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Original Article

Fishers' knowledge improves the accuracy of food web model predictions

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Fisher's knowledge offers a valuable source of information to run parallel to observed data and fill gaps in our scientific knowledge. In this study we demonstrate how fishers' knowledge of historical fishing effort was incorporated into an Ecopath with Ecosim (EwE) model of the Irish Sea to fill the significant gap in scientific knowledge prior to 2003. The Irish Sea model was fitted and results compared using fishing effort time-series based on: (i) scientific knowledge, (ii) fishers' knowledge, (iii) adjusted fishers' knowledge, and (iv) a combination of (i) and (iii), termed "hybrid knowledge." The hybrid model produced the best overall statistical fit, capturing the biomass trends of commercially important stocks. Importantly, the hybrid model also replicated the increase in landings of groups such as "crabs & lobsters" and "epifauna" which were poorly simulated in scenario (i). Incorporating environmental drivers and adjusting vulnerabilities in the foraging arena further improved model fit, therefore the model shows that both fishing and the environment have historically influenced trends in finfish and shellfish stocks in the Irish Sea. The co-production of knowledge approach used here improved the accuracy of model simulations and may prove fundamental for developing ecosystem-based management advice in a global context.

Keywords: Bayesian, climate change, co-production of knowledge, Ecopath, Ecosim, fishing effort, Irish Sea

Introduction

Considerable progress has been, and continues to be made towards the integration of fishers' knowledge into science and management (Stephenson *et al.*, 2016). In developing countries, it is not uncommon for fishers' knowledge to be the primary source of information for fisheries management (Johannes, 1998; Johannes *et al.*, 2000), as it embodies a continuum of information moulded by personal and generational experience (Mackinson *et al.*, 2011). Fishers have valuable knowledge relating to stock sizes (Eddy *et al.*, 2010), habitat preferences (Bergmann *et al.*, 2004), fish behaviour (Moreno *et al.*, 2007), dietary preferences (Drew, 2005), and fishing effort (McCluskey and Lewison, 2008) due to their dependence on local resources. Furthermore, the dialogue required to capture fishers' knowledge can be effective in strengthening credibility, collaboration, and trust between fisheries stakeholders, scientists, and managers as well as leading to a more complete understanding of the ecosystem for all parties (Mackinson, 2001; Mackinson *et al.*, 2011; Stephenson *et al.*, 2016). Recent trends for co-production of knowledge in environmental sciences go one-step further in involving stakeholders throughout the scientific to policy advice process. This means that the incorporation of knowledge becomes genuine knowledge sharing, rather than simply harvesting of an additional data source (Meadow *et al.*, 2015; Wall *et al.*, 2017; Djenontin and Meadow, 2018).

This integrated knowledge type, co-generated through appropriately designed participatory processes, is reflective of the emerging application of "post-normal" science (Colloff *et al.*, 2017; Ainscough *et al.*, 2018). "Normal science," which is expert led and excludes the extended peer community, is often inefficient for informing real world decisions (Funtowicz and Ravetz, 1993). Fisheries science and policy is inherently uncertain, with high stakes and socioeconomic consequences that influence data interpretation. It is therefore necessary to include a range of stakeholders to legitimize scientific direction and outputs so that they may more readily inform policy and management and improve credibility. A co-production approach to knowledge generation offers an inclusive forum to share information and trigger positive social and ecological action (Armitage *et al.*, 2011). Co-production moves away from expert built analytical framework's, which may fail to capture local knowledge (Djenontin and Meadow, 2018). It also increases the degree to which researchers and stakeholders interact (Dilling and Lemos, 2011), improving the alignment of research to stakeholder needs (Shirk *et al.*, 2012) and also improving stakeholders' understanding of the "scientific" approach.

One area which may benefit from a co-production of knowledge approach is ecosystem modelling. Ecosystem models lend themselves to ecological education and elucidation. By their nature, they are capable of bringing to life ecosystem scenarios far too complex to observe or measure *in situ*. However, the parameterization of ecosystem models is demanding; scientific knowledge alone is often too limited to fully realize a model's potential. A "post-normal" approach to ecosystem modelling may therefore be beneficial for both modellers and stakeholders. As of yet, few ecosystem models have incorporated fishers' knowledge into their parameterization although examples do exist for northern British Columbia (Ainsworth and Pitcher, 2005) and the Brazilian northeast coast (Bevilacqua *et al.*, 2016). These examples gathered fishers' knowledge using interview style approaches and used the information to parameterize biological attributes for functional groups and to reconstruct historical stock biomass time series.

In 2015, the first International Council for the Exploration of the Sea (ICES) Integrated Benchmark Assessment for the Irish Sea (WKIrish) was established with dual aims of improving the single-species stock assessments and working towards integrated ecosystem assessment and advice (ICES, 2015a). WKIrish identified Ecopath with Ecosim (EwE) as a potential approach for investigating the drivers underpinning the dynamics of finfish in the Irish Sea (ICES, 2015a). EwE is a suite of software for modelling food webs (Christensen *et al.*, 2008). Ecopath is used to set up a mass-balanced representation of the food web in a reference year and can be used to quantify the flows of energy within an ecosystem (Polovina, 1984). Ecosim is then used to reconstruct the food web dynamics over time since the reference year. Ecosim thus requires time-series to drive the simulation. These time-series are typically fishing effort (or mortality) plus potential environmental drivers.

When building the Irish Sea EwE model, we were only able to find fishing effort data back to 2003 for a number of gear types (pots, gill nets, long-lines, pelagic nets, dredge). However, commercial stock assessment based estimates of biomass are available back to 1973. It is in instances such as these that fishers' knowledge has been championed as a valuable additional source of information (Mackinson and Nottestad, 1998; Johannes *et al.*, 2000). The incorporation of such knowledge into ecosystem models can complement scientific data, provide new insight into system structure and function and increase their reliability and uptake (Bevilacqua *et al.*, 2016). During benchmark workshops for WKIrish, fishers were therefore invited to share their knowledge of historic Irish Sea fishing effort to fill the gaps in the scientific data (ICES, 2018b). To avoid one-directional data harvesting, the results from this study were shared with stakeholders at a follow-up WKIrish event, where a roadmap was developed for future research and collaboration.

Parameterization of EwE models is vulnerable to input uncertainty because of the amount of information required for each functional group (Gal *et al.*, 2014). Recognizing this, Monte Carlo approaches (Kennedy and O'Hagan, 2001) can be used to generate a range of plausible inputs (Heymans *et al.*, 2016; Bentley *et al.*, 2018). Production of the corresponding range of model outputs allows modellers and end-users to make stronger ecological inferences from the results (De La Vega *et al.*, 2018). In this study, we demonstrate how fishers' knowledge on historical fishing effort was incorporated into the Irish Sea EwE model, taking account of uncertainty around this input. The overall aim was to investigate whether incorporating fishers' knowledge would increase the capacity of the model to simulate historic biomass and catch trends, and therefore better understand the drivers of ecosystem change in the Irish Sea. To the best of our knowledge, the work presented here describes the first study to use a co-production of knowledge approach to parameterize a marine ecosystem model.

Methods

Study system

The EwE model of the Irish Sea covers ICES division VIIa, an area of ∼58 000 km^{-2} (Figure 1). Since the 1970s, the status of the commercial fish and shellfish stocks in the Irish Sea has changed dramatically (Kelly *et al.*, 2006). As elsewhere in the North Atlantic, many of the Irish Sea finfish stocks have been historically subject to high levels of fishing mortality leading to reduced spawning stock biomasses (SSBs) and truncated age structures (Brander, 1981, ICES, 2015a, 2016). For example, by the late 1990s, the Irish Sea Atlantic cod (*Gadus morhua*) stock had declined to the point of collapse and a recovery plan was introduced (Anon\., 2000; ICES, 2001). This plan relied upon landing quota reductions, temporary closure of spawning grounds, and the introduction of technical gear regulations (ICES, 2003). However, despite large reductions in the fishing effort of the bottom trawl and seine fleet, cod SSB declined by 68% from 2003 to 2009. Up until 2010, estimates of fishing mortality remained above F_{lim} (limit reference point for fishing mortality) despite reducing fishing mortality being the main aim of the management plan. Cod spawning grounds were also closed during the spawning season but with exceptions (derogations) for *Nephrops* trawlers and certain beam trawls. However, both of these fisheries have bycatches of cod, whiting (*Merlangius merlangus*), and haddock (*Melanogrammus aeglefinus*) (ICES, 2016). Although a lack of discard data during the years of the cod recovery plan prevented an analysis of the impact of these derogated fisheries, it is likely that cod recovery was hindered (Kelly *et al.*, 2006).

WKIrish has updated discard and mortality parameters (ICES, 2016) and revised the age-structured assessments resulting in a re-evaluation of the SSB of Irish Sea cod to be above B_{lim} (limit reference point for SSB) since 2016. Herring (*Clupea harengus*), haddock and plaice (*Pleuronectes platessa*) SSBs are estimated to be well above MSY B_{trigger} (value of SSB that triggers a specific management action), SSB for sole (*Solea solea*) is also increasing but whiting remains well below B_{lim} (ICES, 2017, 2018a) (Supplementary Figure S1).

