5+)        |          | Other codfish |                     |

*Multi-stanza group

2.2.2. Initial parameters

Ecopath balances the model by solving a series of linear equations (Eq. 1). For each equation there must be an unknown value. The four basic values in Ecopath are $B$, $P/B$, $Q/B$ and $EE$. Ideally, $B$, $P/B$ and $Q/B$ should be input values. However, if estimates of $B$ are lacking, the $EE$ can be used as an input value to estimate $B$. In multi-stanza groups, $B$, $P/B$ and $Q/B$ have to be inserted for the leading stanza, whereas only $P/B$ needs to be inserted for all stanzas. Even though $P/B$ and $Q/B$ can be estimated, it is highly recommended that both are part of the input. The assumption of a closed system was made when modelling the marine ecosystem in Iceland. In a closed system, there is no $BA$ nor $E$, thus these values were set to 0.

Ecopath was set up for the year 1984 and the input biomass and landings corresponded to estimates for this year or for the next year with available data. A comprehensive list of the literature used can be found in Table 2.
Table 2: Literature sources of biomass and $Q/B$ estimates and of landings.

| Functional group               | Literature used                        |
|-------------------------------|----------------------------------------|
| Seabirds                      | Lilliendahl and Solmundsson (1997)     |
|                               | Dommasnes et al. (2001)                |
|                               | Umhverfisstofnun (2016)                |
| Minke whale;                  | Sigurjónsson and Vikingsson (1997)     |
| Baleen whales and             | Dommasnes et al. (2001)                |
| Tooth whales                  | Borchers et al. (2009)                 |
|                               | Pike et al. (2009)                     |
|                               | Vikingsson et al. (2013)               |
| Pinniped                      | Gunnarsson et al. (1998)               |
|                               | Dommasnes et al. (2001)                |
|                               | Institute (2014)                       |
| All fish groups               | Froese and Pauly (2010)                |
| Greenland shark (*Somniosus microcephalus*; biomass) | MacKen et al. (2012)                  |
| Cod ($Q/B$)                    | Magnússon and Fássón (1989)            |
| Mollusc; jellyfish; benthos;   |                                        |
| Small zooplankton and crustacean zooplankton | Kleisner and Hoornaert (2016) |

No biomass was found for functional groups dogshark, skate rays, sandeel, large pelagic, small pelagic, flatfish, other demersal, lobster, shrimp, benthos, jellyfish and both zooplankton groups. Since these were not harvested in Iceland in 1984, it was not possible to estimate biomass and as such the $EE$ was used instead. The $EE$ of dogshark and skate rays was set to 0.500. For all remaining groups, $EE$ was set to 0.950. The choice of $EE$ values was made based on recommendations in the literature (Heymans et al. 2016).

2.2.3. Diet composition

Stomach content data of most fish groups was provided by the MFRI [Institute (2014)] and then transformed into diet composition using R [R Core Team (2016)], to be later used in Ecopath. Diet composition of all other groups, as well as of small pelagic fish, other demersal fish and invertebrates was set according to the literature (Table 3).

Table 3: Literature sources of diet composition.

| Functional group             | Literature used                     |
|-----------------------------|-------------------------------------|
| Seabirds                    | Lilliendahl and Solmundsson (1997)  |
|                             | Vikingsson et al. (2014)            |
| Minke whale                 | Vikingsson et al. (2014)            |
| Baleen whales               | Sigurjónsson and Vikingsson (1997)  |
| Tooth whales                | Canning et al. (2009)               |
|                             | Sigurjónsson and Vikingsson (1997)  |
| Pinnipeds                   | Hauksson and Bogason (1997)         |
| Large pelagic fish          | Hutchings (2002)                    |
| Small pelagic fish          | Tyler and Pearcy (1975)             |
| Other demersal fish         | Hutchings (2002)                    |
| All invertebrate groups     | Gunnarsson et al. (1998)            |
2.2.4. Model balancing

After initialising Ecopath for the first time, two groups had $EE > 1$. These were functional group herring 0-3 ($EE = 1.201$) and capelin ($EE = 2.328$). In order to balance the model, $P/B$ of the herring 0-3 group was raised from 0.490 to 0.570 and the $EE$ was set to 0.950 for capelin. The latter decision was based on the hypothesis that capelin biomass has been underestimated in assessments [Magnússon and Pálsson 1989]. According to a study by Magnússon and Pálsson [1989], assessments of capelin biomass have to be approximately doubled to explain consumption by predators.

2.3. Dynamic model

Ecosim is the dynamic part of the EwE modelling suite [Walters et al. 1997, 2000; Christensen and Walters 2004]. Ecopath estimates are used as initial values in Ecosim, which runs a simulation for a user-defined period. The Ecosim model presented here had a time span of 30 years. Ecosim uses a system of differential equations to give a time series of simulated biomass and landings:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_{0i} + F_i + e_i)B_i$$

(2)

Here, $dB_i/dt$ represents the rate of change in biomass of functional group $i$, described in terms of its biomass, $B_i$. $g_i$ is net growth efficiency ($P/Q$), $Q_{ji}$ is the consumption of $j$ by $i$, $Q_{ij}$ is the predation by $j$ on $i$, $M_{0i}$ is the mortality not explained by the model, $F_i$ is the fishing mortality rate, $e_i$ is the emigration rate and $I_i$ is the immigration rate.

