


Original Article

Combining scientific and fishers' knowledge to co-create indicators of food web structure and function

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In this study, we describe the approach taken by the International Council for the Exploration of the Seas Irish Sea benchmark working group (WKIrish), to co-create diet information for six commercial species using fishers' and scientists knowledge and incorporate it into an existing Ecopath food web model of the Irish Sea. To understand how the co-created diet information changed the model we compared a suite of food web indicators before and after the addition of fishers' knowledge (FK). Of the 80 predator–prey interactions suggested by fishers during workshops, 50 were already included in the model. Although the small number of changes made to the model structure had an insignificant impact on the ecosystem-level indicators, indicators of species hierarchical importance and mixed trophic impacts were significantly changed, particularly for commercial species. FK heightened the importance of discards as a source of food for rays, plaice, and whiting and reduced the importance of cod, toothed whales, and plaice as structural components of the food web. FK therefore led to changes which will influence pairwise advice derived from the model. We conclude by providing lessons from WKIrish which we believe were key to the positive co-production experience and development of integrated management.

Keywords: co-production of knowledge approach, ecological network analysis, Ecopath, ecosystem-based management, fishers' knowledge, linear inverse modelling

Introduction

Environmental research is confounded by irreducible uncertainties in scientific knowledge and the need to recognize different legitimate perspectives. As a consequence, [Funtowicz and Ravetz \(1993, 2003\)](#) and [Ravetz \(2006\)](#) suggested that research is more likely to meet the challenges of environmental sustainability when enacted through a democratic and transdisciplinary approach. They coined this approach as “post-normal science,” where the extended peer community and multiple knowledge types are included to more sufficiently inform real world decisions ([Strand,](#)

[2017; Ainscough et al., 2018](#)). Taking a post-normal approach to fisheries management broadens the scientific knowledge basis through the engagement of a wider range of actors and leads to the evolution of research towards a participatory approach ([Wiber et al., 2004; Berghöfer et al., 2008; Hind, 2014; Stephenson et al., 2016](#)). [Stephenson et al. \(2016\)](#) suggest one of the best ways to improve fisheries governance is by involving stakeholders throughout the scientific to policy advice process. This is in line with the recent trends for co-production of knowledge in environmental sciences, where collaboration leads to

genuine knowledge sharing rather than simply harvesting an additional data source (Meadow *et al.*, 2015; Wall *et al.*, 2017; Djenontin and Meadow, 2018). It is also called for in European-level policy documents such as the European Marine Board's foresight document: Navigating the Future V (EMB, 2019), which highlights the need for transdisciplinary and sustainability science.

Fishers' knowledge (FK) holds considerable value as a source of information to support and inform fisheries research and management (Johannes *et al.*, 2000; Haggan *et al.*, 2007; Moreno-Báez *et al.*, 2010; Macdonald *et al.*, 2014; Raymond-Yakoubian *et al.*, 2017; Bentley, Serpetti, *et al.*, 2019). The unique experiences and perspectives of fishers provide not only fishery information, but also the ecological, institutional, social, and economic knowledge often passed from generation to generation (Berkes *et al.*, 2000; Haggan *et al.*, 2007; Silvano and Valbo-Jorgensen, 2008; Martins *et al.*, 2018). This breadth of knowledge can aid fisheries management when combined with scientific knowledge (Mackinson and Nottestad, 1998; Mackinson *et al.*, 2015), particularly where data and resources are lacking (Lopes *et al.*, 2018; Berkström *et al.*, 2019). Whilst fisheries research has historically been dominated by more narrowly focused quantitative fisheries biology (Hind, 2014), the support for ecosystem-based and integrated fisheries management has grown over the past few decades. FK forms part of the best available information needed to inform an integrated management approach (Stephenson *et al.*, 2016; Figus *et al.*, 2017). Progress has thus been made towards the integration of FK into science and management, with successful examples indicating that FK is best implemented through the co-production of knowledge, appropriately designed for the conversion of FK into actionable advice (Röckmann *et al.*, 2012; Mackinson and Wilson, 2014; Stange *et al.*, 2015; Stephenson *et al.*, 2016). Those closest to the fishery, including fishers themselves and also other stakeholders such as NGOs, are increasingly interested in contributing to the scientific process (Jasanoff, 2004; Pita *et al.*, 2010). It is therefore promising to see that the growing instances of positive collaboration experiences are changing attitudes towards FK research and leading management systems to place greater value on alternative knowledge types (Djenontin and Meadow, 2018; Stephenson *et al.*, 2018).

In 2015, scientists, fishers, NGO representatives, and industry managers were invited to work towards the first International Council for the Exploration of the Seas (ICES) integrated benchmark assessment for the Irish Sea: WKIrish (ICES, 2015) using a co-production approach. One of the aims of WKIrish was to combine scientific and stakeholder knowledge to build multi-species food web models that may ultimately be used to provide advice in an ecosystem-based context. One of the potential food web modelling approaches identified by attendees of the initial WKIrish workshop (ICES, 2015) was Ecopath with Ecosim (EwE) (Christensen *et al.*, 2008).

EwE is a food web modelling suite, used globally to assess the ecosystem impact of fisheries and address ecological questions for scientific and policy purposes (Pauly *et al.*, 2000; Christensen and Walters, 2004). Underpinning EwE models is a diet matrix which determines the trophic interactions between species and functional groups (Ulanowicz, 1980; Polovina, 1984b), the nature of pairwise interactions (i.e. the influence of one food web component on another) (Ulanowicz and Puccia, 1990; Schramski *et al.*, 2006; Hines *et al.*, 2016), and the hierarchy of species importance

within the food web (Power *et al.*, 1996; Libralato *et al.*, 2006; Borrett, 2013). At an initial meeting of WKIrish on 14–15 September 2017, fishers proposed that their knowledge of the diets of commercial species would be a valuable source of information to support the data available from stomach records and literature. Studies have previously used FK of species diets to support conventional management decisions in the absence of scientific information, with FK often showing a high degree of concordance with scientific literature (Johannes *et al.*, 2000; Silvano and Begossi, 2010, 2012; Ramires *et al.*, 2015). Bevilacqua *et al.* (2016) investigated whether FK could be used to parameterize an entire ecosystem model by gathering additional knowledge such as fish size, weight, growth rates, longevity, stock size, and catch rates. Whilst Bevilacqua *et al.* (2016) found fishers were able to provide precise information regarding species diets and weights, they were unable to inform on the growth rates, longevity, biomasses, and stock sizes of modelled species. In this instance, FK was more appropriate for parameters which were observable (i.e. stomach contents) compared to those which were not (i.e. growth rates). However, the amount of knowledge fishers possess on their target species may be very different for other locations around the world. For ecosystem modelling, the true benefit of FK may lie in its potential as a source of knowledge to be hybridized with existing scientific information.

Following the initial WKIrish meeting focusing on information sharing and project scoping (WKIrish1), two workshops were held to evaluate the scientific (fisheries) data available for the region (WKIrish2) and update Irish Sea single stock assessments (WKIrish3). In this study, we describe the methodological approach to sharing scientists' and FK of species diets which occurred during the fourth workshop (WKIrish4). We examine how the inclusion of FK impacted the structure and function of the previously constructed Irish Sea EwE model (Bentley *et al.*, 2018; Bentley, Hines, *et al.*, 2019) using a suite of ecological indicators which characterize: (i) the entire food web, (ii) individual functional groups, and (iii) trophic interactions. These indicators are influenced by the flows of energy between its components (Patten *et al.*, 1976; Ulanowicz, 1980, 1986; Borrett *et al.*, 2018) and describe the structure and function of the food web flows. Whilst FK may be limited relative to the parameter demands of an end-to-end ecosystem model, we hypothesize that it will influence model-derived advice, particularly surrounding commercial species, and enable stakeholder buy-in for future management.

Methods

Study system

The existing Irish Sea EwE model covers the extent of ICES Division VIIa ($\approx 58\,000\text{ km}^{-2}$) (Figure 1a). Following declines in commercial finfish stocks, the fisheries landings from the Irish Sea shifted in 1994 from being dominated by finfish such as cod (*Gadus morhua*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*), sole (*Solea solea*), and plaice (*Pleuronectes platessa*) to invertebrates such as Norway lobster (*Nephrops norvegicus*), scallops (*Aequipecten opercularis* and *Pecten maximus*), blue mussels (*Mytilus edulis*), and whelks (*Buccinum undatum*) (Figure 1b).