Ecopath model

Ecopath (version 6.6 beta) was used to construct a model of the Irish Sea Ecosystem representative of 1973 (Bentley *et al.*, 2018). The modelled food web includes 41 functional groups, ranging

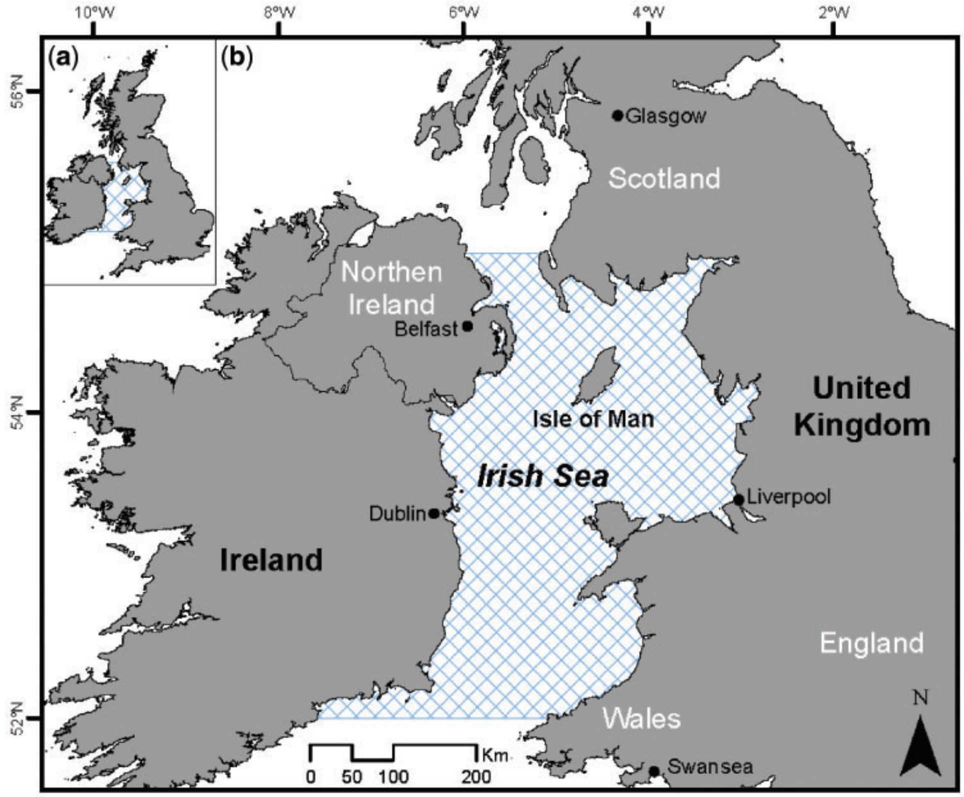

Figure 1. Map of (a) Ireland and the British Isles showing (b) the extent of the model area for the Irish Sea EwE model (hatched area).

from detritus and plankton to seabirds and mammals, with a well-defined fish component (Supplementary Table S1). Functional groups are connected through predator–prey linkages (Supplementary Figure S2). A few important commercial species: cod, whiting, haddock, and plaice were split into adult and juvenile stages to better represent the ontogenetic differences in their physiology and diets (Christensen and Walters, 2004, Bentley *et al.*, 2018). The model's diet matrix was constructed using information held in DAPSTOM (integrated DAtabase and Portal for fish STOMach records) (Pinnegar, 2014) for fish functional groups, and from scientific literature for the mammal, seabird, and invertebrate groups. We followed recommended best practice methods (Heymans *et al.*, 2016) and ecological rules of thumb (Link, 2010) to ensure that ecological realism was maintained in the models structure and function. The Irish Sea model includes eight fishing fleets (beam trawl, otter trawl, *Nephrops* trawl, pelagic nets, gill nets, pots, dredge, and longlines) which reflect those deemed most important by fishers (ICES, 2018b). Landings and discards for 1973 were allocated to fleets using data from ICES and the Scientific, Technical and Economic Committee for Fisheries (STECF, 2018). For an in-depth description of the methods and parameters used to build the Irish Sea Ecopath model, see Bentley *et al.* (2018).

Ecosim model

Ecosim uses initial parameters inherited from the base Ecopath model to simulate food web dynamics over time (Christensen and Walters, 2004; Christensen *et al.*, 2008). The Ecosim model of the Irish Sea runs from 1973 to 2014—the last year for which landings data were available at the time of model construction. To affect a change in the biomass and catch trends of functional groups over time, the model requires time-series of drivers, such as fishing effort, fishing mortality, or environmental change. Ideally, each fishing fleet will have its own effort time series but available series covering the full temporal extent of the model were only available for three of the eight fleets: beam trawl, otter trawl, and *Nephrops* trawl. Data for beam and otter trawls were taken from the Celtic Seas working group (ICES, 2015b), for the *Nephrops* trawls, the effort trend was taken from Coughlan *et al.* (2015) who reconstructed the trend based on catch per unit effort (CPUE). Effort data [kilowatt (KW) days] for the remaining fleets (pelagic nets, gill nets, pots, dredge, and longlines) were available from 2003 onwards through STECF (STECF, 2018). Ecosim uses fishing effort as a relative measure, with effort in the baseline year being equal to 1 and subsequent years reflecting the proportional change. Ecosim therefore requires effort time series from the baseline year, meaning that the available data would limit the model simulation capacity to the trends of functional groups caught by the beam, otter and *Nephrops* vessels. As part of WKIrish, stakeholders were therefore asked to reconstruct historic fishing effort trends through a co-production of knowledge approach.

Fishers knowledge

WKIrish stakeholder workshops (WKIrish4) were held in Dun Laoghaire, Ireland, on the 23–27 October 2017 and in Kilkeel, Northern Ireland, on the 8 December 2017 (ICES, 2018b). The first meeting was attended by nine industry stakeholders, an NGO representative, and a recreational fisherman, the second by 12 industry stakeholders. The stakeholders were invited via their

Producer Organisations (POs). There was no specific selection, however, the POs were asked to invite those fishers who would have knowledge of the fisheries of interest back to 1973. This meant that they were in an age bracket between 45 and 65 years old, with between 30 and 40 years of experience. Several were also sons of fishermen and could convey the knowledge of their predecessors. Each industry stakeholder had worked with, or had knowledge of most of the different gear types, therefore each effort trend was reconstructed as a group exercise. The group included mainly representatives from Ireland, with one person each from Northern Ireland and mainland UK. The knowledge co-production process is illustrated in Figure 2. The process was informed by the guidance given in the GAP2 "Oral Histories Tool," http://gap2.eu/methodological-toolbox/oral-histories/.

Fishers were shown the STECF data on a graph and asked to fill in the 1973–2003 gaps in information to the best of their knowledge. Fishers were asked to perceive fishing effort as a fleets "killing power," avoiding the potential inclination to link effort to factors such as number of vessels or time at sea which may be misrepresentative of fishing effort in KW days. The actual process involved fishers describing changes in the fishing effort as a narrative, the chairman then made a tentative interpretation of that on the graphs pictured in Figure 2. The fishers would then agree or disagree, and the graphed trend altered as they directed until a consensus was arrived at. Every effort was taken to avoid leading the fishers' views in any particular direction, the role of the chairman was simply to interpret what they had said on the graphs. Fishers' trends were incorporated into the Ecosim model during the workshop and preliminary results were shared to provide immediate feedback and enhance the fishers' experience of ecosystem models in action (ICES, 2018b).

The second workshop was held in Kilkeel, Northern Ireland 1 month after the first workshop. This was attended by 12 fishers, with a similar age and experience profile. The main focus of this workshop was on the pelagic effort trends, as this metier in the Irish Sea is mainly operated from this port. The Kilkeel fishers were also shown the other effort trends from the first workshops and asked if they agreed with these, which they did. Many of these fishers would have also worked in the other Irish Sea demersal and *Nephrops* fisheries.

Adjusted fishers' knowledge

During preliminary data testing, the addition of fishers' perceptions of historical fishing effort to the model caused numerous functional groups to collapse. This outcome could be due either to incorrect model parameterization (i.e. the initial catches in Ecopath being too high), or overestimation of the historical changes in fishing effort. The initial catches in Ecopath are taken from official landings reports, and whilst there may be errors in the data reported, altering the model inputs would require assumptions that could not be justified without additional evidence. We therefore proceeded under the assumption that the trends fishers provided were more accurate than the magnitude of change over time.

Bayes' Theorem was used to estimate adjusted fishers' efforts (posterior probability distribution) as a consequence of the ability of unadjusted fishers' efforts (prior probability distribution) to simulate observed trends (likelihood function). Posterior probability distributions are an alternative to *p*-values and provide a direct measure of the degree of belief that can be placed on parameter estimates (Ellison, 2004). The process designed for this study has been conceptually illustrated in Figure 3.