Consumption in Ecosim is calculated based on the foraging arena theory [Walters et al. 1997; Ahrens et al. 2012], in which the biomass of the prey is split into vulnerable and non-vulnerable pools. Consumption is computed as:

$$Q_{ij} = \frac{v_{ij}a_{ij}B_iB_jT_iT_jS_{ij}M_{ij}/D_j}{v_{ij}v_{ij}T_iM_{ij} + a_{ij}M_{ij}B_jS_jT_j/D_j}$$

(3)

Here, $v_{ij}$ is the vulnerability of prey $i$ to predator $j$, $a_{ij}$ is the rate of effective search of $i$ by $j$, $T_i$ is the relative feeding time of $i$, $T_j$ is the relative feeding time of $j$, $S_{ij}$ is the representation of seasonal or long-term forcing effects, $M_{ij}$ represents mediation forcing effects and $D_j$ is the impact of handling time as a limit to consumption.

2.3.1. Model fitting

Ecosim benefits from reference temporal data used to calibrate the model. This reference data includes biomass and/or landings. In addition, biomass, landings, $F$ and environmental variables can be forced to drive the model. To calibrate the model, a time series of both forced and reference values was used (Table 4).
Table 4: Description of the time-series used to calibrate Ecosim. F - Fishing mortality (forced); FB - Forced biomass; RB - Reference biomass; RC - Reference landings; EV - Environmental variables.

| Type | Group | Period       |
|------|-------|--------------|
| F    | Cod 4+; Saithe 4+; Haddock 3+; Blue whiting; Flatfish; Other codfish; Mackerel; Commercial demersal; | 1984-2013 2005-2013 |
| FB   | Mackerel | 1984-2013 |
| RB   | Cod 4+; Saithe 4+; Haddock 3+; Herring 4+; Redfish 8+; Blue whiting; | 1984-2013 |
| RC   | Cod 4+; Saithe 4+; Haddock 3+; Herring 4+; Redfish 8+; Greenland halibut 6+; Capelin; Flatfish; Blue whiting; Mackerel; | 1984-2013 2005-2013 |
| EV   | Temperature | 1984-2013 |

Biomass forcing was used for mackerel. Numbers of mackerel have been increasing in Icelandic waters since around 2007 (Astthorsson et al., 2012). Initial biomass of mackerel was set to low values (0.200 t.km\(^{-2}\)), as new functional groups cannot be introduced in Ecosim. The invasion by mackerel was then simulated by forcing its biomass from 2005 on. This was the chosen method to handle the increasing numbers of mackerel in the ecosystem as a method to simulate species invasion in EwE. Average annual temperature was used as forcing function for PP. The time series was provided the MFRI Institute [2014].

The model was fitted to the time series by conducting anomaly and vulnerability searches. The former reduced the total sum of squares (SSQ) by adjusting the forcing function on PP, while the latter reduced SSQ by adjusting vulnerability parameters. In EwE, the anomaly search uses spline regression to search for time series values of annual relative PP that could explain productivity shifts impacting biomass across the ecosystem (Christensen et al., 2008). Anomaly searches using 5, 10, 15 and 20 spline points were conducted and model selection was done using the Akaike method [Akaike 1974]. The Akaike method for model selection uses the Akaike information criterion (AIC) as a measure of model how well the model fits to the data considering the number of parameters and the lower the AIC, the better the model [Akaike 1974].

2.3.2. Skill assessment

A skill assessment of the model was done using three measures suggested by [Stow et al. 2009]. These were the Pearson’s correlation coefficient (r), the squared Pearson’s correlation coefficient or determination coefficient (R\(^2\)), the modelling efficiency coefficient (MEF; eq. 4) and the reliability index (RI; eq.
5). The model efficiency coefficient and the reliability index are described as:

\[
MEF = \frac{\sum_{i=1}^{n}(O_i - \bar{O})^2 - \sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(O_i - \bar{O})^2}
\]  \tag{4}

And:

\[
RI = \exp \sqrt{\frac{1}{n} \sum_{i=1}^{n} \left( \log \frac{O_i}{P_i} \right)^2}
\]  \tag{5}

Here, \( n \) is the number of observations, \( O_i \) is the \( ith \) of observation, \( \bar{O} \) is the average of the observations and \( P_i \) is the \( ith \) prediction.

The correlation coefficient, \( r \), can range from -1 to 1. An \( r \) value of 0 indicates no correlation, whereas values of 1 indicate that the simulated and reference values variate with an equal trend. Negative \( r \) values indicate inverse variation between simulated and reference values. MEF can vary between \(-\infty\) and 1. Negative values of MEF indicate that the model has a worse fit to the data than an average through the time series; \( MEF = 0 \) indicates that the model has an equal fit to an average through the time series; and \( MEF = 1 \) indicates that the model perfectly fits to the time series. Models with negative MEF can still be useful, if \( r \) is positive. Negative MEF values could be due to differences in magnitude between simulated and observed values, despite the simulations following the same trend as the observations. Finally, RI is a measure of the difference in magnitude between simulated and reference values. It varies between 1 to \(+\infty\) and a value of 1.5 would indicate that the model simulates the reference values with a 50% difference in magnitude.

3. Results and Discussion

3.1. Mass-balance model

The estimated biomass for capelin in 1984 was 4 681 408 tonnes, 2.4 times higher than MFRI estimates for that year \( \text{[Institute] 2014} \). These results are consistent with a previous study by \( \text{Magnússon and Pálsson 1989} \), in which the authors hypothesised that capelin biomass was being grossly underestimated in the assessments and should be approximately doubled in order to explain the amount of capelin that is being consumed by predators.

