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INTEGRATED ECOSYSTEM ASSESSMENT STEERING GROUP

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Report of the Workshop on operational EwE models to inform IEAs (WKEWIEA)

26-30 November 2018

Barcelona, Spain

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Executive summary

The first Workshop on operational EwE models to inform IEAs (WKEWIEA) met from the 26th to the 30th of November 2018 in Barcelona, chaired by Maciej T. Tomczak (Sweden), Maria Angeles Torres (Spain) and Eider Andonegi (Spain). The main goal of WKEWIEA was to identify, analyse and provide light on the potential use of ecosystem models to inform the scientific advice currently provided by ICES. The workshop focused on Ecopath with Ecosim (EwE) models as accepted by the ICES Secretariat, since EwE is the most widely used ecosystem modelling tool across ICES integrated ecosystem assessments (IEA) regional groups.

The group was composed by a variety of experts, including ecosystem modellers, ecosystem researchers and people closely related with or with a deep knowledge of the ICES advisory process (people that actively participate in providing advice on fishing opportunities and also in fisheries and ecosystem overviews).

Different works were presented during the workshop, some providing a general overview of the way EwE models have and/or are being used for solving management and policy related issues, and others showing practical examples how existing models could be used to inform current and future generations of Ecosystem Overviews (EOs). Additionally, discussions focused on the need of a well-accepted and documented protocol that establishes the basis about the requirements of these ecosystem models in order for them to be used to inform various parts of ICES advice, including fishing opportunities.

The main recommendations provided by WKEWIEA to the ICES community are to: i) develop a key run and quality protocol for using EwE models to inform IEAs and ICES advice (together with the Working Group on Multispecies Assessment Methods (WGSAM)); ii) adopt EwE and equivalent models in the ToRs of the ICES IEA regional groups; iii) provide advice for IEA expert groups about indicators from EwE models to be used in IEAs for the state of different ecosystem components; iv) provide some guidelines about the visualization of products (e.g. trade-offs or links quantification). Additionally, WKEWIEA strongly recommends setting up a series of workshops to continue working on how to make EwE (and other ecosystem models) operational for ICES advice, starting with a next workshop in 2019 to deal with the inter-comparability of EwE models to inform IEAs. Intersessional meetings will also be held to organize our work and strengthen the links with other ICES working groups identified as key by the group for achieving these goals.

1 Opening of the meeting

The first meeting of the **Workshop on operational EwE models to inform IEAs (WKEWIEA**) was opened at 13.00 pm on 26th November and adjourned on 30th November 2018, chaired by Maciej Tomczak (Sweden) and Eider Andonegi (Spain) with the apologizes from the third chair, Maria Angeles Torres (Spain) for not been able to physically attend the meeting. Nevertheless, Maria Angeles worked and supported the chairs by correspondence during the whole process. The meeting was attended by 18 participants representing 10 different countries. A full participants list is found in Annex 1.

2 Adoption of the agenda

A preliminary agenda was presented to the group and was adopted with minor changes that are contained in the agenda shown in Annex 2.

3 Terms of reference

The **Workshop on operational EwE models to inform IEAs (WKEWIEA)** needed to address the two tasks in the Terms of Reference described below:

a) Explore the practicalities of integrating information from existing Ecopath with Ecosim and Ecospace models

b) Explore their utility towards informing IEA in ICES areas – explore their potential to inform ICES products such as the Ecosystem Overviews, as an integral part of the ecosystem advice

Several presentations were organized (see the agenda) to get a global context on how EwE models could be used to inform IEAs, and hence ecosystem and fisheries related advice in ICES. All the presenters were asked to showcase their EwE-related work, and to reflect on how that work could be useful to inform IEAs and general ICES advice.

4 Progress report on ToRs and workplan

4.1 Building the working framework

During the first day, aiming at stablishing a common working framework for all participants, the chairs presented the motivation for the workshop. The WS was conceptualized during consecutive WGEAWESS meetings and shared with other IEA groups in ICES to analyse the interest of the whole community, and was contextualized in the framework of the ICES advice and current development of relevant science (i.e. WKDEICE), providing some starting point for following discussions during the week.

Iñigo Martinez from the ICES Secretariat presented how ICES is working to provide ecosystem advice since 2016. See the summary of his talk below:

4.1.1 ICES Ecosystems Overviews: Development and Rationale

By Iñigo Martinez (ICES Secretariat)

The ICES strategic plan highlights the importance of providing the evidence for EBM. Three main outputs are provided to support EBM: advice on fishing opportunities, fisheries overviews, and ecosystem overviews (EOs). All these three products should be considered together to have a complete picture of the ICES advice with the fisheries as the main activity and hence EBFA.