Fishers' trends were transformed into probability distributions, spanning ±99% of the fishers' baseline estimate based on the largest deviation between scientific and fishers' effort magnitudes. Effort magnitude changes resulting in trends which fell below zero were excluded. Biomass and catch trends were simulated for

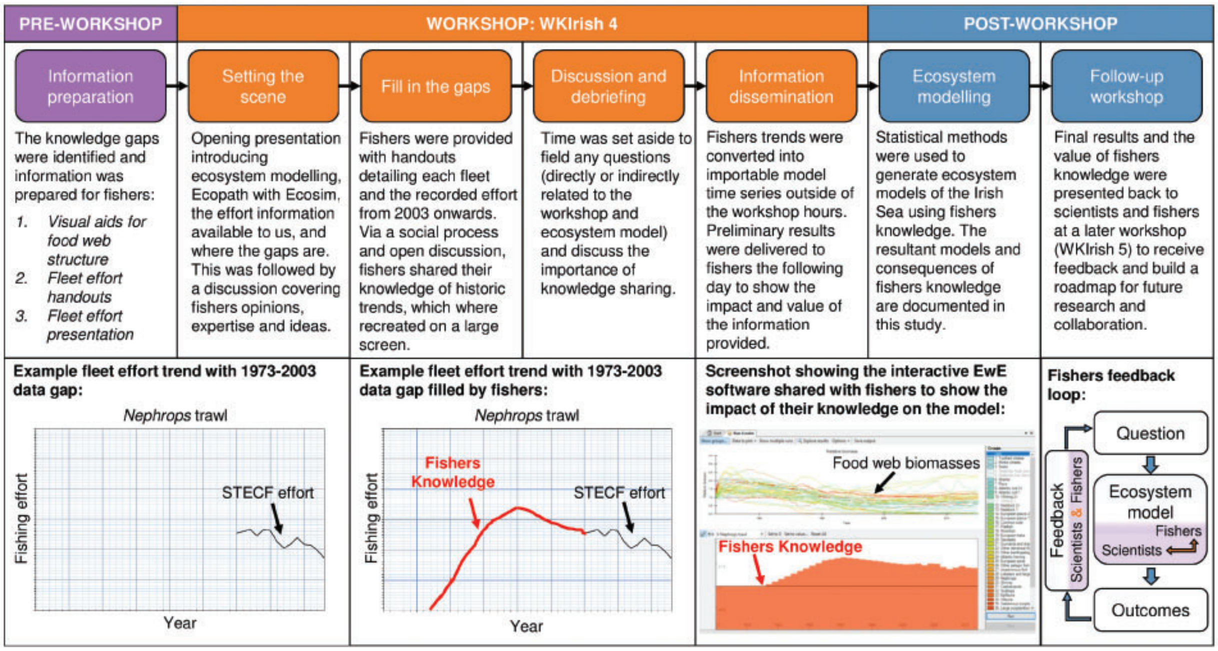

Figure 2. Methodology for the construction of historic fishing effort trends for the Irish Sea using fishers' experiential and inherited knowledge.

10 000 random magnitude combinations (Supplementary Figure S3) using Multi-Sim (Steenbeek *et al.*, 2016). Multi-Sim is an Ecosim plugin which automatically perturbs environmental and anthropogenic drivers (in this case fishing effort) and collates Ecosim results. The sum of squared deviations (SSs) between simulated and observed biomass and catch trends were used to estimate the posterior distribution of fishers' efforts. We implemented a cyclic approach, using posterior distributions as prior distributions for the following cycle, until the overall SS was minimized.

Ecosim scenarios, inputs, and model fitting

The Irish Sea Ecosim model was parameterized using four types of fishing effort information: (i) scientific knowledge only, (ii) fishers' knowledge only, (iii) adjusted fishers' knowledge only, and (iv) hybrid knowledge—which was a combination of (i) and (iii). Each scenario used fishing effort and/or mortality time series to drive fisheries catch (Table 1).

Biomass time series were taken from ICES stock assessments or working group reports where available. For functional groups without dedicated stock assessments, biomass estimates were taken from trawl data available through ICES Database of Trawl Surveys (DATRAS; ICES, 2018c). Catch time series were taken from ICES landing statistics (ICES, 2018d), stock assessments, and working group reports. Whilst catch time series were entered into the model as absolute values, biomass was added as "relative biomass," where the software takes the ratio of "observed" to estimated value for the years where there are observations and estimates a scaling factor. Observations are then scaled and plotted on top on the estimated values. Whilst initial observed and estimated biomass values may not align, model simulations should follow the general trends of observed data. This method was used as a number of time series do not represent absolute values but provide relative trends, such as indicators of plankton biomass, DATRAS survey estimates with uncertain catchability rates, and an index in individuals for *Nephrops norvegicus*.

Temperature functional responses were incorporated into all models (Supplementary Text S1) following the methodologies outlined in recent studies which have used Ecosim to simulate the impact of ocean warming (Bentley *et al.*, 2017; Serpetti *et al.*, 2017; Corrales *et al.*, 2018). Gaussian functional responses to temperature change were designed using temperature tolerance ranges taken from AquaMaps (Kaschner *et al.*, 2016) (Supplementary Figure S4). These responses impact the consumption rates of predators in response to changes in Irish Sea depth integrated temperature (°C) from 1973 to 2014 (Supplementary Figure S5). Temperature functional responses were incorporated into the model prior to the Bayesian effort magnitude search.

After the addition of fishing and temperature drivers, model simulations were fitted against observed data using an automated stepwise fitting plugin (Scott *et al.*, 2016). The automated fitting constructed a series of model iterations to determine which combination of parameters [estimated vulnerabilities and/or primary production (PP) anomaly-described below] provided the best statistical fit for model simulations against observed data, as determined by sum of squares and Akaike's Information Criterion for small sample sizes (AICc) (Akaike, 1974; Burnham and Anderson, 2003). The stepwise fitting estimated up to 54 parameters given that a total of 55 calibration time series were provided (29 biomass, 26 catch). Estimating one parameter less than time series provided ensured statistical strength was maintained (Scott *et al.*, 2016). The fitting procedure was carried out for each model scenario, and for each scenario the iteration with the lowest AICc was selected as the best fit model.

Ecosim uses the foraging arena theory (Ahrens *et al.*, 2012) to quantify "vulnerabilities," which represent the degree to which a change in predator biomass will impact predation mortality for a given prey (Supplementary Text S1). Vulnerabilities can be adjusted in the software interface by applying multipliers to the rate with which a prey moves between being vulnerable and not-vulnerable (Christensen and Walters, 2004). Multipliers can range from one to infinity with two as the default. Vulnerabilities with multipliers greater than two indicate top-down control, where predator biomass drives prey mortality, whereas vulnerabilities with multipliers between one and two suggest bottom-up control, where even large increases in predator biomass cause only a limited increase in the consumption rate of that predator on the given prey, therefore the biomass of the prey regulates predator consumption (Christensen and Walters, 2004; Heymans *et al.*, 2016). Environmental drivers and climate variability indices which impact the dynamics of the marine ecosystem, but are not explicitly incorporated into the model, may be captured by estimating an anomaly function for the production rate of primary producers. In the Irish Sea model this function was applied to the phytoplankton functional group. When estimating the anomaly, we set the maximum number of spline points to five as large scale climatic drivers have multidecadal trends, therefore only one spline point (or change in direction) was required per decade in Ecosim.

The impact of input parameter uncertainty on model predictions was then addressed using the Monte Carlo approach (Kennedy and O'Hagan, 2001). Basic input parameters were assigned data pedigree confidence intervals based on data origin (Supplementary Table S2). For basic input parameters that had data-based uncertainty, confidence intervals were assigned to reflect the plausible range of parameter estimates. One thousand mass-balanced models were produced for each scenario using the EcoSampler plugin (Steenbeek *et al.*, 2018) and 95% confidence intervals were calculated from model outputs.

Results

Fishers effort trends

Fishers provided effort trends for beam trawl, otter trawl, *Nephrops* trawl, pelagic net, gill net, pot, dredge, and longline fleets (Figure 4). Trends were designed using a co-production approach and therefore, in most cases, a single trend was provided for each fleet, however in cases where opinions conflicted, multiple trends were taken for an individual fleet (ICES, 2018b). Fishers effort trends span the 1973–2003 knowledge gap, however during the second workshop in Kilkeel, fishers also estimated trends from 2003 to 2014 for otter trawl and pelagic net fishing effort. Fishers' effort trends for beam trawl, otter trawl, *Nephrops* trawl, and pelagic nets showed general agreement with observed trends (Figure 4).