The combined predation mortality of cod on capelin accounted for 31% of \( M \) of capelin (\( M = 0.311 \); total \( M = 1.014 \)). Blue whiting had the second highest effect on capelin \( M \), with its predation mortality on capelin accounting for 22% of \( M \) (\( M = 0.224 \)).
3.2. Dynamic model

Overall, the Ecosim model performed in a satisfactory manner when replicating previously known dynamics (Table 6 and Figures 2 and 3). The anomaly search using 10 spline points resulted in the fit with the lowest AIC Table 5. The anomaly search on the final model was thus done using 10 spline points. When fitting the model to the time series of biomass and landings by estimating the vulnerability parameters, the original fit ($SSQ = 84.80$) was improved by 4\% ($SSQ = 81.56$). After the addition of temperature as a forcing function of PP to the time series of biomass, F and landings, the original fit was improved by 16\% ($SSQ = 71.04$). Considering these results, temperature was included in the final model as a forcing function of PP.

Table 5: Summary of SSQ and AIC using different number of spline points.

| Spline points | SSQ  | AIC   |
|---------------|------|-------|
| 0             | 75.52| -880.4|
| 5             | 75.01| -944.5|
| 10            | 71.04| -961.4|
| 15            | 72.17| -942.4|
| 20            | 68.53| -957.5|

The best fit was achieved when annual temperature was included in the model, suggesting that fisheries alone cannot explain the Icelandic marine ecosystem. Temperature is considered to be one of the main determining factors in marine fish distribution (Sunday et al., 2012; Genner, 2016). Cod has been shown to change its habitat use in the southern North sea according to surface temperature (Freitas et al., 2016). Considering the fundamental role temperature plays in fish ecology, it is not surprising that the addition of temperature to the model resulted in a better fit.
Table 6: Skill assessment per group, where $r$ is the Pearson’s correlation coefficient, $R^2$ is the determination coefficient, MEF is the modelling efficiency and RI is the reliability index. Reference values for a good fit: $0.7 \leq r \leq 1$; $0.5 \leq R^2 \leq 1$; $0 < MEF \leq 1$; $1 \leq RI \leq 1.5$.

| Functional group | Biomass | | | Catches | | |
|---|---|---|---|---|---|---|
| Cod 4+ | 0.605 | 0.366 | -1.079 | 1.291 | 0.810 | 0.656 | 0.172 | 1.291 |
| Saithe 4+ | 0.750 | 0.563 | 0.599 | 1.242 | 0.844 | 0.712 | 0.479 | 1.242 |
| Haddock 3+ | 0.768 | 0.590 | 0.635 | 1.241 | 0.623 | 0.388 | 0.471 | 1.241 |
| Herring 4+ | 0.323 | 0.104 | -0.223 | 1.398 | 0.577 | 0.333 | 0.047 | 1.398 |
| Redfish 8+ | 0.567 | 0.321 | 0.147 | 1.230 | 0.796 | 0.634 | 0.279 | 1.230 |
| Greenland halibut 6+ | 0.188 | 0.035 | -0.354 | 1.909 |
| Capelin | 0.763 | 0.583 | -0.419 | 2.006 |
| Blue whiting | 0.535 | 0.286 | -0.012 | 1.909 | 0.929 | 0.863 | 0.424 | 1.755 |
| Mackerel | 1.000 | 1.000 | 1.000 | 1.000 |
| Flatfish | 0.778 | 0.605 | 0.391 | 1.238 |
| Other codfish | 0.754 | 0.568 | 0.506 | 1.251 |
| Commercial demersal | 0.687 | 0.472 | -0.444 | 1.318 |

The skill assessment had overall satisfactory results ($0.7 \leq r \leq 1$; $0.5 \leq R^2 \leq 1$; $0 < MEF \leq 1$; $1 \leq RI \leq 1.5$; Table 6). There was a general tendency from the model to replicate the landings better than the biomass. With the exception of group haddock 3+, fitted biomass had higher $R^2$ values than fitted landings (Table 6). These results are unsurprising, as the landings were actual observations, while the biomass used were previous estimates by the MFRI [Institute] [2014].

There were three groups (cod 4+, herring 4+ and blue whiting) for which the model had a worse fit for biomass than a straight line through the average of the reference values ($MEF < 0$; Table 6). The model performed poorly when predicting the landings of Greenland halibut 6+, capelin and commercial demersal fish as well ($MEF < 0$; Table 6). The MEF is sensitive to the difference between the simulated and the reference values (Eq. 4) and can be negative even when the $R^2$ is within reasonably good range ($0.5 \leq R^2 \leq 1$), as was the case of capelin landings (Table 6). The model underestimated capelin landings with a difference in magnitude of approximately 100% ($RI = 2.006$; Table 6), which could account for the low MEF value.

The model was calibrated using biomass estimates from single-species assessments, as well as $F$ calculated using those estimates. This method was chosen, as there were no biomass estimates from multi-species assessments available and because of how Ecopath internally computes $F$ as $Y/B$. The use of biomass estimated by single species assessments in a multi-species context could have contributed to the poor skill assessments results observed for herring 4+ and redfish 8+ biomass, as well as for Greenland halibut 6+ landings.
With the exception of mackerel, all groups had $R_I > 1.2$, which indicates that the simulated biomass and landings varied at least 20% in magnitude in relation to the reference biomass and landings (Table 6). However, none of these differences in magnitude were constant through the simulations, indicating that there were no systematic errors (Figures 2 and 3).