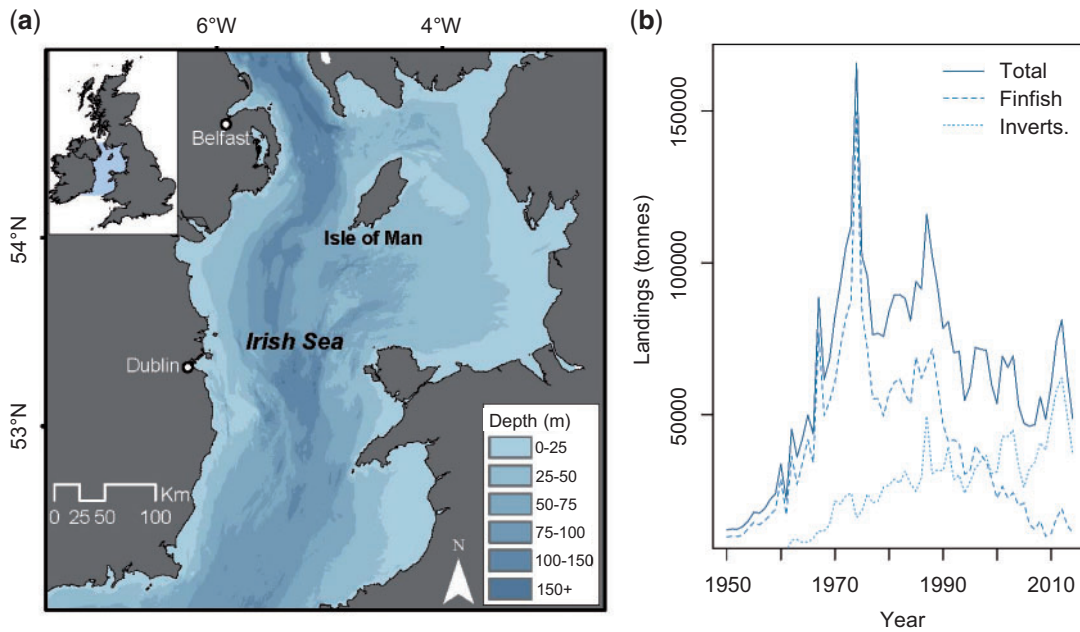


Figure 1. Study area. (a) Map of the British Isles and Ireland with inset showing the extent of the Irish Sea Ecopath model and (b) ICES landings statistics (tonnes) for the Irish Sea from 1950–2014.

Ecopath model

The Ecopath approach was initially presented by Polovina (1984a, b) to estimate the biomass and food consumption of functional groups within an ecosystem and was subsequently combined with approaches from theoretical ecology for the analysis of energy flows between functional groups (Ulanowicz and Kay, 1991). The system has since been optimized for use in fisheries assessment and ecological investigations (Christensen and Pauly, 1992; Walters *et al.*, 1997, 1999; Christensen *et al.*, 2008). The model structure comprises a mass-balanced network of functional groups, consisting of single or multiple species, whose biomass pools are trophically linked. There are two master equations in Ecopath, the first describes how the production of each functional group can be split into components [Equation (1)] and the second describes the energy balance for each group [Equation (2)].

$$\begin{aligned} \text{Production} = & \text{catches} + \text{predation mortality} \\ & + \text{biomass accumulation} + \text{net migration} \\ & + \text{other mortality} \end{aligned} \quad (1)$$

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}. \quad (2)$$

The initial Irish Sea model was developed by Bentley *et al.* (2018) using Ecopath version 6.6 beta and represents a mass-balanced snapshot of the food web in 1973. The model includes 41 functional groups ranging from detritus and plankton to elasmobranchs and marine mammals with a well-defined fish component. Four important commercial species: cod, whiting, haddock, and plaice were split into adult and juvenile stages using the best practice suggested by Heymans *et al.* (2016), to capture ontogenetic diet shifts and different exploitation patterns with size. The model's initial diet matrix for fish was built using information held in the Cefas integrated DAtabase and Portal for STOMach (DAPSTOM) records (Pinnegar, 2014; Bentley, Hines,

et al., 2019). Diets for mammals, seabirds, and invertebrates were taken from literature sources as described in Bentley *et al.* (2018). The Irish Sea model includes eight fishing fleets (beam trawl, otter trawl, *Nephrops* trawl, pelagic nets, gill nets, pots, dredges, and other gears). Fisheries landings and discards were parameterized using information from ICES (2018a) and STECF (2018). The recommended rules of thumb and best practices outlined by Link (2010) and Heymans *et al.* (2016) to ensure ecological realism in model structure and function were followed. For an in-depth description of the methods and parameters, see Bentley *et al.* (2018).

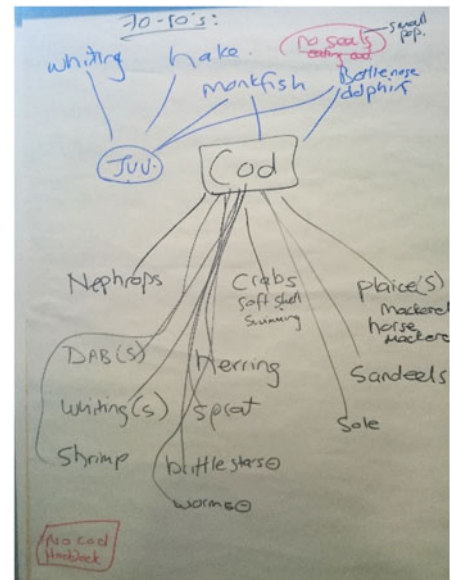
Fishers' knowledge

FK regarding the diets of commercially important species was shared during a WKIrish workshop (WKIrish4) held in Dun Laoghaire, Ireland, on 23–27 October 2017 (ICES, 2018c). The meeting was attended by nine scientists, nine fishing industry stakeholders (fishers' and their representatives), an NGO representative, and a recreational fisherman. The scientist attendees were from multiple disciplines, primarily focused on the Irish Sea region, and included multi-species modellers, marine mammal experts, and fisheries scientists. Their role was to participate in the group discussions and share their knowledge with stakeholders. Stakeholders from the fishing industry were selected by their producer organizations, who were asked to invite those who would have knowledge dating back to the 1970s. Stakeholders from the fishing industry therefore had between 30 and 40 years of fishing experience, with several coming from families with multigenerational experience.

The aim of the workshop was to build a diet matrix which included scientific knowledge and FK of predator–prey interactions for the species they commonly encountered in their operations, and where they would have observed stomach contents whilst processing catches. During the workshop, cod, whiting, haddock,

Table 1. Workshop methodology.

| | |
|--|---|
| <p>Stage 1: pre-workshop Research impetus and preparation</p> | <ul style="list-style-type: none"> • During WKIrish1, stakeholders expressed knowledge of commercial species diets as well as an interest in using this knowledge in an ecosystem modelling context. • Between WKIrish1 and WKIrish4, the EwE model was constructed using stomach record data and literature, with the foresight that new interactions from stakeholders would be incorporated during WKIrish4. |
| <p>Stage 2: workshop:WKIrish 4 Introduction and workshop aims (2 h)</p> | <ul style="list-style-type: none"> • The workshop began with a briefing presentation, familiarizing stakeholders with ecosystem modelling. (20–30 min) • The aims of the workshop were discussed. (1 h) • Visual aids were provided of the models functional groups. |
| <p>Information collection (3 h)</p> | <ul style="list-style-type: none"> • Discussion took place to identify the species stakeholders were familiar with. (30–40 min) • Diets for the six commercial species commonly encountered by fishers' (rays, cod, whiting, haddock, plaice, Norway lobster) were collected one at a time with participants gathered around a flipchart. • Food webs were drawn by a scientific member of the workshop whilst stakeholders provided information. • Visual aids were projected onto monitors to support discussion, i.e. if a participant was talking about a specific species, that species would be projected to inform others in the room. |
| <p>Discussion (1 h)</p> | <ul style="list-style-type: none"> • Time was put aside to discuss the workshop and answer stakeholder questions and share scientific knowledge on the subject of species diets. |
| <p>Stage 3: post-workshop Network analysis</p> | <ul style="list-style-type: none"> • Stakeholder information was incorporated into the ecosystem models diet matrix. Comparisons were made between model statistics with and without stakeholder's additions. |
| <p>Follow-up workshop</p> | <ul style="list-style-type: none"> • Final results and the value of FK were presented back to participants during WKIrish 5 via an oral presentation. Research briefs were also produced for stakeholders to convey the research undertaken from 2017 to 2018. |



Example stakeholder diet for Atlantic cod produced during WKIrish4

Using fishers' experiential and inherited knowledge to better understand the predator–prey interactions of commercial species in the Irish Sea.

plaice, rays (*Raja* spp.), and Norway lobster were identified as the species for which fishers' felt they had substantial knowledge. The knowledge co-production process is shown in Table 1. The process was informed by guidance given in the GAP2 “Oral Histories Tool,” <http://gap2.eu/methodological-toolbox/oral-histories/>.

Each of the six selected species was considered in turn, with fishers' being asked to provide knowledge as far back in time as possible, ideally to the early 1970s as the EwE snapshot was constructed to represent the system in 1973. Every effort was taken to avoid leading fishers' responses; the only guidance from the scientists was to focus discussion species by species. Thereafter, the inclusion and strength of any interaction was driven only by the stakeholders. Fishers were asked to list the predator–prey interactions for the species of interest, along with any qualitative information that might influence how the information was entered into the model (i.e. were interactions observed frequently or infrequently). Where possible, fishers' were asked to differentiate between juvenile and adult fish for functional groups with multi-stanzas. Fishers were finally asked about any other information they could contribute regarding diets of mammals and

seabirds. An example of a completed appraisal for cod is presented in stage 2 of Table 1.