For beam trawls, fishers felt effort had increased up till 2000 but had then declined. The overall trends for this gear were in good agreement with available scientific data. For otter trawls fishers proposed two trends, version 1 increased from 1985 to 1990, declining after 1995, whereas version 2 dramatically declined from 1975 to 1995 and plateaued from there. The otter

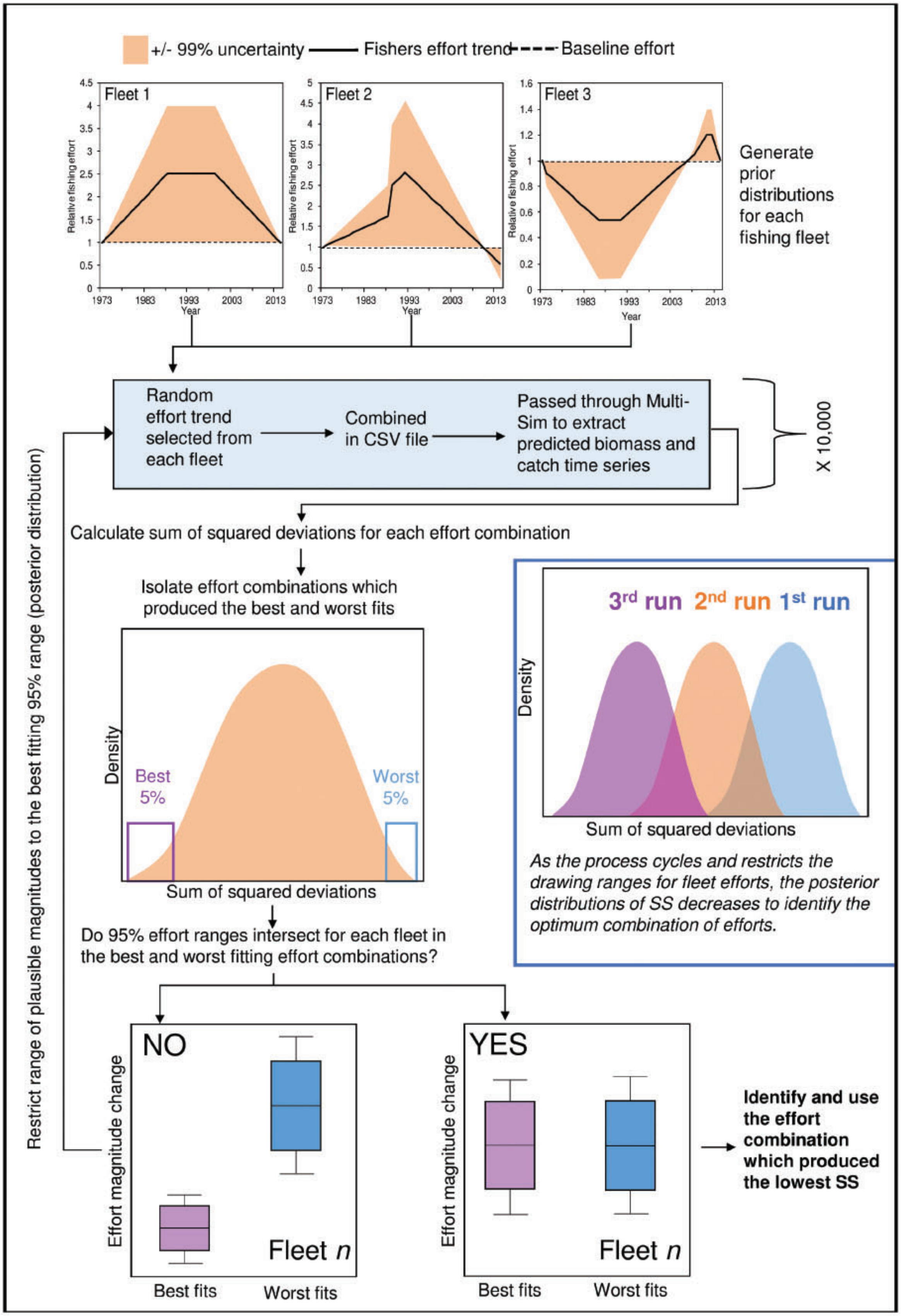

Figure 3. Conceptual diagram of the Bayesian inference cycle designed to optimize the magnitude of fishers' efforts to reduce the sum of SSs between observed and predicted biomass and catch time series for functional groups in the Irish Sea EwE model.

Table 1. Fishing time series (effort and mortality) used to drive four Irish Sea Ecosim scenarios: (i) scientific knowledge only (S1), (ii) fishers knowledge only (S2), (iii) adjusted fishers knowledge only (S3), and (iv) hybrid knowledge (S4).

	S1	S2	S3	S4
Fleet fishing effort				
Beam trawl	■	░	░ [a]	■
Otter trawl	■	░	░ [a]	■
Nephrops trawl	■	░	░ [a]	■
Pelagic nets	–	░	░ [a]	░ [a]
Gill nets	–	░	░ [a]	░ [a]
Pots	–	░	░ [a]	░ [a]
Dredge	–	░	░ [a]	░ [a]
Long line	–	░	░ [a]	░ [a]
Group fishing mortality				
European plaice	■	–	–	■
Common sole	■	–	–	■
Flatfish	■	–	–	■
Atlantic herring	■	–	–	–
European sprat	■	–	–	■

Dark shading, scientific knowledge; Light shading, Fishers knowledge.

[a] Denotes adjusted fishers time series.

–Denotes the absence of a driver.

trend for version 2 shows greater similarity to scientific data (Figure 4a). For *Nephrops* trawls, fishers suggested effort had increased up until the early 1990s and slowly declined to present day. This trend shows good agreement with scientific data (Figure 4a). Fishers provided two trends for pelagic nets (Figure 4a). Effort in version 1 drastically declined in the early 1980s and increased in the late 1980s/early 1990s. From 1995 on, fishers felt effort had declined. This trend showed decent agreement with the fishing mortality (F) of herring in the Irish Sea. Version 2 of fishers' pelagic net trend showed poor agreement with scientific data, increasing from 1980 to 1990 and then declining in the early 2000s. No scientific data was available to compare against fishers' trends for gill net, dredge, longline, or potting fishing effort. For gill nets, fishers felt effort had increased in the mid-1980s but then declined from the mid-1990s onwards (Figure 4b). Fishers suggested potting effort to have continuously increased since 1990, slowly at first but much more rapidly from 1995 onwards. For dredge effort, fishers felt effort had decreased rapidly during the early 1990s. Fishers explained how longline effort had increased since 1980, with a large increase around 2000.

Whilst the trends are consistent between scientific data and fishers' effort time series, the magnitude of change for beam, otter and *Nephrops* trawls are much larger according to fishers' knowledge (Figure 4).

Adjusted fishers' effort trends

In total, 40 000 combinations of fishers' efforts with altered magnitudes were tested to identify which combination minimized the model's SS pre-fitting. This equated to four loops (10 000 combinations each) of the Bayesian inference cycle depicted in Figure 3. After the first loop, *Nephrops* trawl effort was restricted to a smaller magnitude range (−65 to −99%). At the end of the second loop the effort range for *Nephrops* trawl was further reduced (−82 to −99%) with the addition of a beam trawl restriction (−78 to −99%). After the third loop the effort of *Nephrops* (−95 to −99%), beam (−94 to −99%), and otter (−6 to −99%) trawls were all limited to lower magnitudes. After the fourth run, the 95% distribution of efforts from the top 500 models overlapped with the 95% distributions of the worst 500 models, therefore we could no longer subdivide effort ranges with confidence.

Fleets with multiple effort trends were selected evenly to ensure the randomly generated combinations were not biased towards certain trend versions. Overall, 82% of the 500 combinations with the lowest SS used beam trawl version 2, 91% used otter trawl version 2, and 96% used pelagic net version 1. There was therefore a clear statistical preference for these trends over their counterparts.

The lowest SS produced by the first 10 000 iterations was 58 716. With range restrictions, the lowest SS dropped to 6330 after the second loop, 3562 after the third loop and a minimum of 2947 after the fourth and final loop. The magnitude changes for the lowest SS were as follows: beam trawl version 2: −96%; otter trawl version 2: −61%; *Nephrops* trawl: −99%; pelagic nets version 1: +13%; gill nets: −70%; pots: +43%; dredge: +23%; longlines: −24% (Figure 5). These effort trends were used for the adjusted fishers' effort Ecosim scenario.

Ecosim scenario results

Simulations were produced using the fishing effort scenarios detailed in Table 1 above. Simulated biomass and catch trends were fitted to time series via the adjustment of predator vulnerabilities and a PP anomaly applied to phytoplankton. For each data scenario the best fitting model was identified by the lowest AICc.

Scenario 1: scientific knowledge

Using scientific information, a best fit model was produced with an AICc of −592 and an SS of 1039. Of the 1039 SS, 308 can be attributed to biomass predictions and 731 to catch. Biomass predictions for commercial stocks (cod, whiting, haddock, plaice, sole, herring, and *Nephrops*) tended to follow the trajectories of observed data (Figure 6). However, this scenario failed to capture the observed catch dynamics for functional groups which were not primarily driven by any of the incorporated effort or F time-series. For example, the steep catch increase in "lobsters and large crabs" and "epifauna" was not replicated, resulting in high SS contributions from these groups (Figure 7). The epifauna functional group includes commercially caught species such as common whelk (*Buccinum undatum*), European edible sea urchin (*Echinus esculentus*), common mussel (*Mytilus edulis*), and velvet swimming crab (*Necora puber*) among others (Bentley *et al.*, 2018).

Monte Carlo analysis highlighted the uncertainty in model predictions based on the potential range of input parameters (Figures 6 and 7). Uncertainty ranges show that input alterations were unable to improve the fit of catch predictions lacking fishing drivers.

The best-fit model estimated 37 vulnerabilities (15 top-down, 22 bottom-up) (Supplementary Table S3) and a PP anomaly with three spline points (Figure 8). The estimated PP function significantly negatively correlated with the North Atlantic Oscillation index (NAO) (Hurrell, 1995), the Atlantic Multidecadal Oscillation (AMO) (Edwards, Beaugrand, *et al.*, 2013), and depth integrated temperature (Supplementary Figure S6).