The skill assessment of mackerel caches shows optimal results for all measures (Table 6). These can be explained by the use of forced biomass for this group. Using forced biomass for mackerel in EwE can have consequences for the modelled trophic dynamics, as it could lead to over-fitting. Over-fitting the model can, in turn, lead to unnatural simulations of the groups with direct trophic links to this group. However, the use of fisheries and temperature was not enough to satisfactorily simulate the invasion by mackerel.
3.2.1. Trophic flows

Ecosim uses a vulnerability scale of 1 to $+\infty$, where $v = 2$ represents mixed-trophic control, $v < 2$ represents bottom-up control and $v > 2$, represents top-down control (Christensen et al., 2008). The higher the vulnerability, the stronger top-down effect a predator has on its prey, this being relevant for values up to $v = 100$.

Of the groups with vulnerability parameters freed from default, only cod 4+ had $v < 2$ (Table 7), suggesting that this group is affected by the abundance and/or availability of their prey; as contrast to acting as a controlling force over them. The groups capelin, blue whiting and commercial demersal had $v = 1.979$, $v = 2.156$ and $v = 2.000$, respectively (Table 7), which suggests that these groups have mixed trophic control. The remaining groups had $v > 100$, suggesting top-down control from these groups over their prey (Table 7). Only high TL predators ($TL > 3$; Figure 4) had their vulnerability parameters freed from default (Table 7), as these were the only groups with time-series of biomass and/or landings available, and these usually are linked to their prey through top-down control. As such, it is not possible to speculate about which type of trophic control dominates the Icelandic marine ecosystem from this model.
The vulnerability search was done by predator. When freeing vulnerabilities from default in this manner, it is assumed that how vulnerable a prey is to their predator depends mostly on the predator’s foraging behaviour \(^{[Christensen and Pauly, 1992]}\). Conducting the vulnerability search by predator will thus lead to one vulnerability value for every predator-prey interaction of a given predator \(^{[Christensen and Pauly, 1992]}\). Assuming that a predator’s foraging behaviour remains unchanged independently of the prey sought might not always depict reality. An example of this is cod, which was estimated to be affected by bottom-up control \((v < 2; \text{Table 7})\) by this model. However, a previous study has shown that cod has top-down control over shrimp, but is affected by bottom-up control by capelin \(^{[Stefansson et al., 1998]}\). The vulnerability search method used prevents individual predator/prey pairs from having a unique vulnerability value. The vulnerability search was done in this manner as it was the only option available to restrict it to the groups with time series.

| Predator          | Functional group | \(v\) |
|-------------------|------------------|-------|
| Cod 4+            | Capelin          | 1.186 |
| Saithe 4+         | Blue whiting     | >100  |
| Haddock 3+        | Mackerel         | >100  |
| Herring 4+        | Flatfish         | >100  |
| Redfish 8+        | Other codfish    | >100  |
| Greenland halibut 6+ | Commercial demersal | 2.000 |
3.3. Comparison with other models

There were two previously published Ecopath models describing the Icelandic marine ecosystem in 1950 and 1997 (Buchary, E.A.; Mendy, A.N and Buchary, E.A., respectively, in Guénette et al., 2001; Mendy, 1998). The model for 1950 included an Ecosim simulation, ran from 1950 to 1997.

In the 1950 study, the author constructed the model to be comparable to the Ecopath model for 1997 (Buchary, E.A. in Guénette et al., 2001). The 1950 model Ecopath was an attempt to reconstruct the ecosystem for that year (Buchary, E.A. in Guénette et al., 2001; Mendy, 1998), by estimating the biomass for most functional groups. The author then used a time series of F and reference biomass (calculated as Y/F) of cod and herring to fit the model (Buchary, E.A. in Guénette et al., 2001). No vulnerability search was done in this study and all vulnerabilities were set to 0.3 (Buchary, E.A. in Guénette et al., 2001). There were differences between the input biomass and landings of the 1997 model (Mendy, A.N and Buchary, E.A. in Guénette et al., 2001; Mendy, 1998) and the simulations by the present model for the same year for most groups. It is reasonable to think that these discrepancies were due to different modelling assumptions such as modelled area and species density, as the differences are also found between the input data of the older model and the data sources for the current model.

Both the 1950 and 1997 models used 25 functional groups each (Buchary, E.A.; Mendy, A.N and Buchary, E.A., respectively, in Guénette et al., 2001; Mendy, 1998) in contrast to the 35 functional groups of the here presented model. The current model was more complete than the 1950 and 1997 models, as it included more detailed functional groups, a more complete time series than the one used in the 1950 model and because of it being fitted to the time series through vulnerability and anomaly searches. Furthermore, a skill assessment was carried out in the current model, which was not the case for the previous models.

3.4. Final remarks

It was estimated by this model that commercial fishes like haddock, redfish, Greenland halibut, flatfish and other codfish have top-down control over their prey. These being predators implies that their more or less heavy removal from the system could have serious implications for the ecosystem dynamics and should be taken into account by fisheries management authorities. Furthermore, mid trophic level species like herring and mackerel were also estimated to have top-down control over their prey. These species have a direct trophic link to lower trophic level organisms and their exploitation should surely take this into account.

The use of EE to estimate biomass in Ecopath, might raise concerns, as it is inversely related to biomass. An alternative to using EE could be using species density from other EwE models in neighbouring areas. However, using this method would imply assuming that either the marine ecosystem in Iceland would have the same physical, hydrological and biological dynamics as the
neighbouring areas or that species density is independent of these. This would be an assumption with potentially serious consequences, as the distribution of species in marine systems is thought to be linked to biotic and abiotic factors (Genner [2016]). This model provides insight on the marine trophic web in Iceland and it could be used as a tool to investigate how different fishing policies could impact the trophic web dynamics in Icelandic waters.