Incorporating FK into EwE

Fishers' diet links were quantified in the model on a case-by-case basis. New interactions were added to the model diet matrix whilst ensuring that the combined predation and fishing mortality placed on each functional group did not exceed production, as for an Ecopath model to be mass balanced total consumption cannot exceed the production of the species. To ensure diets remained balanced, additions of new prey proportions were counterbalanced by adjusting other prey proportions within the range of plausible values (Bentley et al., 2018). Due to the inherent uncertainty in quantifying qualitative information, the diets of functional groups which were altered by FK were assigned large confidence intervals ($\pm 80\%$) in the models “pedigree” routine (Table 2) (Christensen and Walters, 2004), which serves a dual purpose by allowing the user to describe the origin of the data whilst also assigning confidence intervals based on data origin. The large confidence intervals assigned to diets altered by fishers ensured, when later applying Monte Carlo simulations (see “Assessing the impact of FK on food web structure and function”

Table 2. Confidence intervals assigned to predator diets within Ecopath.

| | Functional group | Confidence intervals | |
|----|------------------------------|----------------------|---------|
| | | Without FK | With FK |
| 1 | Toothed whales | 0.5 | 0.5 |
| 2 | Minke whales | 0.5 | 0.5 |
| 3 | Seals | 0.5 | 0.8 |
| 4 | Seabirds (high discard diet) | 0.5 | 0.8 |
| 5 | Seabirds (low discard diet) | 0.5 | 0.8 |
| 6 | Sharks | 0.1 | 0.8 |
| 7 | Rays | 0.1 | 0.8 |
| 8 | Adult cod | 0.1 | 0.1 |
| 9 | Juvenile cod | 0.1 | 0.1 |
| 10 | Adult whiting | 0.1 | 0.8 |
| 11 | Juvenile whiting | 0.1 | 0.1 |
| 12 | Adult haddock | 0.1 | 0.1 |
| 13 | Juvenile haddock | 0.1 | 0.1 |
| 14 | Adult plaice | 0.1 | 0.8 |
| 15 | Juvenile plaice | 0.1 | 0.8 |
| 16 | Common sole | 0.1 | 0.1 |
| 17 | Flatfish | 0.1 | 0.1 |
| 18 | Monkfish | 0.1 | 0.8 |
| 19 | European hake | 0.1 | 0.8 |
| 20 | Sandeels | 0.1 | 0.1 |
| 21 | Gurnards and dragonets | 0.1 | 0.1 |
| 22 | Other demersal fish | 0.1 | 0.1 |
| 23 | Other benthopelagic fish | 0.1 | 0.1 |
| 24 | Atlantic herring | 0.1 | 0.1 |
| 25 | European sprat | 0.1 | 0.1 |
| 26 | Other pelagic fish | 0.1 | 0.1 |
| 27 | Anadromous fish | 0.1 | 0.1 |
| 28 | Lobsters and large crabs | 0.5 | 0.5 |
| 29 | Norway lobster | 0.5 | 0.8 |
| 30 | Shrimp | 0.5 | 0.5 |
| 31 | Cephalopods | 0.5 | 0.5 |
| 32 | Scallops | 0.5 | 0.5 |
| 33 | Epifauna | 0.5 | 0.5 |
| 34 | Infauna | 0.5 | 0.5 |
| 35 | Gelatinous zooplankton | 0.5 | 0.5 |
| 36 | Large zooplankton | 0.5 | 0.5 |
| 37 | Small zooplankton | 0.5 | 0.5 |
| 38 | Seaweed | 0.5 | 0.5 |
| 39 | Phytoplankton | 0.5 | 0.5 |

Diets taken from local stomach data were assigned low confidence intervals of 0.1, diets taken from literature were assigned confidence intervals of 0.5. Diets altered by FK were assigned higher confidence intervals of 0.8.

section), that a large range of parameters could be tested to reflect data uncertainty in model outputs.

Assessing the impact of FK on food web structure and function

To quantify the impact of incorporating FK into the Irish Sea food web model, we calculated a suite of ecological network analysis (ENA) indicators both before and after changes were made. ENA indices are capable of identifying the impact of stress and disturbance on ecosystem status and trophic conditions (Dame and Christian, 2007). There is therefore a sense that ENA indices can be used for ecosystem and fisheries management (Longo et al., 2015; Raoux et al., 2019). Whilst efforts are underway to establish the most appropriate indicators to assess

ecosystem status (Borrett et al., 2018; Schückel et al., 2018), the development of methods to perform sensitivity and uncertainty analysis for ENA is essential to make stronger inferences regarding network thresholds (Borrett et al., 2016) and the differences between networks (Hines et al., 2018). Eight indicators were used (Table 3), four of which [total system throughput (TSTp), average path length (APL), Finn's cycling index (FCI), and Shannon based flow diversity (H)—see Table 2 for definitions] have recently been proposed as key indicators for food web assessment for management advice (Schückel et al., 2018; Fath et al., 2019; Safi et al., 2019). The selected indicators explore the impact of incorporating FK on ecosystem structure and function [TST, APL, FCI, indirect flow intensity (IFI), H], on species importance in the food web [trophic level (TL) and relative trophic impact (RTI)], and on pairwise dependencies [mixed trophic impact (MTI)].

Calculating indicators and uncertainty in Ecopath

TL and RTI were calculated using the Ecopath software (Christensen et al., 2008). The inbuilt Monte Carlo routine (Kennedy and O'hagan, 2001; Heymans et al., 2016) was used to generate 500 permutations of (i) the original Ecopath model without FK and (2) the modified version of the original model with FK using the “pedigree” based confidence intervals assigned to the diets of each functional group (Table 2). Model iterations were stored using the EcoSampler plugin (Steenbeek et al., 2018). Estimates of TL and RTI were extracted for the calculation of 95% confidence intervals.

Calculating indicators and uncertainty using enaR

The remaining indicators (TST, APL, FCI, IFI, H, and MTI) were calculated in RStudio (version 1.0.153) (RStudioTeam, 2015) using recent advances in uncertainty analyses for ENA which facilitate the estimation of data-based flow uncertainty (Hines et al., 2018; Bentley, Hines, et al., 2019). Following the methodology of Bentley, Hines, et al. (2019), the Irish Sea food web models, both with and without FK, were transformed into network objects using the “network” package (version 1.14-377) (Butts, 2008) for analysis with the “enaR” package (version 3.0.0) (Borrett and Lau, 2014). Each network edge (energy flows, exports, and respirations) was assigned an upper and lower limit calculated using the 95% confidence intervals for prey contribution to predator diet from the DAPSTOM records.

Limits were assigned to each network flow using the enaUncertainty function from the enaR package (Lau et al., 2017). This function uses a linear inverse modelling (LIM) algorithm from the limSolve package (version 1.5.5.3) (Soetaert et al., 2009; Van Den Meersche et al., 2009) in combination with Monte Carlo sampling to generate a plausible set of network permutations. For flows which were not taken from DAPSTOM, where no dietary uncertainty data were available (i.e. FK and interactions from literature), symmetric upper and lower network parameter limits were set at $\pm 25\%$ of the balanced models estimates as, after testing limits from ± 0 to $\pm 100\%$ uncertainty, this was found to be the point at which the effect of uncertainty in these edges was maximized (i.e. further increases in uncertainty generated a predictable and symmetrical melt of indicator distributions).

Overall, 10 000 balanced network permutations were generated for the Irish Sea model without FK, and another 10 000 for the model with FK. All permutations had edge values that fell within

Table 3. List of food web indicators used to compare the Irish Sea food web model with and without FK.

| Food web indicator | Equation | Indicator description | References |
|----------------------|--|--|--|
| TL | $TL_i = 1 + \sum_j (TL_j \times DC_{ij})$ | TL _i signifies the position group <i>i</i> occupies within the food web, where TL _j is the fractional TL of prey <i>j</i> and DC _{ij} is the fraction of <i>j</i> in the diet of <i>i</i> . | Odum and Heald (1975) and Christensen <i>et al.</i> (2008) |
| RTI (ϵ_i) | $\epsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2}$ | RTI (ϵ_i) is calculated for group <i>i</i> using their estimated pairwise MTIs (m_{ij}), taking into consideration that m_{ij} can be positive or negative to calculate an overall effect on the food web. | Libralato <i>et al.</i> (2006) |
| TSTp | $TSTp = \frac{\text{Internal flows} + \text{External flows}}{\text{Inputs}}$ | TSTp is a measure of the amount of material moving through a system and is seen as an indicator of system size and activity. | Rutledge <i>et al.</i> (1976), Ulanowicz (1980, 1997, 1986), and Borrett and Lau (2014) |
| APL | $APL = \frac{TST}{\text{Inputs}}$ | APL is a measure of the retention time of material within the system and is expected to be higher in systems with high degrees of flow diversity and cycling (Christensen, 1995). It also characterizes the amount of activity that the system organization can generate for each unit of input into the system, and is therefore similar to the multiplier effect in economics. | Samuelson and Scott (1967), Finn (1976), Christensen (1995), and Borrett and Lau (2014) |
| FCI | $FCI = \frac{\text{Cycled flow}}{TST}$ | Cycled flow is defined as material that is recycled before exiting the network. FCI therefore indicates the retention time of material within a system and can be used to interpret ecosystem stability and health. | Finn (1976), Baird and Ulanowicz (1993), Vasconcellos <i>et al.</i> (1997), and Borrett and Lau (2014) |
| IFI | $IFI = \frac{\text{Indirect flow}}{TST}$ | IFI characterizes the indirect effects within a system, which can be critical components of complex adaptive systems that can act as a stabilizing force in the face of external perturbations | Borrett <i>et al.</i> (2006) and Borrett and Lau (2014) |
| H | $H = -1 \sum_{i=1}^n p_i \log(p_i)$ | This Shannon entropy-based metric of total flow diversity captures the effects of both richness (the length of the vector, <i>n</i>) and the evenness of the distribution. In this application p_i is the proportion of group <i>i</i> relative to the total number of groups. | MacArthur (1955) and Borrett and Lau (2014) |
| MTI | $q_{ij} \equiv g_{ij} - h_{ji}$ | MTI quantifies the net impact (q_{ij}) of a network compartment on another as the difference between the positive impact the prey has on the predator (g_{ij}) minus the negative impact the predator has on its prey (h_{ji}). | Ulanowicz and Puccia (1990) and Borrett and Lau (2014) |

the assigned upper and lower limits and were therefore considered equally plausible. Indicators were calculated for each network permutation to produce indicator distributions for each model. Indicators were compared to and without FK to identify whether FK significantly impacted their distributions. We defined the impact of FK to be significant if there was no overlap between the 95% confidence intervals for indicator distributions (Hines *et al.*, 2018).