Scenario 2: fishers' knowledge

Using fishers' knowledge resulted in a best fit model with an AICc of 5768 and a much higher SS of 25 299 (biomass = 11 545,

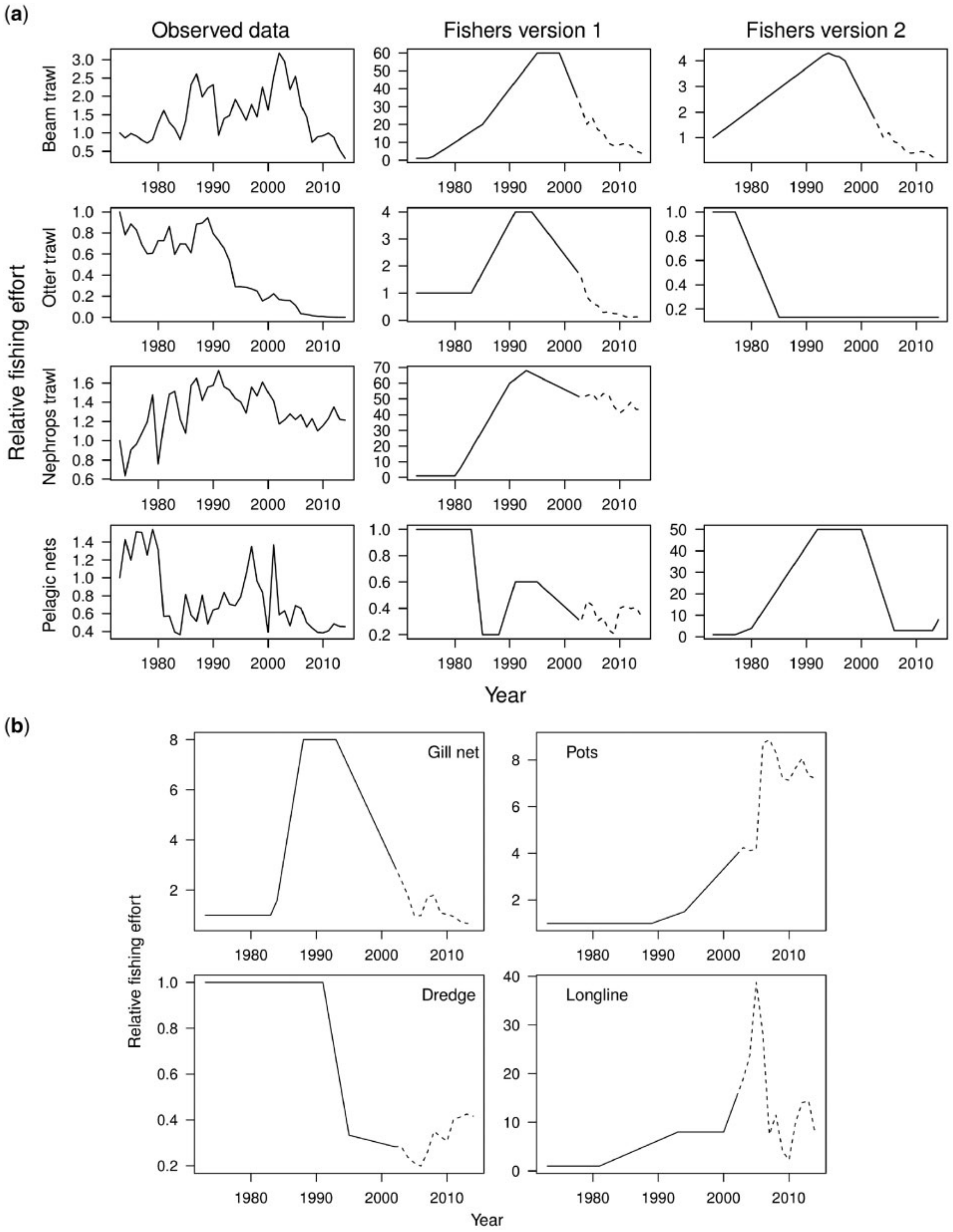

Figure 4. Fishing effort trends for fleets in the Irish Sea. (a) Gear types with observed data from 1973 to 2014 in comparison to fishers' effort trends; (b) Fishers' effort trends for gear types which do not have observed data for 1973–2014. For numerous fishers' effort trends, fishers' filled only the 1973–2003 knowledge gap, therefore dashed lines indicate observed effort from the Scientific, Technical, and Economic Committee for Fisheries (STECF, 2018). Observed data for beam and otter trawls were taken from the Celtic Seas working group (ICES, 2015b), for the Nephrops trawls, the effort trend was taken from Coughlan *et al.* (2015) who reconstructed the trend based on CPUE. Fishers trends for pelagic net effort are compared to the relative instantaneous fishing mortality of herring in the Irish Sea, calculated as catch/biomass.

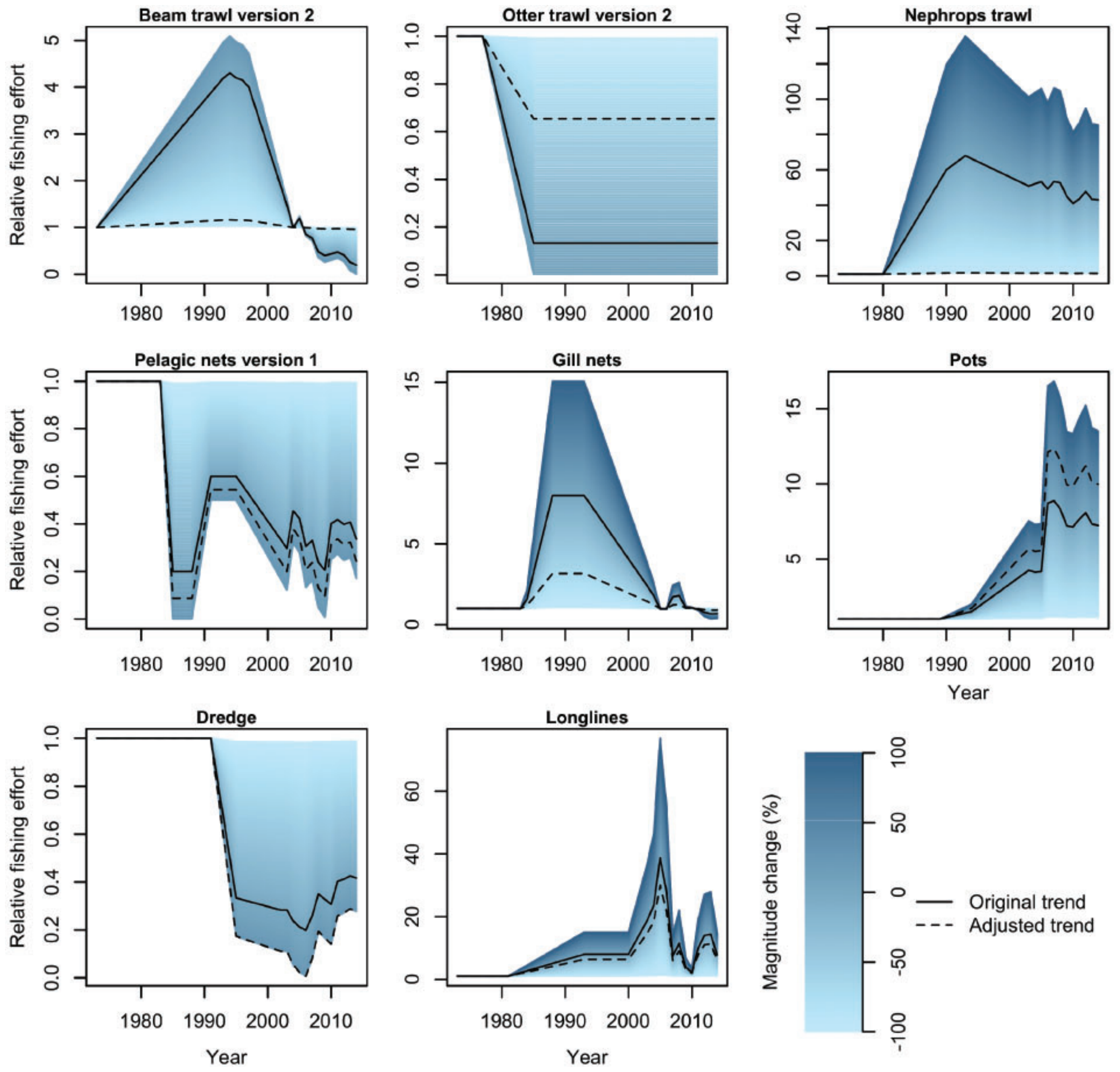

Figure 5. Fishers effort trends for fleets in the Irish Sea. Trends are surrounded by ±99% magnitude shifted trends. The dashed lines signify the combination of trends best able to reduce the models sum of SSs and were used in the final model.

catch = 13 754). Biomasses of commercially important stocks plummeted under the efforts suggested by fishers. However, the addition of effort trends for fleets previously lacking, resulted in more accurate catch dynamics for epifauna (Table 2). The overall unstable state of the ecosystem model with these drivers resulted in large MC uncertainties.

The best-fit model estimated 32 vulnerabilities (9 top-down, 23 bottom-up) and a PP anomaly with five spline points. The PP anomaly did not correlate with depth integrated temperature, however it did correlate with the NAO and AMO. In this case the correlation was positive, with PP increasing from the start of the time series (Figure 8). This likely represents the models attempt to "revive" collapsed functional groups via bottom-up mechanisms.