4. Acknowledgements

This study has received funding from the European Union’s Seventh Framework Programme for research, technological development and demonstration under grant agreement no. 613571 for the project MareFrame and from the European Commission’s Horizon 2020 Research and Innovation Programme under Grant Agreement No. 634495 for the project Science, Technology, and Society Initiative to minimize Unwanted Catches in European Fisheries (Minouw).

Furthermore, the authors would like to acknowledge the MFRI for providing the data that made the work presented here possible, Maciej T. Tomczak, in providing useful comments on an early version of the paper and Villy Christiansen for giving helpful input on the time series fitting.

References

Ahrens, R. N. M., Walters, C. J., Christensen, V., 2012. Foraging arena theory. Fish and Fisheries 13 (1), 41–59.
URL <GotoISI>://WOS:000298740900004

Akaike, H., 1974. New look at statistical-model identification. Ieee Transactions on Automatic Control AC19 (6), 716–723.
URL <GotoISI>://WOS:A1974U921700011

Astthorsson, O. S., Gislason, A., Gudmundsdottir, A., 1994. Distribution, abundance and length of pelagic juvenile cod in icelandic waters in relation to environmental conditions. In: ICES Marine Science Symposia. Vol. 198. Copenhagen, Denmark: International Council for the Exploration of the Sea, 1991-,, pp. 529–541.

Astthorsson, O. S., Gislason, A., Jonsson, S., 2007. Climate variability and the icelandic marine ecosystem. Deep Sea Research Part II: Topical Studies in Oceanography 54 (23), 2456–2477.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., Oskarsson, G. J., 2012. Climate-related variations in the occurrence and distribution of mackerel (scomber scombrus) in icelandic waters. ICES Journal of Marine Science: Journal du Conseil 69 (7), 1289–1297.
Borchers, D. L., Pike, D. G., Gunnlaugsson, T., Vikingsson, G., 2009. Minke whale abundance estimation from the nass 1987 and 2001 aerial cue–counting surveys taking appropriate account of distance estimation errors. NAMMCO Scientific Publications 7, 95–110.

Canning, S. J., Santos, M. B., Reid, R. J., Evans, P. G. H., Sabin, R. C., Bailey, N., Pierce, G. J., 2008. Seasonal distribution of white-beaked dolphins (lagenorhynchus albirostris) in uk waters with new information on diet and habitat use. Journal of the Marine Biological Association of the United Kingdom 88 (6), 1159–1166.

Christensen, V., Pauly, D., 1992. Ecopath-ii - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61 (3-4), 169–185.

Christensen, V., Walters, C., Pauly, D., Forrest, R., 2008. Ecopath with ecosim version 6 user guide. Lenfest Ocean Futures Project, 235.

Christensen, V., Walters, C. J., 2004. Ecopath with ecosim: methods, capabilities and limitations. Ecological Modelling 172 (2-4), 109–139.

Cook, R. M., Sinclair, A., Stefansson, G., 1997. Potential collapse of north sea cod stocks. Nature 385 (6616), 521–522.

Dommasnes, A., Christensen, V., Ellertsen, B., Kvanme, C., Melle, W., Nottestad, L., Torstein, P., Tjelmeland, S., Zeller, D., 2001. An ecopath model for the norwegian sea and barents sea. Fish. Cent. Res. Rep. 9 (4), 213–240.

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., Moland, E., 2016. Temperature-associated habitat selection in a cold-water marine fish. Journal of Animal Ecology 85 (3), 628–637.

Froese, R., Pauly, D., 2016. Fishbase. www.fishbase.org

Genner, M. J., 2016. Staying out of the heat: how habitat use is determined by local temperature. Journal of Animal Ecology 85 (3), 611–613.

Guénette, S., Christensen, V., Pauly, D., 2001. Fisheries impacts on north atlantic ecosystems: Models and analyses. https://open.library.ubc.ca/cIRcle/collections/52383/items/1.0348145
Gunnarsson, K., Jónsson, G., Pálsson, K., 1998. Sjávarnytjar við Ísland, mál og menning. Reykjavík (1998).

Hanna, S. S., 1999. From single-species to biodiversity - making the transition in fisheries management. Biodiversity and Conservation 8 (1), 45–54. URL <GotoISI>://WOS:000081404300005

Hauksson, E., Bogason, V., 1997. Comparative feeding of grey (halichoerus grypus) and common seals (phoca vitulina) in coastal waters of Iceland, with a note on the diet of hooded (cystophora cristata) and harp seals (phoca groenlandica). J. Northwest Atl. Fish. Sci 22, 125–135.

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in ecopath with ecosim food-web models for ecosystem-based management. Ecological Modelling 331, 173–184. URL <GotoISI>://WOS:000376831700016

Hutchings, J. A., 2002. Ecology and biodiversity of commercially unexploited marine fishes in the northwest Atlantic. Final Report, Dalhousie University, Halifax, Nova Scotia.

Institute, M. F. R., 2014. State of marine stocks in Icelandic waters 2013/2014 - prospects for the quota year 2014/2015.

Jonsson, S., Valdimarsson, H., 2005. Recent developments in oceanographic research in Icelandic waters. In: Developments in Quaternary Sciences. Vol. 5. Elsevier, pp. 79–92.