Following the calculation of indicator distributions, we applied a secondary uncertainty analysis. Unlike the primary uncertainty analysis which explored whether network metrics were different given the assigned uncertainty to network edges, here we acknowledged that the original networks (without and with FK) were not identical, and therefore question how much (or little) edge uncertainty was necessary to obscure the differences between networks. Questioning the level of uncertainty at which differences between network objects become apparent strengthens conclusions from comparative assessments (Hines *et al.*, 2016). In this study, we conducted comparisons using the uncertainty proportions assigned to each edge and an uncertainty scalar, as introduced by Hines *et al.* (2018). The scalar is a proportion of the assumed uncertainty, ranging from 0.03 to 0.1, where the original assumed uncertainty is equal to 1. Upper and lower uncertainty limits were calculated as:

$$\text{lower} = O_{ij} - ((O_{ij} - L_{ij}) \times \text{Uncertainty scalar})$$

$$\text{upper} = O_{ij} + ((U_{ij} - O_{ij}) \times \text{Uncertainty scalar}),$$

where O_{ij} is the original edge value between groups *i* and *j*, L_{ij} is the lower edge limit and U_{ij} is the upper edge limit. Calculating upper and lower edges independently facilitates the calculation of asymmetric uncertainty for edges with asymmetric upper and lower limits. The range of 0.03–0.1 was selected as at this level of uncertainty we began to see differences between indicators with and without FK. We did not test above 0.1 as significant differences were obscured beyond this point. This window will likely be different for each model comparison.

Results

Fishers' knowledge

Fishers identified a total of 80 predator–prey interactions involving rays, cod, haddock, whiting, plaice, or Norway lobster (Figure 2, Table 4). Of these, 50 were already included in the Irish Sea EwE model without FK, thus fishers identified 30 new linkages. The addition of these new predator–prey interactions increased the number of edges in the food web network from 479

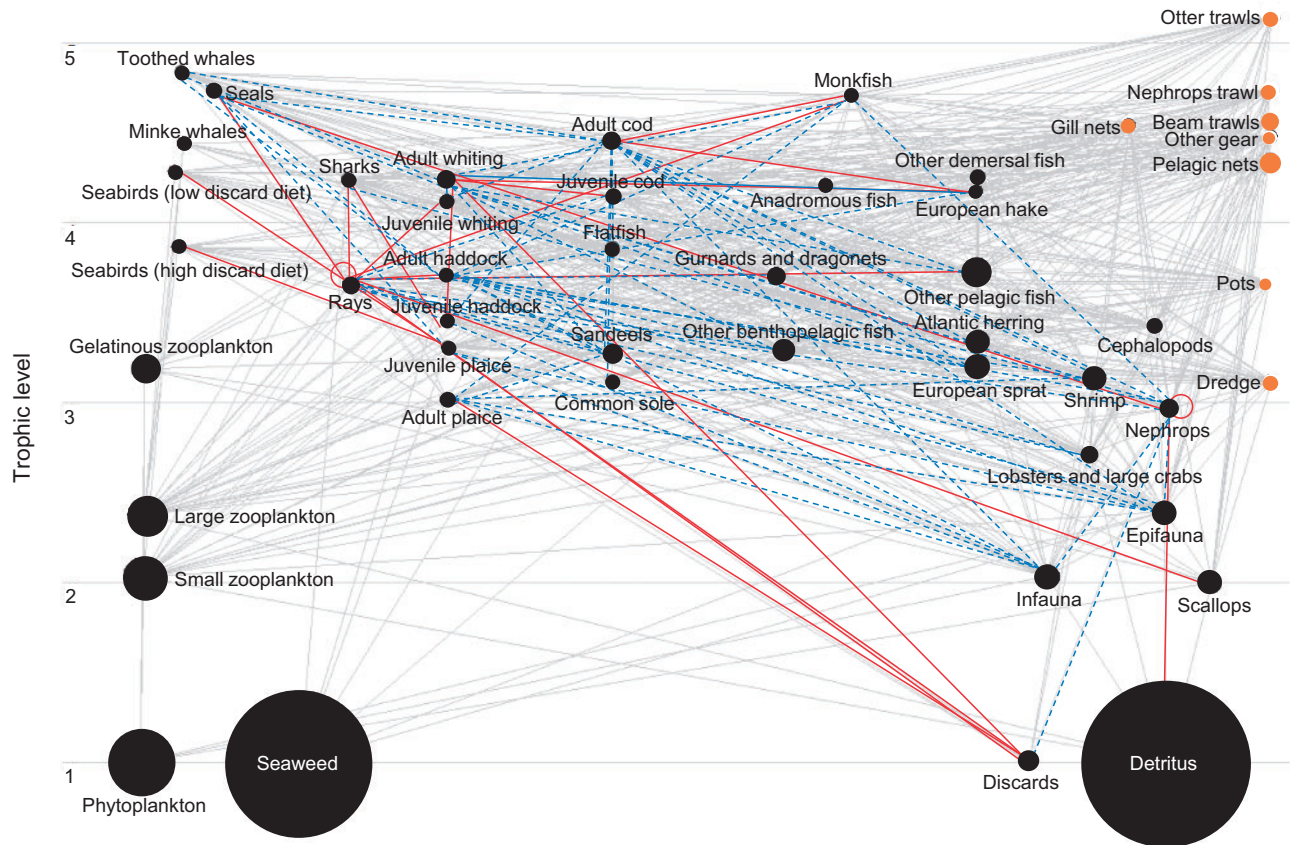


Figure 2. Energy flow and biomass diagram for the Irish Sea Ecopath food web model. Functional groups (black) and fleets (orange) are represented by nodes. The relative size of nodes for functional groups denotes their biomass in the ecosystem, whereas the relative size of nodes for fishing fleets represents catch volume. Lines represent the flow of energy and the y-axis denotes group trophic level. Thin grey lines=interactions included based on scientific data, thick (red) lines=new interactions from fishers' knowledge, thick dashed (blue) lines=interactions from fishers' knowledge which were already in the model. See online for color version.

to 509. New predators were identified for rays, cod, haddock, whiting, plaice, and Norway lobster. Notably, monkfish (*Lophius piscatorius*) was identified as a predator on rays, cod, whiting, and haddock. Within functional group predation was identified for rays and Norway lobster and discard consumption was identified for rays, whiting, and plaice. Despite multiple prey being suggested for cod and haddock, no new prey items were identified reflecting the opportunistic diet of these species, as indicated also by DAPSTOM data used for "without FK" model construction. Including FK altered the diet profile for rays the most, with five new prey items being identified (not including within-group predation). FK also proved valuable in providing insights into new interactions between commercial species and marine mammals and seabirds, including the consumption of rays and Norway lobster by seals and the consumption of juvenile plaice by seabirds. Overall, 14% of the flows in the model were modified to accommodate FK (Table 4).

Changes to species-level indicators

The addition of FK had small impacts on the TLs of the functional groups (Figure 3). Small declines were generated in the baseline TLs of seals, rays, adult whiting, juvenile plaice, and adult plaice, whereas the TL of monkfish increased. Only the TLs of juvenile and adult plaice were significantly altered by incorporating

FK, where the 95% confidence intervals from plausible models were used to make statistical comparisons.

RTI identifies groups which have the largest effects on the food web. The groups with the highest RTI with and without FK were epifauna, zooplankton, and phytoplankton. In the model without FK, adult cod also had a high RTI, however fishers' additions significantly reduced this, as well as the RTI of toothed whales and adult plaice. The RTI for adult whiting and European hake increased in the model with FK. RTI for the remaining groups showed a lack of significant difference between the model with FK vs. the model without FK.

Changes to ecosystem-level indicators

Sets of 10 000 plausible models were generated for the Irish Sea Ecopath models with and without FK. These sets were used to produce distributions of ENA metrics for comparative assessment. The 95% ranges of all the network metrics overlapped so no significant differences were observed between the metrics estimated with and without FK (Figure 4).