Scenario 3: adjusted fishers' knowledge

The use of the previously described adjusted fishers' efforts improved the fit of model predictions in comparison to the unadjusted fishers' efforts. The AICc of the best fit model was 591 with a SS of 1661: 355 of the SS was attributed to biomass and 1306 came from catch predictions. Biomass predictions for commercial stocks tended to generally follow observed data, with predictions for cod, haddock, and herring achieving greater fits compared to those produced using scientific knowledge (Figure 6). However, the biomass fit worsened for plaice, sole, whiting, and *Nephrops*. Catch predictions were much improved for lobsters and large crabs, epifauna, herring, and shrimp (Figure 7, Table 2).

Uncertainty ranges were more conservative than unadjusted fishers' trends and tended to resemble uncertainty scales

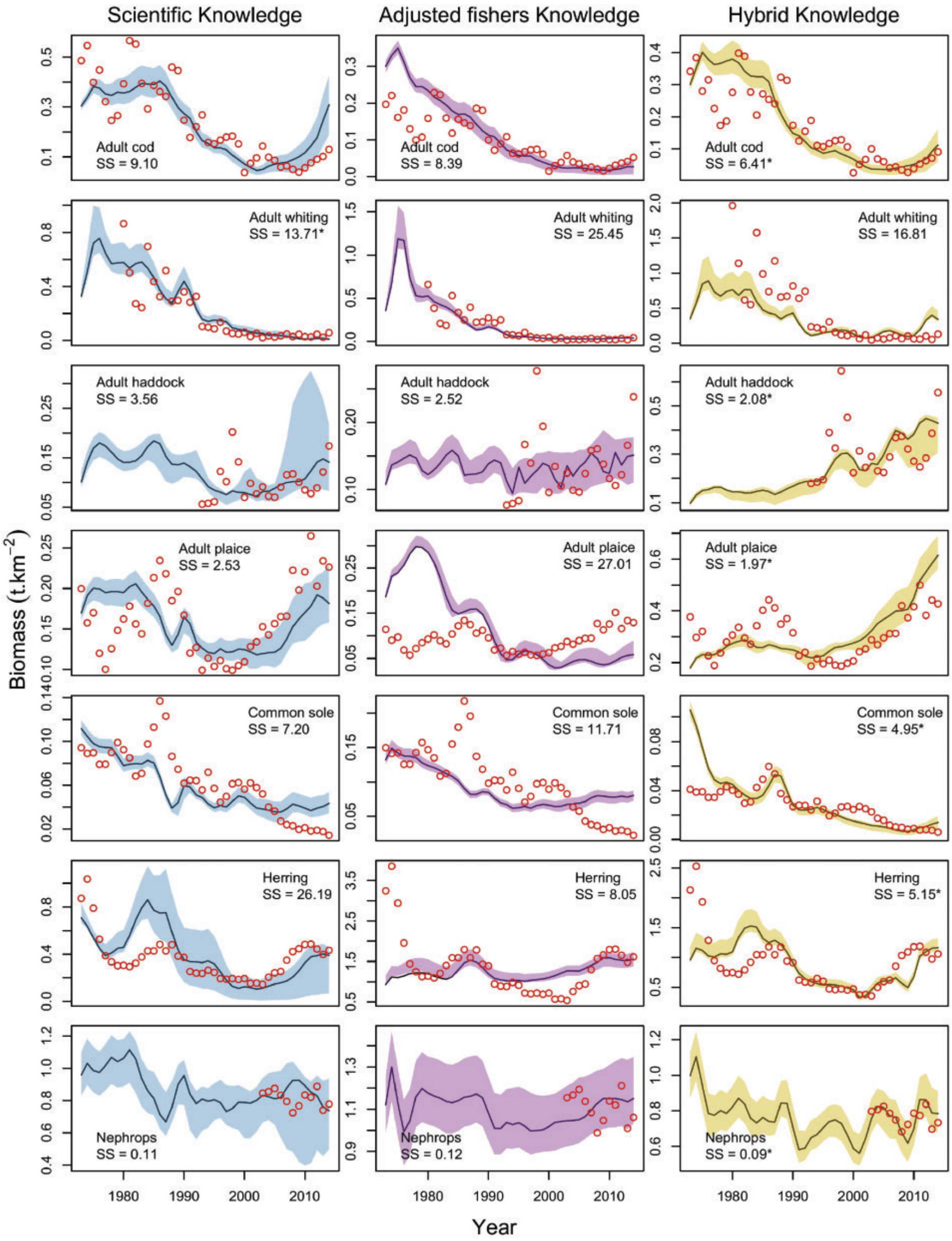

Figure 6. Biomass trends for the commercially important stocks in the Irish Sea EwE model. Solid lines indicate model predictions and dots represent scaled observational data. Predictions are surrounded by 95% confidence intervals calculated using a Monte Carlo approach, generating 1000 models within the range of plausible input estimates. Model simulations presented were generated using three sources of fishing effort data: (i) Scientific knowledge, (ii) adjusted fishers' knowledge, (iv) hybrid knowledge.

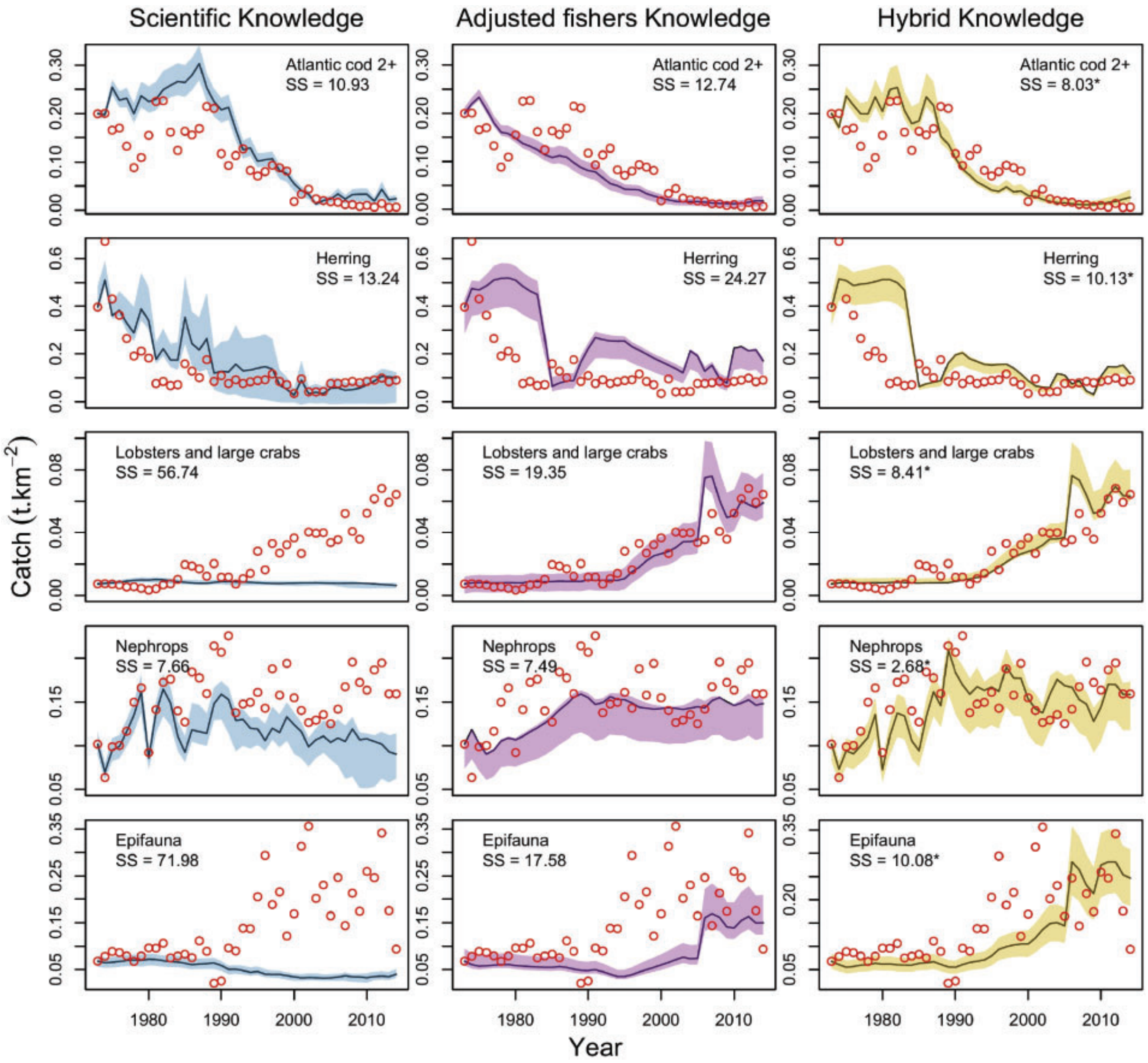

Figure 7. Catch trends for a selection of functional groups in the Irish Sea EwE model. Solid lines indicate model predictions and dots represent observed data. Predictions are surrounded by 95% confidence intervals calculated using a Monte Carlo approach, generating 1000 models within the range of plausible input estimates. Model simulations presented were generated using three sources of fishing effort data: (i) Scientific knowledge, (ii) adjusted fishers' knowledge, (iv) hybrid knowledge.

obtained using scientific knowledge, suggesting greater model stability.