Kleisner, K., Hoornaert, C., 2016. Primary production. URL www.seaaroundus.org

Lilliendahl, K., Solmundsson, J., 1997. An estimate of summer food consumption of six seabird species in Iceland. Ices Journal of Marine Science 54 (4), 624–630. URL <GotoISI>://WOS:A1997XU44800013

MacNeil, M. A., McMeans, B. C., Hussey, N. E., Vecsei, P., Svavarsson, J., Kovacs, K. M., Lydersen, C., Treble, M. A., Skomal, G. B., Ramsey, M., Fisk, A. T., 2012. Biology of the Greenland shark somniosus microcephalus. Journal of Fish Biology 80 (5), 991–1018. URL <GotoISI>://WOS:000302722800006

Magnússon, K. G., Pálsson, I. K., 1989. Trophic ecological relationships of Icelandic cod. In: ICES Rapp. Proc.-Verb. Vol. 188. pp. 206–224.

Malmberg, S., Jonsson, S., 1997. Timing of deep convection in the Greenland and Iceland seas. Ices Journal of Marine Science 54 (3), 300–309. URL <GotoISI>://WOS:A1997XG98100003
Mendy, A. N., 1998. Trophic modelling as a tool to evaluate and manage Iceland’s multispecies fisheries.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. Ices Journal of Marine Science 57 (3), 697–706.
URL <GotoISI>: //WOS:000088880200026

Petursdottir, H., Falk-Petersen, S., Gislason, A., 2012. Trophic interactions of meso- and macrozooplankton and fish in the Iceland sea as evaluated by fatty acid and stable isotope analysis. Ices Journal of Marine Science 69 (7), 1277–1288.

Pike, D. G., Paxton, C. G., Gunnlaugsson, T., Vikingson, G., 2009. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986-2001. NAMMCO Scientific Publications 7, 117–142.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J., Sainsbury, K. J., 2004. Ecosystem-based fishery management. Science 305 (5682), 346–347.
URL <GotoISI>: //WOS:000222662400022

Popescu, I., Poulsen, K., 2012. Icelandic fisheries: a review. Policy Department B: Structural and Cohesion Policies Fisheries Note, European Parliament.

R Core Team, 2016. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Sigurjonsdottir, J., Vikingson, G. A., 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science 22, 271–287.

Stefansson, G., Rosenberg, A. A., 2005. Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation and protected areas. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360 (1453), 133–146.

Stefansson, G., Skuladottir, U., Steinarsson, B. A. E., 1998. Aspects of the ecology of a boreal system. Ices Journal of Marine Science 55, 859–862.

Stow, C. A., Jolliff, J., McGillicuddy, D. J., Doney, S. C., Allen, J. I., Friedrichs, M. A., Rose, K. A., Wallhead, P., 2009. Skill assessment for coupled biological/physical models of marine systems. Journal of Marine Systems 76 (1), 4–15.
Sturludottir, E., Desjardins, C., Elvarsson, B., Fulton, E. A., Gorton, R., Logemann, K., Stefansson, G., 2018. End-to-end model of icelandic waters using the atlantis framework: Exploring system dynamics and model reliability. Fisheries Research 207, 9–24.

Sunday, J. M., Bates, A. E., Dulvy, N. K., 2012. Thermal tolerance and the global redistribution of animals. Nature Climate Change 2 (9), 686–690. URL <GotoISI>://WOS:000309029100016

Tyler, H. R., Pearcy, W. G., 1975. Feeding habits of 3 species of lanternfishes (family myctophidae) off oregon, usa. Marine Biology 32 (1), 7–11. URL <GotoISI>://WOS:A1975AS18300002

Umhverfisstofnun, 2016. Veiditolur. URL http://ust.is/?PageId=2ab56c6a-246d-11e4-93bd-00505695691b

Vikingsson, G. A., Elvarsson, B. P., Olafsdottir, D., Sigurjonsson, J., Chosson, V., Galan, A., 2014. Recent changes in the diet composition of common minke whales (balaenoptera acutorostrata) in icelandic waters. a consequence of climate change? Marine Biology Research 10 (2), 138–152. URL <GotoISI>://WOS:000324978700004

Vikingsson, G., Pike, D. G., Desportes, G., Øien, N., Gunnlaugsson, T., Bloch, D., 2009. Distribution and abundance of fin whales (balaenoptera physalus) in the northeast and central atlantic as inferred from the north atlantic sightings surveys 1987–2001. NAMMCO Sci. Publ 7, 49–72.

Vikingsson, G. A., Ólafsdóttir, D., Sigurjónsson, J., 2003. Geographical, and seasonal variation in the diet of harbour porpoises (phocoena phocoena) in icelandic coastal waters. NAMMCO Scientific Publications 5, 243–270.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7 (2), 139–172. URL <GotoISI>://WOS:A1997XD41200001

Walters, C., Pauly, D., Christensen, V., Kitchell, J. F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim ii. Ecosystems 3 (1), 70–83. URL <GotoISI>://WOS:000085509300011
### Appendix A

Table A.1: Description to the species level of the functional groups used in the EwE model for Icelandic waters.