Uncertainty sensitivity analysis highlighted how little data variability was needed to reveal significant differences between indicator estimates from the model without FK vs. the model with FK. Differences in the distributions of FCI, IFI, and H were observed between the two models when the uncertainty ranges

Table 4. Changes made to the Irish Sea Ecopath diet matrix using FK.

| Predator/prey FK | Seals | | Seabirds (high discard) | | Seabirds (low discard) | | Sharks | | Rays | | Adult whiting | | Adult plaice | | Juvenile plaice | | Monkfish | | European hake | | Norway lobster | | |
|--------------------------|--------------|-------|----------------------------|-------|---------------------------|-------|--------------|--------------|--------------|--------------|---------------|--------------|--------------|-------|--------------------|-------|----------|-------|------------------|--------------|-------------------|-------|--|
| | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | Before | After | |
| | | | | | | | | | | | | | | | | | | | | | | | |
| Sharks | 0.009 | 0.009 | | | | | | | | | | | | | | | | | | | | | |
| Rays | <u>0.045</u> | | | | | | | | | | | | | | | | | | | | | | |
| Adult cod | 0.040 | 0.040 | | 0.014 | 0.014 | 0.014 | 0.001 | 0.001 | 0.049 | 0.045 | <u>0.010</u> | | | | | | | | | | | | |
| Juvenile cod | 0.009 | 0.009 | 0.012 | 0.012 | | | 0.001 | 0.001 | 0.011 | 0.010 | | <u>0.005</u> | | | | | | | | <u>0.010</u> | | | |
| Adult whiting | 0.031 | 0.031 | | | | | 0.004 | 0.004 | | | 0.032 | 0.030 | | | | | | | | | | | |
| Juvenile whiting | 0.005 | 0.005 | 0.027 | 0.027 | | | 0.012 | 0.012 | | | <u>0.020</u> | 0.074 | 0.070 | | | | | | | | | | |
| Adult haddock | 0.005 | 0.005 | | | | | <u>0.005</u> | <u>0.005</u> | | | | | | | | | | | | | | | |
| Juvenile haddock | 0.005 | 0.005 | | | | | <u>0.035</u> | <u>0.035</u> | | | | | | | | | | | | | | | |
| Adult plaice | 0.002 | 0.002 | | | | | 0.001 | 0.001 | | | | | | | | | | | | <u>0.005</u> | 0.009 | | |
| Juvenile plaice | 0.020 | 0.020 | <u>0.020</u> | | | | 0.020 | 0.020 | | | | | | | | | | | | | | | |
| Common sole | 0.020 | 0.020 | | | | | 0.008 | 0.008 | 0.004 | 0.004 | | | | | | | | | | | | | |
| Flatfish | 0.057 | 0.057 | 0.047 | 0.027 | 0.030 | 0.010 | 0.130 | 0.100 | 0.055 | 0.050 | 0.045 | 0.042 | | | | | | | | | | | |
| Monkfish | 0.001 | 0.001 | | | 0.027 | 0.027 | | | | | | | | | | | | | | | | | |
| European hake | | | | | | | | | | | | | | | | | | | | | | | |
| Sandeels | 0.060 | 0.060 | 0.091 | 0.091 | 0.329 | 0.329 | 0.002 | 0.002 | 0.083 | 0.076 | 0.005 | <u>0.016</u> | | | | | | | | | | | |
| Gurnards and dragonets | 0.023 | 0.023 | 0.036 | 0.036 | 0.073 | 0.073 | 0.070 | 0.070 | 0.003 | 0.003 | | | | | | | | | | | | | |
| Other demersal fish | 0.220 | 0.185 | 0.083 | 0.083 | 0.020 | 0.020 | 0.007 | 0.007 | | | | | | | | | | | | | | | |
| Other benthopelagic fish | 0.221 | 0.195 | 0.040 | 0.040 | 0.013 | 0.013 | 0.208 | 0.178 | 0.003 | 0.003 | 0.160 | 0.150 | | | | | | | | | | | |
| Atlantic herring | 0.045 | 0.045 | 0.087 | 0.087 | 0.124 | 0.124 | 0.011 | 0.011 | | | 0.021 | 0.020 | | | | | | | | | | | |
| European sprat | 0.045 | 0.045 | 0.087 | 0.087 | 0.125 | 0.125 | 0.002 | 0.002 | 0.299 | 0.280 | | | | | | | | | | | | | |
| Other pelagic fish | 0.075 | 0.075 | 0.118 | 0.118 | 0.094 | 0.094 | 0.176 | 0.176 | <u>0.005</u> | 0.160 | 0.150 | | | | | | | | | | | | |
| Anadromous fish | 0.090 | 0.090 | | | 0.017 | 0.017 | | | | | | | | | | | | | | | | | |
| Lobsters and large crabs | 0.008 | 0.008 | | | 0.013 | 0.013 | 0.014 | 0.014 | 0.014 | 0.013 | | | | | | | | | | | | | |
| Norway lobster | <u>0.016</u> | | | | | | 0.075 | 0.075 | 0.110 | 0.050 | 0.007 | <u>0.007</u> | | | | | | | | | | | |
| Shrimp | | | | | | | 0.002 | 0.002 | 0.022 | 0.020 | 0.002 | 0.002 | | | | | | | | | | | |
| Cephalopods | 0.035 | 0.035 | 0.002 | 0.002 | | | 0.037 | 0.037 | 0.007 | 0.007 | 0.015 | 0.015 | | | | | | | | | | | |
| Scallops | | | | | | | 0.007 | 0.007 | | | | | | | | | | | | | | | |
| Epifauna | | | 0.107 | 0.107 | 0.001 | 0.001 | 0.206 | 0.206 | 0.493 | 0.448 | 0.141 | 0.132 | | | | | | | | | | | |
| Infaua | | | 0.050 | 0.050 | 0.082 | 0.082 | 0.005 | 0.005 | 0.140 | 0.127 | 0.037 | 0.035 | | | | | | | | | | | |
| Gelatinous zooplankton | | | | | | | | | | | | | | | | | | | | | | | |
| Large zooplankton | | | 0.013 | 0.013 | 0.017 | 0.017 | <0.001 | <0.001 | 0.002 | 0.002 | <0.001 | <0.001 | | | | | | | | | | | |
| Small zooplankton | | | | | | | <0.001 | <0.001 | 0.003 | 0.003 | 0.001 | 0.001 | | | | | | | | | | | |
| Seaweed | | | | | | | 0.001 | 0.001 | | | | | | | | | | | | | | | |
| Discards | | | 0.201 | 0.201 | 0.019 | 0.019 | | | <u>0.050</u> | <u>0.020</u> | <u>0.020</u> | <u>0.259</u> | | | | | | | | | | | |
| Detritus | | | | | | | | | | | | | | | | | | | | | | | |

New interactions are underlined.

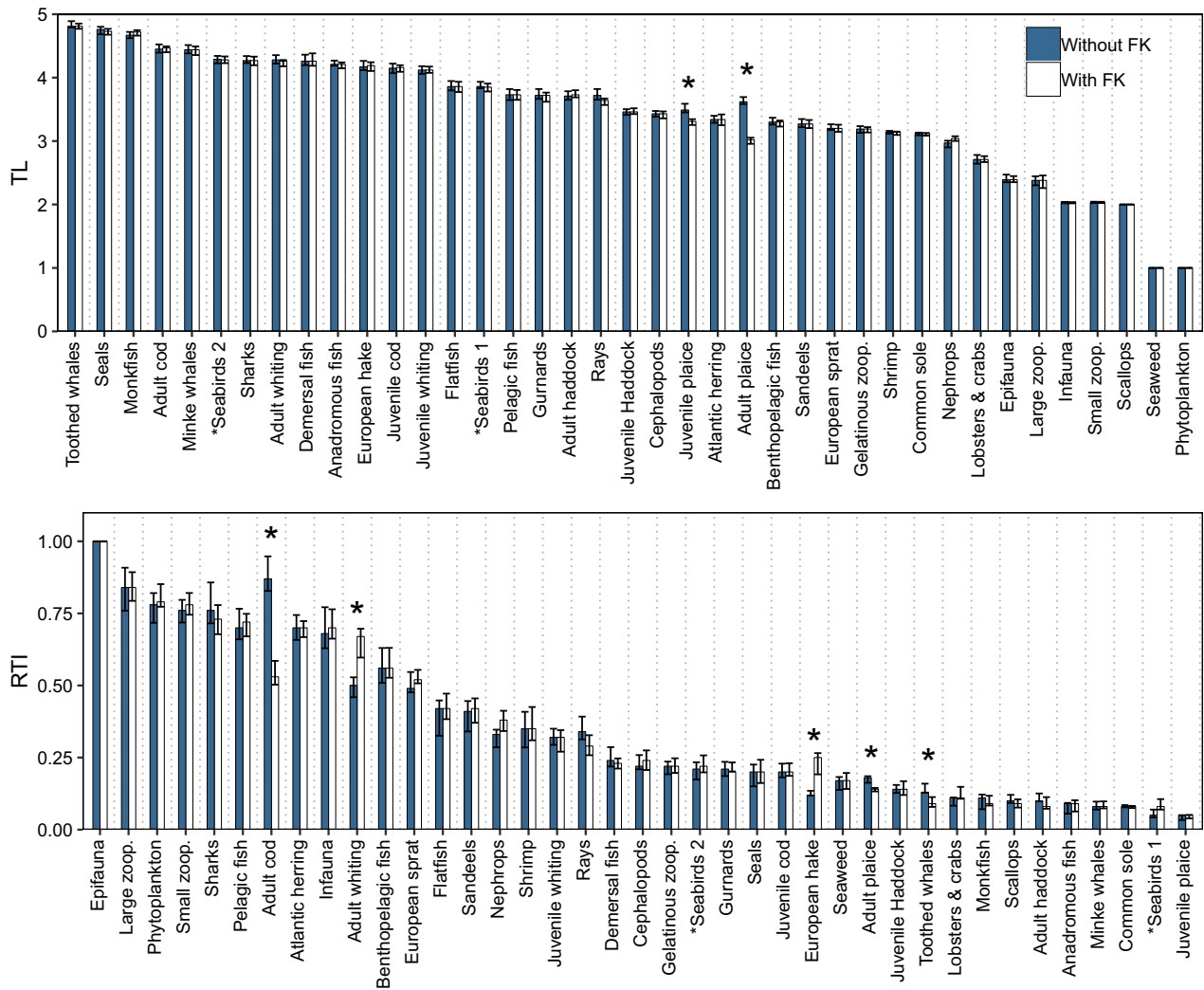


Figure 3. Trophic Level (TL) and Relative Total Importance (RTI; Libralato et al, 2006) network metrics, ranked highest to lowest, before and after the addition of new predator-prey links suggested by fishers'. Bars indicate baseline Ecopath estimates of all living functional groups of the two models (without vs. with fishers' knowledge (FK)) and error bars indicate 95% confidence intervals calculated using a Monte Carlo approach. Stars indicate significant differences between metrics with and without fishers' knowledge. * Seabirds 1 = high discard diet; Seabirds 2 = low discard diet.

around predator-prey interactions were below 4–5% of their original uncertainty. For TSTp and APL), significant differences were not observed above 3% of the original uncertainty.