Using adjusted fishers' effort, the best fit model included 35 vulnerabilities (12 top-down, 22 bottom-up) and a PP anomaly with three spline points. As in scenario 1, the PP function significantly negatively correlated with the NAO, AMO, and depth integrated temperature (Figure 8, Supplementary Figure S5).

Scenario 4: hybrid knowledge

The hybrid knowledge scenario used both scientific and fishers' knowledge to retain the strengths of scenarios 1 and 3 whilst discounting their weaknesses. The scientific scenario produced a better model fit than the adjusted fishers' scenario (Table 2). However, adjusted fishers' drivers produced superior fits for the biomass trends of rays, cod, juvenile whiting, haddock, juvenile plaice, and herring. Catch fits were also improved for adult whiting, lobsters and large crabs, *Nephrops*, shrimp and epifauna under adjusted fishers' efforts. The combination of fishers' and scientific knowledge produced the best-obtained catch fits for 76% of functional groups and the best biomass fits for 55% (Table 2).

By combining scientific knowledge with fishers' knowledge, the best-fit model achieved an AICc of −1451 and a SS of 842 (biomass SS = 278; catch SS = 564). The hybrid knowledge scenario was therefore the best fitting scenario tested. Biomass predictions were improved for all commercial stocks with the exception of whiting (Figure 6). Catch predictions remained well fitted for groups such as epifauna and lobsters and crabs whilst the fit of other groups (such as cod and *Nephrops*) improved with the annual variability of the data-based effort trends (Figure 7).

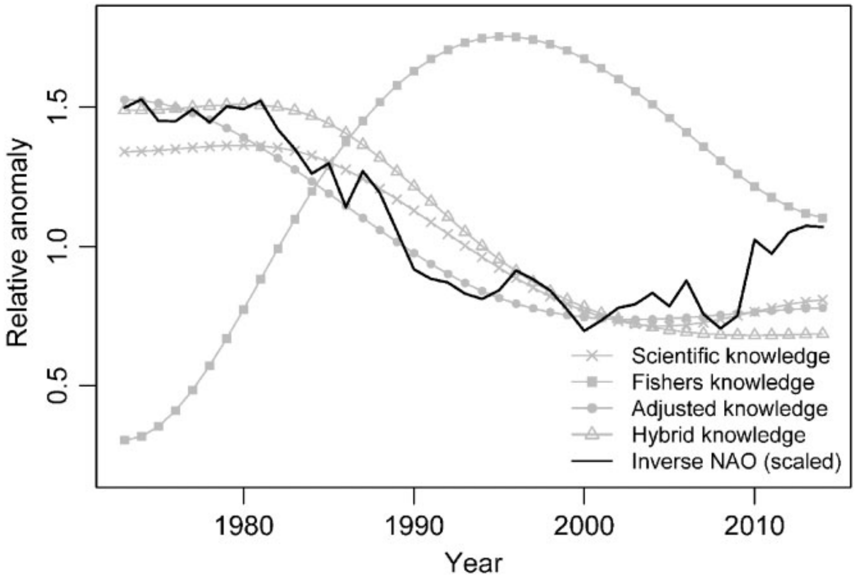

Figure 8. Primary production anomalies for Irish Sea Ecosim models using different fishing effort knowledge types. The Inverse North Atlantic Oscillation trend has been rescaled to the magnitude of the hybrid knowledge trend.

Model uncertainty ranges were less dynamic than previous scenarios, suggesting an increased confidence in model results in light of the plausible input parameter distributions.

The best fitting hybrid model was obtained with 36 vulnerabilities (8 top-down, 28 bottom-up) and a PP anomaly with four spline points. The PP anomaly produced by this scenario also significantly negatively correlated with the NAO, AMO, and depth integrated temperature (Figure 8, Supplementary Figure S6).

Discussion

This study shows the usefulness of the co-production process. The WKIrish workshops relied entirely upon listening to fishers and learning from their experience and knowledge. The process was relatively informal, unrestrained, and care was taken not to impose any preconceived ideas, following the GAP2 project guidelines. With the light guidance of a chairperson, fishers primarily determined the direction and flow of the meetings, taking time to discuss questions, whilst the scientists recorded the information needed for the model. The scientific interpretations of what the fishers had said were then presented back to them and modified if it did not reflect what they agreed, thus iterating on a consensus.

A general review of the co-production process points to the importance of trust building between researchers and stakeholders as a necessary pre-cursor to successful collaboration (Djenontin and Meadow, 2018). In this specific case, the initial impetus for the work came from the stakeholders via the EU North Western Waters Advisory Committee (NWWAC) showing an early engagement. The first workshop in Dun Laoghaire was co-chaired by a PO representative, nominated by the NWWAC. The second, in Kilkeel, was organized by another PO representative and member of the NWWAC. This gave a solid foundation for the mutual trust that was an essential part of the workshops, which themselves further cemented that trust. However, poorly managed attempts to harvest stakeholders' knowledge can lead to further resentment and alienation towards the research community. The "ethics" of knowledge co-production thus needs careful consideration so that stakeholders actually benefit, and feel that they are benefitting, from sharing their knowledge (Marshall *et al.*, 2017).

One of the issues with the co-production approach was the creation of multiple trend versions for the beam trawl, otter trawl, and pelagic nets fleets. This was, in part, due to changes in the people contributing to these trend evaluations. Whilst the Bayesian approach was designed to choose a preferred trend on the basis of statistical fit, it is also important to explore why these different trends were produced. Reconstructed effort trajectories were very similar for the beam trawl fleet, however large differences were observed in the fishers' effort trends for otter trawl and pelagic nets. The difference in the otter trawl effort projections is most likely because, in 1973, the differences between the otter fleet (TR1, targeting whitefish) and the *Nephrops* fleet (TR2, targeting *Nephrops*) did not really exist. Much the same gear was used in both fisheries. The distinction then evolved over some years. Recent analyses have treated the fleets as differentiated into TR1 and TR2 to capture the change and these designations were used in the model. Version 1 of the otter trend seems to capture the effort of TR1 and TR2 combined, whereas version 2 recognized the switch between TR1 and TR2, noting the decrease in TR1 effort in alignment with the increase in TR2 effort. It is this switch which makes version 2 more statistically viable as a trend to drive the landings of whitefish in the model. Versions 1 and 2 of the pelagic effort shared a similar peak in effort between 1990 and 2000, however they have different perspectives of effort in 1973. The pelagic fishery would be predominantly for herring. Version 1, produced by fishers at the Dun Laoghaire meeting, starts with high effort and then decreases to the mid-1980s. Version 2, designed by semi-pelagic fishers at the Kilkeel meeting, starts with low effort and then increases. The semi-pelagic vessels would fish both herring and demersal fish. It is likely that the Kilkeel trend reflects the specific effort of the Northern Irish semi-pelagic fleet in isolation, whereas the Dun Laoghaire trend, reconstructed by fishers from multiple fleets, captures the overall pelagic effort in the Irish Sea. The 1973–1980 effort proposed in

Table 2. Sum of SS contributions from each functional group in the Irish Sea Ecosim model under four fishing effort parameterizations: S1) scientific knowledge, S2) fishers' knowledge, S3) adjusted fishers' knowledge, and S4) hybrid knowledge.

	Biomass				**Catch**			
Group name	**S1**	**S2**	**S3**	**S4**	**S1**	**S2**	**S3**	**S4**
Toothed whales	0.37[a]	3.61	1.16	0.84	–	–	–	–
Minke whales	1.32[a]	1.78	1.34	1.57	–	–	–	–
Seabirds (high discard diet)	1.8	0.59[a]	18.59	3.17	–	–	–	–
Seabirds (low discard diet)	2.14	1.06[a]	9.72	1.76	–	–	–	–
Sharks	2.82[a]	73.94	4.57	10.51	57.11	298.15	67.95	34.48[a]
Rays	4.53	9.1	3.19	1.79[a]	9.4	64.43	18.39	7.54[a]
Atlantic cod 2+	9.1	5590.53	8.39	6.41[a]	10.93	4652.9	12.74	8.03[a]
Atlantic cod 1	15.14	5086.42	9.99	6.83[a]	20.1	4471.99	27.81	16.06[a]
Whiting 2+	13.71[a]	20.17	25.45	16.81	94.38	74.84	75.43	52.08[a]
Whiting 1	11.44	25.72	6.36[a]	8.54	18.09[a]	145.8	39.8	51.12
Haddock 2+	3.56	11.91	2.52	2.08[a]	9.63[a]	63.03	42.84	29.63
Haddock 1	37.71	42.54	30.55[a]	38.77	34.64[a]	55.09	56.34	55.28
European plaice 2+	2.53	57.01	27.01	1.97[a]	12.71	105.8	13.46	5.46[a]
European plaice 1	68.11	114.4	62.52	50[a]	63.6	287.08	101.96	42.66[a]
Common sole	7.2	24.94	11.71	4.95[a]	11.55	62.6	19.42	7.38[a]
Flatfish	1.08	2.21	1.13	1.03[a]	10.08	536.42	23.1	3.12[a]
Monkfish	7.94	7.33	10.46	6.33[a]	20.43	60.11	34.67	14.08[a]
European hake	17.2	144.63	21.74	15.73[a]	28.73	460.76	35.07	12.29[a]
Sandeels	14	9.39[a]	12.39	9.97	–	–	–	–
Gurnards and dragonets	0.5	0.34	0.28	0.27[a]	2.73[a]	259.88	19.95	22.2
Other demersal fish	6.06	7.48	7.14	6.13[a]	19.96	136.33	58.05	13.37[a]
Other benthopelagic fish	4.74	1.7[a]	6.83	21.92	11.6[a]	324.21	39.52	17.77
Atlantic herring	26.19	81.44	8.05	5.15[a]	13.24	107.62	24.27	10.13[a]
European sprat	9.99	4.01[a]	18.64	6.4	14.94	525.17	291.18	10.27[a]
Other pelagic fish	–	–	–	–	69.61	315.77	103.12	68.78[a]
Lobsters and large crabs	–	–	–	–	56.74	135.2	19.35	8.41[a]
Nephrops	0.11	13.31	0.12	0.09[a]	7.66	122.12	7.49	2.68[a]
Shrimp	–	–	–	–	22.24	153.76	16.61	15.07[a]
Cephalopods	–	–	–	–	26.19	174.42	48.97	25.89[a]
Scallops	–	–	–	–	12.7[a]	75.75	91.12	19.47
Epifauna	–	–	–	–	71.98	45.95	17.58	10.8[a]
Gelatinous zooplankton	3.45	2.21	2.5	1.6[a]	–	–	–	–
Large zooplankton	11.51	63.84	9.71[a]	22	–	–	–	–
Small zooplankton	10.96	109.73	5.48	4.17[a]	–	–	–	–
Phytoplankton	12.3[a]	33.24	26.96	21.45	–	–	–	–
Sum	307.5	11544.6	354.5	278.2[a]	731.0	13754.2	1306.2	564.1[a]
Percentage of best fit	17.2%	17.2%	10.3%	55.2%	23.1%	0.0%	0.0%	76.9%