| Type           | Functional Group | Species                                      |
|---------------|------------------|----------------------------------------------|
| Seabirds      | Seabirds         | *Alca torda*                                 |
|               |                  | *Fratercula arctica*                         |
|               |                  | *Fulmarus Glacialis*                         |
|               |                  | *Rissa tridactyla*                           |
|               |                  | *Uria aalge*                                 |
| Marine Mammals| Minke whale      | *Balaenoptera acutorostrata*                 |
|               | Baleen whales    | *Balaenoptera borealis*                      |
|               |                  | *Balaenoptera physalus*                      |
|               |                  | *Megaptera novaeangliae*                     |
|               | Tooth whales     | *Globicephala melas*                         |
|               |                  | *Hyperoodon ampullatus*                      |
|               |                  | *Lagenorhyncus acutus*                       |
|               |                  | *Lagenorhyncus albirostris*                  |
|               |                  | *Orcinus orca*                               |
|               |                  | *Phocoena phocoena*                          |
|               |                  | *Physeter macrocephalus*                     |
|               | Pinniped         | *Halichoerus grypus*                         |
| Fish          | Greenland shark | *Somniosus microcephalus*                    |
|               | Dogshark         | *Apristurus aphyodes*                        |
|               |                  | *Apristurus laurussoni*                      |
|               |                  | *Centroscyllium fabricii*                    |
|               |                  | *Etmopterus princeps*                        |
|               | Skate rays       | *Raja sp.*                                   |
|               | Cod*             | *Gadus morhua*                               |
|               | Saithe*          | *Pollachius virens*                          |
|               | Haddock*         | *Melanogrammus aeglefinus*                   |
|               | Herring*         | *Clupea harengus*                            |
|               | Redfish*         | *Sebastes norvegicus*                        |
|               |                  | *Sebastes mentella*                          |
|               |                  | *Sebastes viviparus*                         |
|               | Greenland halibut*| *Reinhardtius hippoglossoides*               |
|               | Capelin          | *Mallotus villosus*                          |
|               | Blue whiting     | *Micromesistius poutassou*                   |
|               | Mackerel         | *Scomber scombrus*                           |
|               | Sandeel          | *Ammodytes sp.*                              |
|               | Large pelagic    | *Magnisudis atlantica*                       |
|               | Small pelagic    | *Myctophiidae*                               |
|               | Other codfish    | *Brosme brosme*                              |
|               |                  | *Merlangius merlangus*                       |
| Type                  | Functional Group          | Species                        |
|----------------------|---------------------------|--------------------------------|
|                      |                           | *Molva dipterygia*             |
|                      |                           | *Molva molva*                  |
| Commercial demersal  |                           | *Anarhicas sp.*                |
|                      |                           | *Cyclopterus lumpus*           |
|                      |                           | *Lophius piscatorius*          |
| Other demersal       |                           | *Cottidae*                     |
|                      |                           | *Lumpenidae*                   |
|                      |                           | *Macroridae*                   |
|                      |                           | *Zoarcinae*                    |
| Molluscs              | Cephalopod                | *Octopoda*                     |
|                      |                           | *Teuthida*                     |
|                      |                           | *Sepiida*                      |
|                      | Mollusc                   | *Arctica islandica*            |
|                      |                           | *Bivalvia*                     |
| Crustaceans          | Lobster                   | *Nephropidae*                  |
|                      |                           | *Nephrops norvegicus*          |
|                      | Shrimp                    | *Caridea*                      |
|                      |                           | *Pandalus sp.*                 |
| Benthos              | Benthos                   | *Anomura*                      |
|                      |                           | *Brachyura*                    |
|                      |                           | *Polichaeata*                  |
| Cnidarians           | Jellyfish                 | *Scyphozoa*                    |
| Plankton             | Krill                     | *Euphasiidae*                  |
|                      | Crustacean zooplankton    | *Amphipoda*                    |
|                      |                           | *Copepoda*                     |
|                      |                           | *Ostracoda*                    |
|                      | Small zooplankton         | *Chaetognatha*                 |
|                      |                            | *Ciliophora*                   |
|                      | Phytozooplankton          | *Algae*                        |
|                      | Detritus                  |                                |

*Multi-stanza group*
Table A.2: Input data for the balanced Ecopath model for Icelandic waters. Biomass and landings are given in thousands of tonnes.