The ICES environmental advice is relatively new and needs to be provided in context for the scope and the framework to be understood, with a correct interpretation by recipients (see outputs from WKECOFRAME2, 2018). ICES environmental advice needs to be consistent with other pieces of ICES Advice and needs to be evidence based, transparent and legitimate.

The ecosystem overviews objective is to provide a concise, up-to-date, evidence-based overview of each of the ICES ecoregions and is divided in 5 main sections:

1. Ecoregion description: boundaries and management
2. Key signals within the environment and ecosystem
3. Top pressures on the ecosystem
4. State of ecosystem components
5. Climate change (2018)

The ecosystem overviews currently use qualitative methods to identify and focus on the top five priority pressures and associated human activities that can be locally managed within each ecoregion. They thus put fishing activities into the context of the trends and status of the marine ecosystem as a whole. EOs also try to highlight consequences of trade-offs between objectives.

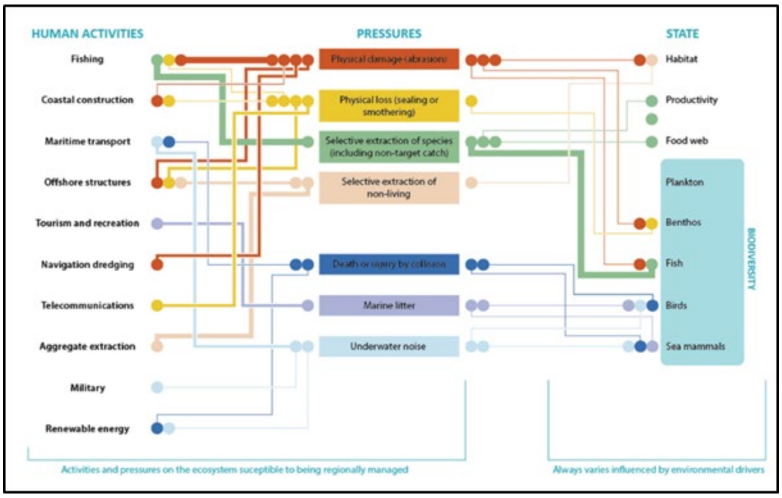


Figure 4.1.1.1. Example of ecoregion overview main diagram with the major regional pressures, human activities, and ecosystem state components. Climate change affects human activities, the intensity of the pressures, and some aspects of state, as well as the links between these.

So far ICES has developed EOs for seven Ecoregions; Bay of Biscay and Iberian Coast, Greater North Sea, Celtic Seas, Barents Sea, Norwegian Sea, Icelandic waters and Baltic Sea: http://www.ices.dk/community/advisory-process/Pages/Ecosystem-overviews.aspx

Current overviews use qualitative methods based on knowledge from across the ICES network combined with the quality assurance and advice drafting experience. However, a new generation of overviews with more quantitative methods to further assess these pressures are currently being developed. These new overviews will reinforce the online application, consider social and economic objectives an incorporate ecosystem services and not only pressures.

There would be also stronger expectations for data provision and access to underlying data for the future ICES ecosystem overviews (see FAIR principles for data). Therefore, data supporting new products are expected to (1) have a Digital Object Identifier (DOI) (2) conform to ISO standards, and (3) refer to international standards and units. Data access rights must be clear, and could include a data usage license (ref. to the ICES data policy) and links to download with internationally recognized download formats. All data should be accompanied by a clear vocabulary and auxiliary data (manuals and protocols) that describe the methods used or referenced by weblinks.

In addition, ICES is implementing a Transparent Assessment Framework (TAF: taf.ices.dk) that links data inputs with decision-making and models to data outputs. This framework should assure archiving, transparency and reproducibility in the long term.

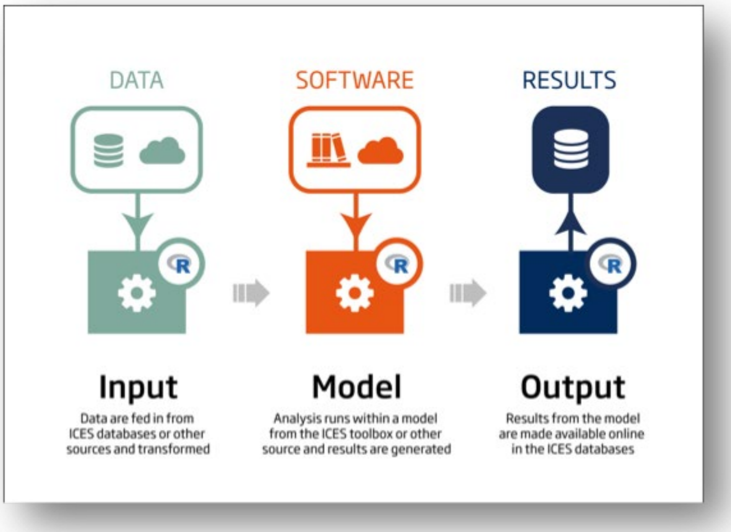


Figure 4.1.1.2. Transparent Assessment Framework (TAF) conceptual model.