SS was calculated by comparing model biomass and catch predictions to observed data where available. The table includes the total SS (sum) and percentage of best-fits obtained for each parameterization.

[a] Denotes the best biomass and catch fit obtained for each functional group.

Dun Laoghaire followed the Irish herring fishery dynamics described in Molloy (2006), where upwards of 30 boats participated in the fishery during its peak period in the early 1970s, yet declined to two or three boats in the 1980s after the price of herring dropped and the fleet lost interest.

The fishing effort trends fishers provided showed good agreement with scientific estimates for vessels using beam trawl, otter trawl, *Nephrops* trawl, and pelagic gears. However, when incorporated into the Irish Sea Ecosim model they caused multiple stock collapses. The Bayesian approach suggested that fishers' perceptions of historical changes in *Nephrops* trawl, beam trawl, and otter trawl effort were too high. The reasons behind this are uncertain but it may be the effort terminology used during the workshops led to overestimation of fishing effort, or the perceptions may actually reflect the magnitudes of change as apparent to fishers. It cannot be ruled out that errors in the Ecopath model and not the fishers' effort trends, may have led to incompatibilities between fishers' trends and the model. However, this is difficult to address as the models catch parameterization was grounded in the best available data, and therefore *ad hoc* alterations seem unjustifiable.

The overall best fitting Irish Sea model used a combination of effort drivers based on both fishers' and scientific knowledge (scenario 4). This hybrid model retained the annual dynamics obtained using scientific effort trends but gained the ability to account for the observed landings of groups caught by gears that were under-represented by scientific knowledge, namely potting, dredging, long lines, pelagic nets, and gillnets. Whilst the dynamics of the main commercial finfish stocks were relatively well reproduced using scientific knowledge only (scenario 1), incorporating fishers' knowledge into the hybrid scheme improved the models capacity to recreate the dynamics of functional groups such as lobsters and crabs. This is particularly important given that the catches of these groups have increased markedly in the Irish Sea since the 1990s.

The variables selected in the hybrid model included fishing effort, a PP anomaly, and a combination of top-down and bottom-up vulnerabilities. Ideally it would have been preferable to simultaneously search for vulnerabilities, PP anomalies, and fishing effort magnitudes to find the optimal combination and better understand the uncertainty in the final fishing effort magnitudes. However, this is currently not technically possible but may be possible in future versions if a plugin was to be developed to automate the process. Therefore at present, optimizing for fishing effort magnitudes prior to searching for vulnerabilities and anomalies is the best option available. It can be argued that the vulnerabilities from the scientific model could be used when searching for optimal fishing magnitudes, however, the vulnerabilities and anomalies estimated will aim to compensate for the constant fishing effort of gill nets, pots, longlines, pelagic nets, and dredge, as the vulnerability search function is an "observation error" fitting procedure (Christensen and Walters, 2004). Therefore, the set of trophic parameters estimated would be unique to the initial fishing efforts and may not be suitable for estimating magnitudes for the additional fishers' efforts.

Only 8 of the 36 parameterized predator vulnerabilities in the hybrid model were top-down, meaning the vast majority suggest bottom-up mechanisms control functional groups in the Irish Sea, as concluded recently from Irish Sea Ecological Network Analyses (Bentley *et al.*, 2019). This suggests that changes in plankton communities, such as those driven by multidecadal oscillations (Fromentin and Planque, 1996; Edwards, Beaugrand, *et al.*, 2013) or climate change (Richardson and Schoeman, 2004; Edwards, Bresnan, *et al.*, 2013), may have a strong influence on the dynamics of higher trophic levels. The majority of vulnerabilities estimated for the other best fit scenarios (scientific, fishers, adjusted fishers) were also bottom-up, however the individual vulnerabilities amongst these models were different, implying different ecological interactions. This means that the differences observed between scenarios could also be influenced by different vulnerability values or PP anomaly assumed.

The impact of the PP anomaly propagated through the hybrid models food web due to the overall bottom-up nature of the system. Whilst the PP anomaly negatively correlates with both the NAO and AMO, the estimated anomaly shows greater similarity to the inverse NAO trend which has previously been used to drive productivity in an Ecosim model of the Irish Sea (Mackinson *et al.*, 2009). The AMO has also previously been found to correlate with PP anomalies for the West Coast of Scotland (Serpetti *et al.*, 2017) and the Norwegian and Barents Seas (Bentley *et al.*, 2017) Ecosim models. In future work, the inverse NAO should be directly used as a bottom-up driver for the Irish Sea.

Known ecological responses to the NAO include changes in timing for recruitment (i.e. finfish), reproduction (i.e. birds), altered population dynamics (i.e. birds and mammals), and changes to spatial distributions (i.e. birds and finfish) and interspecific relationships (i.e. finfish and invertebrates) (Ottersen *et al.*, 2001). The NAO may affect the recruitment of cod through local environmental variables such as temperature, salinity, oxygen, advection, and turbulence (Planque and Fox, 1998; Attrill and Power, 2002; Stige *et al.*, 2006) and has been shown to strongly negatively correlate with cod recruitment in the Irish Sea (Brander and Mohn, 2004). The fact that cod recovery in the Irish Sea did not yield the expected gain may therefore stem from environmental factors, such as system productivity, temperature, and predation, influencing the survival and growth of larvae and juveniles. Therefore, even if area closures and gear restrictions reduced the fishing mortality, our model indicates that the recovery may have been hampered by the prevailing environmental conditions, as previously hypothesized by Kelly *et al.* (2006).

The next stage in the co-production will be further involvement of the stakeholders in generating policy advice based on the model. After a follow up discussion at WKIrish5, where fishers were shown model results, a roadmap was discussed for future collaboration. Fishers highlighted their interest in the ecosystem impacts of the landings obligation, area closures, and climate change. To help with the development of model scenarios going forward, fishers will be asked to identify likely trends over the next few years (e.g. in effort and metier), and the likely impacts of these on both the commercial fish stocks and the wider ecosystem. They will also be invited to consider possible changes in management approach that can be investigated with the model. An evaluation of the success, or otherwise, of these outcomes will be critical. This process has already started and will be maintained as the model is taken to a key run evaluation and peer review by the ICES Working Group on Multispecies Assessment Methods. This study therefore highlights the importance of positive engagement as well as the validity of fishers' knowledge for use in ecosystem modelling and fisheries research.

Finally, the methods and approaches we established here may be of particular interest to researchers aiming to model ecosystems with limited local scientific knowledge to generate ecosystem-based fisheries management advice. The approach may also be applicable to a wider range of topics. This might include spatial distribution of the fish species, locations of nursery and spawning grounds, or other aspects of fishers' behaviour, e.g. targeting behaviour.

Conclusion

Using the Irish Sea as an example, we demonstrated that combining fishers' and scientific knowledge regarding historic fishing effort led to the best statistically fitted EwE food web model. This model has improved capability to recreate the biomass and catch trends of commercially important stocks, especially shellfish that have become increasingly important in the catches. The revised Irish Sea EwE model is subsequently more capable of answering future questions posed by stakeholders and management. The hybrid model will be used to provide ecosystem-based management advice via WKIrish and to investigate the impact of fishing and environmental change on food web dynamics in the Irish Sea. Specifically, we aim to quantify the historic impact of the environment in greater detail. Hopefully this will elucidate why cod, and other species, did not recover as expected whilst also highlighting the potential benefit of incorporating bottom-up processes into long-term management plans. We conclude that successful co-production needs to involve stakeholders at multiple stages of research (Lemos and Morehouse, 2005).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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