Changes to pairwise species dependencies

The MTI routine was used to explore how a small increase in the biomass of any functional group impacted the biomass of the other groups. The routine was applied to each of the 10 000 model iterations with and without FK to calculate the plausible MTI ranges and visualize the impact of including FK. An average MTI matrix was created for the model with FK using the 10 000 iterations (Figure 5). Increases in the biomasses of lower TLs, notably phytoplankton, had the largest positive impacts on the biomasses of other functional groups, whereas increases in the biomasses of higher trophic groups negatively impacted their prey species, such as the impact of adult cod on haddock. Cannibalistic functional groups negatively impacted themselves.

MTI values are relative and comparable between groups, therefore cumulative MTIs were calculated for each functional group to explore their average impact on other groups as well as the average impact of other groups on them. The full range of MTI values were utilized from the 10 000 models to provide 95% confidence intervals around the cumulative MTIs (Figure 5). Increases in the biomasses of phytoplankton, epifauna, infauna, zooplankton, and detritus had positive cumulative impacts on the system biomass. Sandeels, herring, sprat (*Sprattus sprattus*), and other pelagic fish also positively impacted the systems biomass, with predominantly positive MTI ranges. Sharks, rays, cod, and whiting showed largely negative MTI ranges, suggesting that increases in their biomass would, on average, negatively impact other groups. When looking at the impacted functional groups we find that the average cumulative MTI tends to increase with increasing TL. Discards and detritus also show positive responses to increases in system biomass.

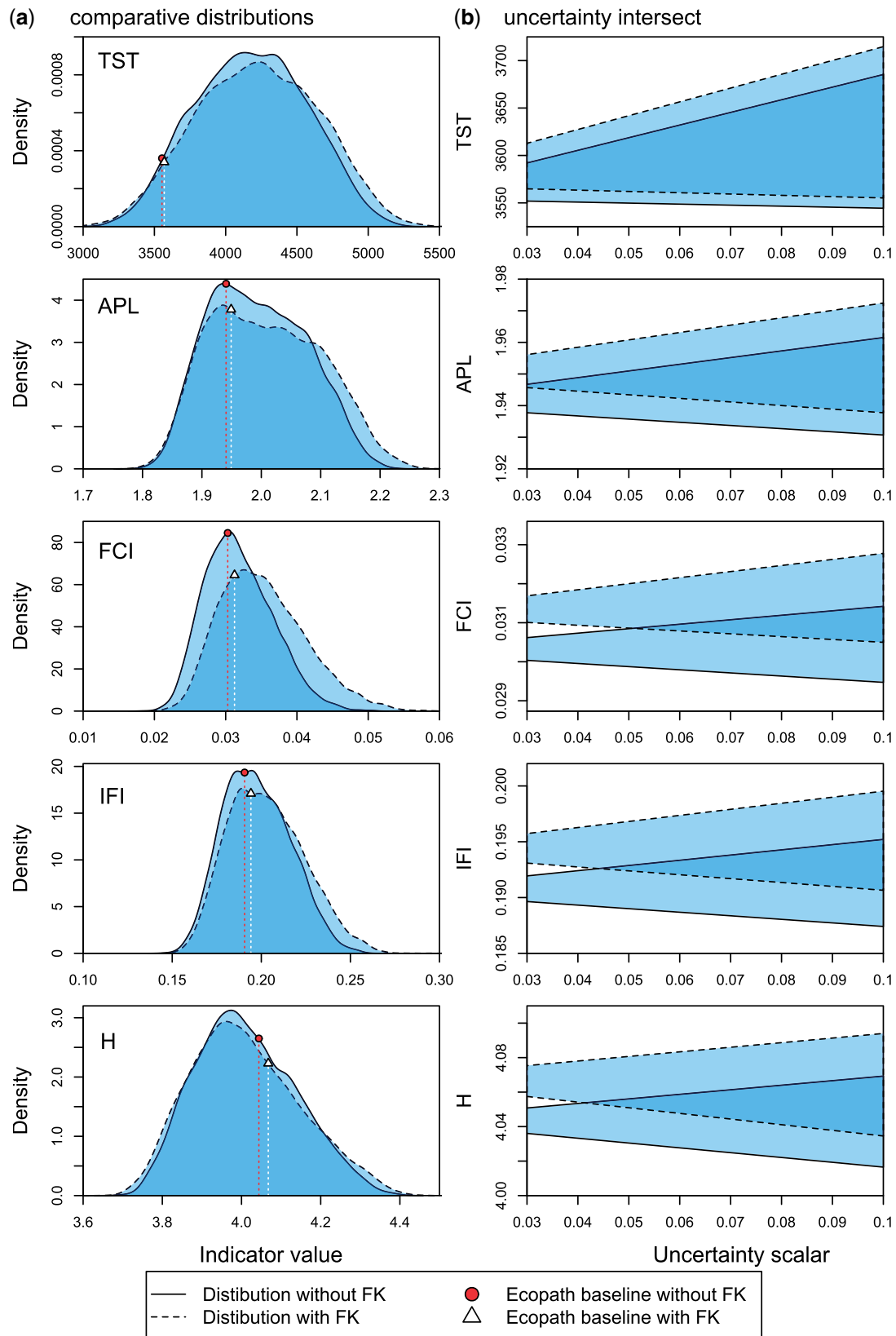


Figure 4. (a) Probability density plots showing the distribution of TSTp, APL, FCI, IFI and H in the Irish Sea networks using data guided uncertainty. Network metrics were calculated before and after fisher’s knowledge (FK) was incorporated into the models diet matrix. Vertical lines indicate original metrics of the two baseline models. (b) Asymmetric uncertainty analysis showing the uncertainty necessary to obscure the differences between network metrics with and without fishers’ knowledge using scalar asymmetric uncertainty ranging from 3–10%. See Table 3 for indicator definitions.

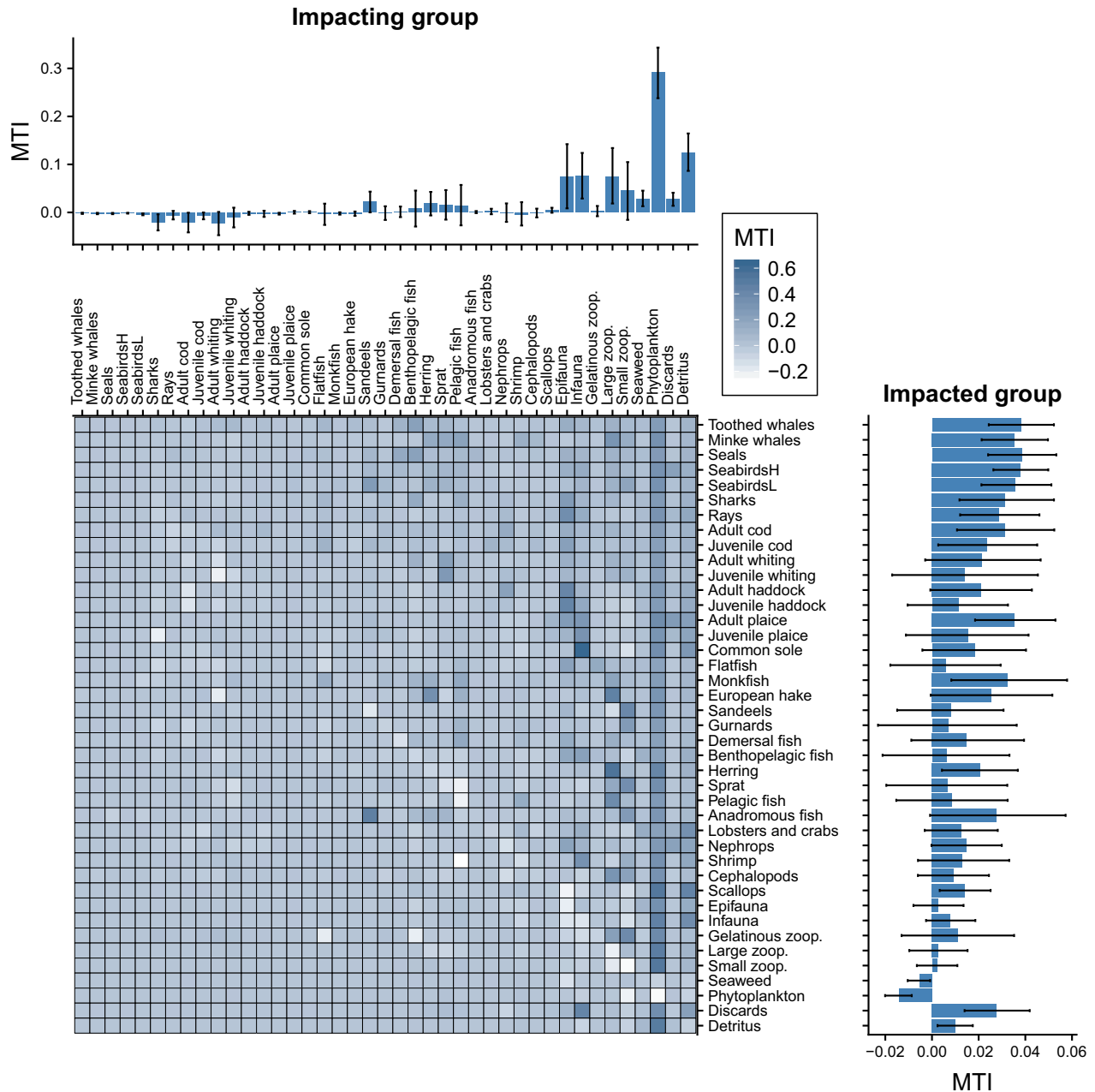


Figure 5. Mixed trophic impact (MTI) analysis for the Irish Sea food web co-created by scientists and stakeholders. Values in the MTI matrix represent the average impacts across 10,000 model iterations. Bars highlight the average cumulative MTI's for each group, showing how they impact the food web and how they are impacted by the food web. Error bars show the 95% confidence intervals for cumulative impacts based on the 10,000 models produced.