| Functional group         | Biomass | P/B | Q/B | EE   | Landings |
|--------------------------|---------|-----|-----|------|----------|
| Seabirds                 | 2.831   | 0.177| 38.00 | 0.191|
| Minke whale              | 81.65   | 0.042| 6.340| 0.985|
| Baleen whale             | 189.5   | 0.060| 4.000| 5.449|
| Tooth whale              | 26.84   | 0.063| 15.00|     |
| Pinniped                 | 1.538   | 0.141| 15.00| 0.078|
| Greenland shark          | 17.50   | 0.043| 0.500| 0.051|
| Dogshark                 | 0.320   | 4.834| 0.500|     |
| Sable rays               | 0.225   | 1.750| 0.500| 2.000|
| Cod                       |         |     |     |      |
| Cod 0-3                  | 289.4   | 0.500| 4.120| 8.694|
| Cod 4+                   | 914.0   | 0.520| 1.850| 282.0|
| Saithe                    |         |     |     |      |
| Saithe 0-3               | 116.9   | 0.500| 9.687| 0.088|
| Saithe 4+                | 287.0   | 0.520| 4.760| 63.00|
| Haddock                   |         |     |     |      |
| Haddock 0-2              | 119.9   | 0.900| 9.794| 0.872|
| Haddock 3+               | 147.8   | 0.900| 4.960| 48.00|
| Herring                  |         |     |     |      |
| Herring 0-3              | 953.2   | 0.570| 10.82| 0.723|
| Herring 4+               | 387.3   | 0.950| 7.345| 49.58|
| Redfish                   |         |     |     |      |
| Redfish 0-7              | 837.9   | 0.220| 4.684|     |
| Redfish 8+               | 883.6   | 0.380| 2.800| 109.0|
| Greenland halibut        |         |     |     |      |
| Greenland halibut 0-5    | 110.9   | 0.300| 2.557|     |
| Greenland halibut 6+     | 220.0   | 0.340| 1.400| 30.21|
| Capelin                  | 1.262   | 4.800| 0.950| 865.0|
| Blue whiting             | 1159    | 0.780| 9.060| 7.077|
| Mackerel                 | 151.6   | 0.390| 4.400|     |
| Sandeel                  | 0.640   | 6.700| 0.950|     |
| Large pelagic            | 0.555   | 5.700| 0.950|     |
| Small pelagic            | 0.785   | 9.800| 0.950|     |
| Flatfish                 | 0.326   | 3.420| 0.950| 13.57|
| Other codfish            | 0.577   | 2.300| 0.950| 9.856|
| Commercial demersal      | 431.7   | 0.712| 1.400| 24.67|
| Other demersal           | 0.265   | 3.100| 0.950|     |
| Cephalopod               | 1995    | 2.440| 12.00|     |
| Mollusc                  | 1.500   | 5.000| 0.950| 15.58|
| Lobster                  | 0.354   | 5.850| 0.950| 2.459|
| Shrimp                   | 1.250   | 5.000| 0.950| 24.42|
| Benthos                  | 1.500   | 9.750| 0.950|     |
| Jellyfish                | 3.000   | 10.00| 0.950|     |
| Krill                    | 2.500   | 15.00| 0.950|     |
| Crustacean Zooplankton   | 4.000   | 15.00| 0.950|     |
| Small Zooplankton        | 13.00   | 25.00| 0.950|     |
| Phytoplankton            | 12151   | 117.6|     |      |
| Detritus                 | 0.027   |     |     |      |
Table A.3: Output for the Ecopath model for Icelandic waters. Biomass is given in thousands of tonnes.

| Functional group         | Trophic level | Biomass | EE   | Q/B  |
|--------------------------|---------------|---------|------|------|
| Seabirds                 | 4.160         | 2.831   | 0.379| 0.005|
| Minke whale              | 4.261         | 81.65   | 0.287| 0.007|
| Baleen whale             | 3.333         | 189.5   | 0.479| 0.015|
| Tooth whale              | 4.666         | 26.84   | 0.000| 0.004|
| Pinniped                 | 4.934         | 1.538   | 0.360| 0.009|
| Greenland shark          | 4.778         | 17.50   | 0.068| 0.086|
| Dogfish                  | 4.142         | 13.05   | 0.500| 0.066|
| Skate rays               | 3.897         | 220.30  | 0.500| 0.129|
| Cod                      |               |         |      |      |
| Cod 0-3                  | 4.036         | 289.4   | 0.752| 0.121|
| Cod 4+                   | 4.179         | 914.0   | 0.817| 0.281|
| Saithe                   |               |         |      |      |
| Saithe 0-3               | 3.913         | 116.9   | 0.927| 0.052|
| Saithe 4+                | 4.021         | 287.0   | 0.950| 0.109|
| Haddock                  |               |         |      |      |
| Haddock 0-2              | 3.657         | 119.9   | 0.631| 0.092|
| Haddock 3+               | 3.760         | 147.8   | 0.975| 0.181|
| Herring                  |               |         |      |      |
| Herring 0-3              | 3.223         | 953.2   | 0.913| 0.053|
| Herring 4+               | 3.250         | 387.3   | 0.948| 0.129|
| Redfish                  |               |         |      |      |
| Redfish 0-7              | 3.481         | 837.9   | 0.577| 0.047|
| Redfish 8+               | 3.668         | 883.6   | 0.648| 0.136|
| Greenland halibut        |               |         |      |      |
| Greenland halibut 0-5    | 4.160         | 110.9   | 0.242| 0.117|
| Greenland halibut 6+     | 4.370         | 220.0   | 0.404| 0.243|
| Capelin                  | 3.250         | 468.1   | 0.950| 0.263|
| Blue whiting             | 3.523         | 1159    | 0.220| 0.086|
| Mackerel                 | 3.248         | 151.6   | 0.776| 0.089|
| Sandeel                  | 3.250         | 3030    | 0.950| 0.096|
| Large pelagic            | 3.250         | 68.76   | 0.950| 0.097|
| Small pelagic            | 3.250         | 2193    | 0.950| 0.080|
| Flatfish                 | 4.118         | 279.1   | 0.950| 0.095|
| Other codfish            | 4.235         | 470.2   | 0.950| 0.251|
| Commercial demersal      | 3.779         | 431.7   | 0.386| 0.508|
| Other demersal           | 3.416         | 2861    | 0.950| 0.085|
| Cephalopod               | 3.151         | 1995    | 0.420| 0.203|
| Mollusc                  | 2.000         | 481.1   | 0.950| 0.300|
| Lobster                  | 3.359         | 1784    | 0.950| 0.060|
| Shrimp                   | 2.853         | 4217    | 0.950| 0.250|
| Benthos                  | 2.248         | 38230   | 0.950| 0.154|
| Jellyfish                | 3.150         | 22.48   | 0.950| 0.300|
| Krill                    | 2.250         | 39521   | 0.950| 0.167|
| Crustacean Zooplankton   | 2.164         | 14741   | 0.950| 0.267|
| Small Zooplankton        | 2.000         | 16707   | 0.950| 0.520|
| Phytoplankton            | 1.000         | 12151   | 0.656|      |
| Detritus                 | 1.000         | 20466   | 0.471|      |