To investigate the impact of FK on the MTI routine, we compared the distributions of plausible MTI values between models sets with and without FK (Figure 6). The greatest changes in MTI distributions were seen for the group interactions which included one of the six species altered by FK. On average, the percentage overlap for distributions of MTI values for the six species targeted by FK was reduced by 30% with the addition of FK. However, the indirect consequences of these changes propagated through the food web, with the average percentage overlap for distributions of MTI values for all other groups being reduced by 18% after the addition of FK. Overall, 168 of the MTI distributions from the model

with FK shared <50% overlap with the distributions from the model without FK. Of these 168 interactions, 67 shared <95% overlap with estimates prior to the addition of FK, and were therefore significantly altered. Adult plaice, rays, and discards showed the largest changes in the ways they impacted other groups whereas adult plaice, rays, Norway lobster, and hake experienced the largest changes in the ways they were impacted by other groups.

Discussion

A number of new food web interactions was identified and added to the Irish Sea Ecopath model through a co-production of

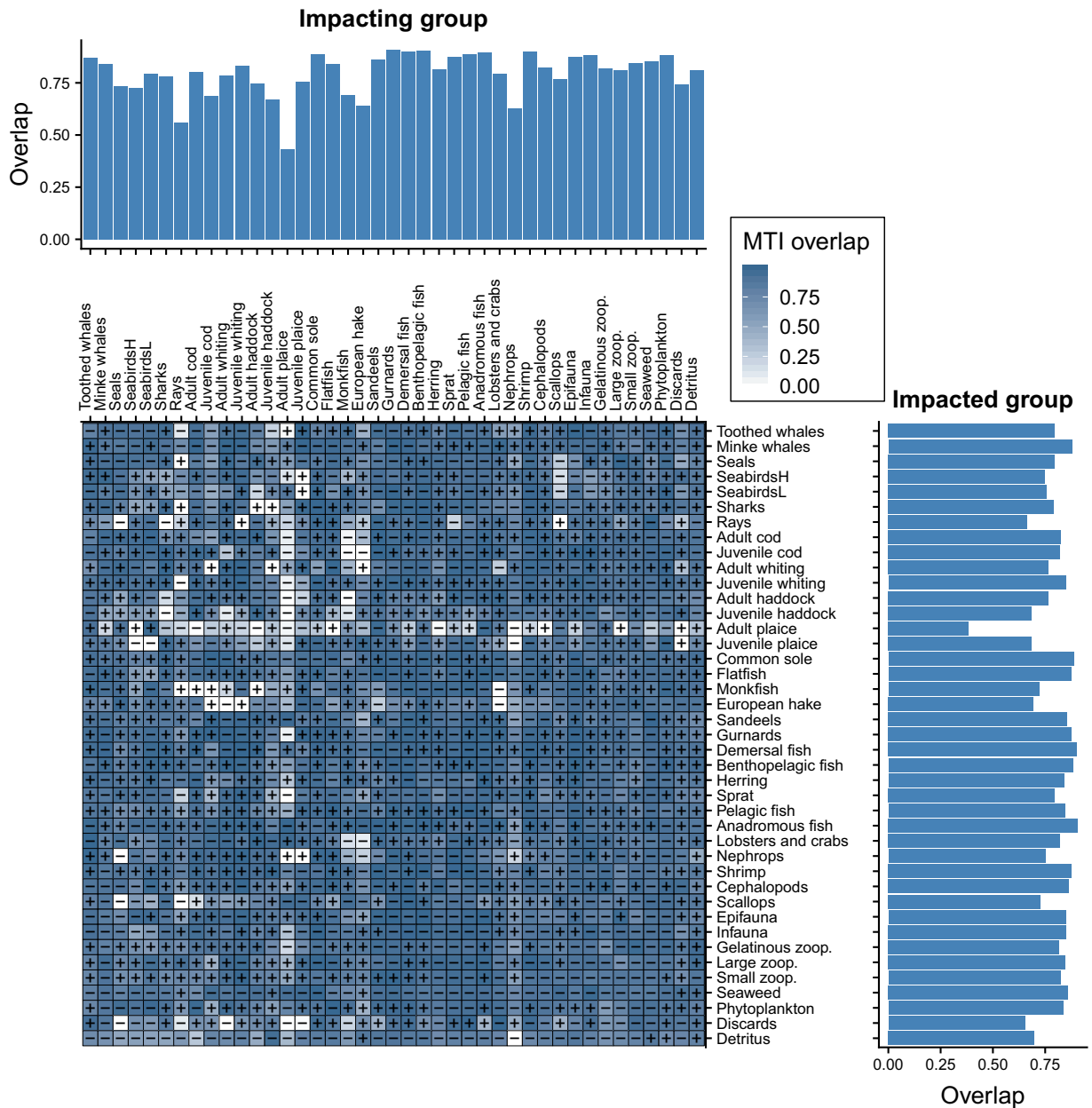


Figure 6. Impact of fishers' knowledge on mixed trophic impact (MTI) analyses. Proportional overlaps were calculated between MTI distributions with and without fishers' knowledge. The direction of distribution shifts were defined as positive (+) or negative (-). Bars highlight the average overlap for each impacted and impacting group. Values towards zero indicate large differences in MTI estimates with the inclusion of fishers' knowledge.

knowledge approach. The difficulty in assigning qualitative information to a quantitative model was addressed through LIM uncertainty analysis (Hines *et al.*, 2018) and the assignment of large confidence intervals (Christensen *et al.*, 2008) to diets which included FK. Whilst this introduced more uncertainty into the diet matrix, we consider it preferable to address larger uncertainty ranges than to omit trophic interactions. If interactions are not included in the Ecopath model, they will not be incorporated into further spatial and temporal extensions so that model scenarios intended to inform management will not be able to replicate these interactions.

Fishers' have been shown on multiple occasions to have a detailed and accurate understanding of the diets of the species they

frequently observe and process (Silvano and Begossi, 2010, 2012; Ramirez *et al.*, 2015; Bevilacqua *et al.*, 2016). Our study revealed good agreement between FK and the available data, as 63% of fishers suggested predator-prey interactions were already included in the model. Having information from FK and scientific knowledge in agreement aids to validate and reinforce both sources of information. It also encourages greater confidence in the new interactions put forward by fishers', which have implications for model outputs used to inform fisheries and ecosystem management and enhance fishers' uptake of management measures based on these models. FK is therefore a valid, yet underutilized, source of information which could be used to improve fisheries

management (Stephenson *et al.*, 2016). However, factors such as fishers' experience, the degree to which they work spatially, the times of year they fish, education levels, and the trust between fishers and scientists will impact the knowledge held and shared (Johannes *et al.*, 2000; Hind, 2014; Baigún, 2015). Therefore trust and relationship building is a necessary pre-cursor to a successful co-production process (Djenontin and Meadow, 2018).

Food web indicators

Given the levels of uncertainty assumed as plausible, we were unable to detect significant differences in ecosystem-level indicators when comparing models before and after the addition of FK. The high overlap in ecosystem-level metrics is not entirely surprising given the relatively small amount of changes FK made to the network structure. We further investigated the level of uncertainty at which statistically meaningful differences would become apparent. Our findings indicate that even at 10% of the original uncertainty there would still be considerable overlap in most of the system-level metrics, strengthening the conclusion that the differences are negligible. When using only 4–5% of the original uncertainty, H, FCI, and IFI) were significantly different with FK. This brings to attention the importance of the data range being used to accurately determine differences. When comparing two separate ecosystems, or an ecosystem changing over time, using limited data to establish uncertainty bounds may lead to Type 1 errors, i.e. the perception of a genuine difference when there is not one. The opposite is also true, where too much assigned uncertainty can lead to Type 2 errors, i.e. the perception of no difference when there is one. Sensitivity analyses, such as the example provided here, should therefore be further developed and used to check ENA results, considering available data, to make more informed conclusions. Furthermore, indicators are also sensitive to network structure and topology, making it difficult to compare indicators from models with different structures (i.e. one which account for a microbial loop against one which does not) (Bentley, Hines, *et al.*, 2019). Developing methods to address these sensitivities represents a vital step in the maturation of ENA as we consider applying it more broadly for environmental management.

Detritus (dissolved and particulate organic carbon) and lower trophic organisms, such as primary producers, invertebrates, and the microbial loop, have been identified as the dominant/structural components of numerous ecosystems globally (Libralato *et al.*, 2006; Pavés and González, 2008; Heymans *et al.*, 2014; Ulanowicz *et al.*, 2014; D'alelio *et al.*, 2016). Our findings indicate that the Irish Sea is consistent with this trend. Indicator analysis highlighted zooplankton, phytoplankton and epifauna as the food web components with the greatest relative total impact (RTI). Adding FK had no impact on the high importance of lower trophic-level organisms, however, the addition of FK altered the TL of adult and juvenile plaice and the importance of toothed whales, adult cod, adult whiting, adult plaice, and hake. TLs of functional groups are determined by the TLs of their prey (Odum and Heald, 1975). Fishers' advised that plaice eat Norway lobster as discards only, as they do not find that they consume whole Norway lobster, often just the heads, which are discarded at sea during processing. As discards is a detrital group, this alteration significantly lowered the TL of plaice in the Irish Sea. This also drew attention to the importance of cautiously assigning stomach record data, as records do not always differentiate between

primary consumption and scavenging. Collaboration between fishers and scientists to create conceptual food webs therefore improved the credibility of the ecosystem model, reinforcing the idea that early involvement of stakeholders is a crucial first step for the effective co-development of participatory research (Djenontin and Meadow, 2018).

Incorporating FK changed the diet of adult whiting and hake and significantly increased their RTI (Figure 3), increasing their impact and importance within the system. Conversely, FK-based changes reduced the impact that a change in the biomass of adult cod, adult plaice, rays, and toothed whales had on other food web components. The modelled change in the importance of toothed whales is a consequence of declines in the importance of their prey species (i.e. cod and plaice).

The largest changes which occurred as a consequence of incorporating FK into the Irish Sea EwE model were to the nature of pairwise group interactions. The MTI routine is a useful tool to quantify and visualize the combined direct and indirect impacts that an increase in any of the functional groups is predicted to have on all other groups (Ulanowicz and Puccia, 1990). Adding fishers' information to the model changed the MTI results for all functional group interactions. Most changes were insignificant due to the high overlap between MTI indicators with and without FK, however 67 of the MTI distributions from the model with FK shared <5% of the parameter space estimated by the model without FK. These changes were important as they primarily altered the MTI information of the commercial components of the food web. The role of adult plaice in the food web was changed dramatically due to its increased consumption of discards and reduced TL. Monkfish and hake became more ferocious predators in the model with FK, experiencing greater biomass increases in response to small increases in the biomasses of cod, whiting, and haddock, whilst small increases in the biomasses of monkfish and hake are estimated to have a more negative impact on the biomasses of cod, whiting, and haddock. As the MTI analysis is often used for identifying keystone species (Libralato *et al.*, 2006), the addition of FK might change the perception of keystone species in an ecosystem. This information helps us to better understand how the impacts of stressors such as fishing or climate change, which directly impact one or multiple food web components, could be indirectly propagated throughout the ecosystem. FK therefore led to network changes which will influence pairwise advice derived from the model to support ecosystem-based management and policy.

Impact of FK on the modelled role of discards

One area where FK can be used to inform policy is the role of fisheries discards in the food web. Previous analysis without FK highlighted the importance of discards as a controlling group over seabirds, crabs and lobsters, and Norway lobster in 10 000 network parameterizations (Bentley, Hines, *et al.*, 2019). By adding FK, the impact of discards on plaice, whiting, and rays significantly increased. The model developed through a co-production approach suggests that the EU landing obligation (European Union, 2013) which requires all catches of regulated commercial species to be landed, thus reducing discards, may have trophic implications for a wider range of functional groups than previously thought. However, it is challenging to identify how significant this impact would be, as none of these functional groups solely depend on discards (Heath *et al.*, 2014; Depestele *et al.*,

2019). Nevertheless, this alteration demonstrates the capacity of participatory research to reveal unforeseen impacts of anthropogenic and environmental change.

FK: localized benefits and global discourse

Transdisciplinary approaches and co-design are now being called for at both the scientific and policy level (EMB, 2019). The positive impacts of scientific research are likely to be strengthened by engaging stakeholders in its design, development, and delivery and by providing feedback on the impact and value of their contribution (Johannes *et al.*, 2000; Reed, 2008; Mackinson *et al.*, 2011; Djenontin and Meadow, 2018). ICES is at the forefront in providing scientific advice on European fisheries and therefore is in an ideal position to develop and promote such participatory research and guide its integration into management (Mackinson *et al.*, 2011).

Focusing on the localized benefits of the WKIrish experience, the co-production of knowledge approach improved the rigor of the Irish Sea model and provided an opportunity to test and develop new methodologies to forward the field of research (Bentley, Serpetti, *et al.*, 2019; Pedreschi *et al.*, 2019). From a stakeholder perspective, inclusion of their information influenced the structure of the model, which increased their buy-in and engagement with the process, and continue to guide the direction of future collaboration and research objectives (ICES, 2018b). Fishers' recommended that researchers prioritize ecosystem modelling in the future, with the desire to better understand (i) the roles of food web components not currently under management, (ii) the impact of area closures on commercial stocks and the ecosystem, and (iii) how best to maximize the sustainability of fisheries and socio-economic benefits.

In the context of the global scientific discourse, experts expect that stakeholder participation in research will become fundamental for the delivery of credible and more readily usable results to support and legitimize management (Stephenson *et al.*, 2016; Raymond-Yakoubian *et al.*, 2017; EMB, 2019). For this to succeed we need to provide standards and frameworks from which to develop our participatory approach. WKIrish serves as an example of successful participatory research which is en-route to incorporate co-produced ecosystem information into ICES fisheries advice (ICES, 2018b). Through WKIrish, FK was used to feed into studies on species diets, historical fishing effort (Bentley, Serpetti, *et al.*, 2019), and integrated ecosystem assessments (Pedreschi *et al.*, 2019). However, through the methodologies established here and in other co-production studies, FK could be used to feed into studies on temporal and spatial abundances (Macdonald *et al.*, 2014), population dynamics (Decelles *et al.*, 2017), and socio-economic dynamics (Scholz *et al.*, 2004), to inform different management processes and policy dimensions. We list below the lessons from WKIrish which we believe were key to the positive co-production experience and will be useful for the wider FK and co-production discourse:

- The research was initially requested by the fishing industry and linked to impending changes in the policy advice for Irish Sea fisheries, establishing immediate stakeholder buy-in and research engagement.
- Working relationships and trust between stakeholders and scientists were established prior to WKIrish. Harnessing pre-

existing relationships facilitated open discussions and negated the often-combated issue of mistrust.

- Stakeholders participated at all stages of WKIrish, including definition of the problem, development of the benchmark structure, data collection, data analysis, testing results, and knowledge dissemination.
- Knowledge was shared, not harvested, and time was taken to reach mutual understandings by combining multiple knowledge sources from stakeholders in an open and informal forum.
- Results and the value of stakeholder contributions were disseminated back to stakeholders via presentations and printed research briefs (summaries) to overcome the inaccessibility of primary scientific information.

Study limitations

There are two main limitations to this study. First, from the discussion with fishers, only six species, in a food web model with 41 compartments, were considered and respective trophic interactions modified. Furthermore, 63% of interactions identified by fishers were already included in the model without FK. Whilst more a reality than a limitation, this limited the scope to observe any impact of FK on whole system indicators (TST, FCI, APL, IFI, H) was therefore limited as these indicators are products of all the flows of energy throughout the system, of which only 14% were modified. In addition, system indicators tend to be more critically influenced by the few strong links with big energy flows, such as those between primary producers and lower TLs, than they are by the relatively small and diverse energy flows at higher TLs which were altered by FK (Ulanowicz *et al.*, 2014). Yet as this was an exercise in co-production, the path taken remains preferable for the development of a food web model using the best available knowledge. To ask fishers to define diets for species they were unfamiliar with would have been counterproductive for the models rigor and stakeholder buy-in, reducing the models credibility as a tool for the production of ecosystem information.

Second, fishers provided qualitative information which was quantified in the model based on the values already assembled from scientific data. This approach ensured the model remained mass-balanced (i.e. demands on functional group did not exceed their production) and provided an environment within which qualitative diet information could be readily quantified relative to other parameters in the model such as species biomass, consumption rates, and production rates. However, by not quantifying FK independently of scientific knowledge, the plausible inputs for fishers' new additions were restrained by scientific data. Again, whilst this limited the scope of impact of FK on food web indicators, this approach provided a means to co-create knowledge using qualitative FK within the boundaries of the available quantified scientific knowledge.

Conclusion

Work is on-going towards the practical application of the co-created Irish Sea model as a tool to provide ecosystem information to support resource management. Through ICES groups WKIrish, WKEWIEA (Operational EwE models to inform IEAs), and WGEAWESS (Ecosystem Assessment of Western European Shelf Seas), protocols are being developed to assess the quality of EwE models and identify data products which can be integrated

into ecosystem assessments and fisheries advice. For example, WKIrish are developing methods to incorporate ecosystem information as an additional factor to consider when selecting a fishing pressure from the FMSY ranges (ICES, 2018b). FMSY is the fishing mortality consistent with achieving Maximum Sustainable Yield, which ICES provides to fisheries managers as an adaptable range between $FMSY_{upper}$ and $FMSY_{lower}$. If a species is being negatively impacted by ecosystem or food web dynamics (i.e. low system productivity or high natural mortality), then managers may be advised to apply an FMSY at the lower end of the range to minimize the cumulative impact their actions may have on the system, and *vice versa*.

WKIrish has been key to increasing the interest of stakeholders in the continued development of an ecosystem modelling capacity for the Irish Sea. By disseminating results back to fishers', we were able to demonstrate the visible impact and value of their knowledge and together build a road map for future collaboration (ICES, 2018b). Based on our experience, we can recommend that the approach taken by WKIrish should be considered for other ICES regions, and by other organizations which hold a similar position of influence. Not only have we learned more about the ecosystem, but through stakeholder buy-in, the process has strengthened relationships between fishers' and scientists and serves as a positive example of the co-production approach.

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