During the following two days, different works were shown by the workshop participants. Some examples demonstrated how EwE models were being used to address management related issues in a global and/or regional scale, showing cases from both ICES and non-ICES international areas.

The summaries of those talks (following the order of the agenda) are shown in the subsections below.

Section 4.2 contains the bulk of presentations that aimed to provide an overview of how ecosystem models in general and EwE models in particular are being used to address management and policy related issues. Section 4.3 contains presentations focused on providing considerations, recommendations and potential alternatives about the use of ecosystem models. Section 4.4contains presentations that detail practical examples where EwE models have been applied for EU-ICES areas and how they could be used to inform existing Ecosystem Overviews. Finally, section 4.5 presents other potential ways of using EwE models to inform advice were shown, dealing with different issues such as including the spatial dimension using Ecospace, incorporating fisher's knowledge in EwE models and also the use of geographically-nested ecosystem model to support MPAs related issues.

4.2 How are EwE and other ecosystem models used to support management and policy related issues?

4.2.1 Are ecosystem models used for management and policy?

By Villy Christensen (University of British Columbia)

There is widespread interest in and demand for models of aquatic ecosystems, and this presentation showed an overview of how ecosystem models are used for management and policy based on a review focused on the most widely used ecosystem model type, Ecopath with Ecosim (EwE). There are around 500 published - EwE models, and many of these are available for download in an online database - (www.Ecobase.Ecopath.org). The review evaluated the current status of using EwE for management and policy and was structured around seven topics, (1) fisheries management, focused on evaluation of ecological, economic and social factors and trade-offs, and for setting and evaluation of reference points, and increasingly as operating models for Management Strategy Evaluation (MSE); (2) fishing regulations, where development of STECF Multi Annual Plans, evaluations of the EU Landing Obligation and other bycatch studies are of interest; (3) indicators, with focus on the EU Marine Strategy Framework Directive; (4) evaluations of the fisheries sector, notably value chain analysis describing economic and social factors throughout the supply chain to the consumers; (5) spatial management, which includes development of MSE frameworks as operational tools for ecosystem based management, and applications aimed at developing toolboxes for evaluating impact of nuclear reactor incidences on seafood; (6) environmental impact assessments are a focus of much development, and includes evaluations of impact of dams, marine renewable energy, and major infrastructure; and (7) climate change research, based on coupling of physical, biogeochemical and foodweb models climate change, or linking to Earth System models to evaluate potential impacts of climate change, which impacts policies through IPBES, IPCC, Fisheries Management Councils, a.o.

4.2.2 A modelling framework for the Mediterranean Sea ecosystem in support of EU policies

By Chiara Piroddi (JRC, European Union)

The Marine Strategy Framework Directive (MSFD) is foreseeing that all EU Member States take the necessary measures to maintain or progressively achieve Good Environmental Status (GES) in the marine environment by year 2020. In recent years, the JRC has delivered to the Commission scientific and technical support to the implementation of the Marine Strategy Framework Directive (MSFD). As part of this initiative, in particular, the development of models aiming at helping the evaluation and implementation of policies conductive of achieving GES in the different European basins. Under this framework, this presentation showed the Marine Modelling Framework (MF) developed at DG JRC with the aim of providing policy-support to EU initiatives dealing with the environmental status of EU regional seas. The general structure of the MF was presented as well as a schematic representation on how such tools could be used, through modelled derived indicators, in the MSFD policy evaluation cycle (selected descriptor/criteria were presented and linked to the modelled derived indicators). A general overview of current implementations and progress of these approaches at EU scale was shown, together with some specific examples of present and past applications of the MF for the Mediterranean Sea, which was the first regional sea of being assessed by JRC.

4.2.3 Using EwE models for management issues – the US example

By Howard Townsend (NOAA)

National Marine Fisheries Services (NMFS) uses a range of ecosystem models for living marine resource management. The primary reason to use ecosystem modeling is to systematically and simultaneously evaluate multiple factors affecting LMRs. Models are used in a holistic, EBFM context as well as to inform single-species management issues (Table 4.2.3.1).

Table 4.2.3.1. Different use of ecosystem models in the EBFM and classic FM context.

EBFM Context	Informing single species management
To systematically catalogue information for an ecosystem and thereby systematically identify data gaps	To predict LMR species responses to a range of management options

To explore hypotheses of how the ecosystem, ocean, trust spp., and fisheries behave	To predict LMR species responses to climate change, oceanography, esp. with respect to distribution
To systematically evaluate relativity of risk	To provide mass balance constraints to stock-assessment, Protected Resource model outputs
To quantitatively evaluate social, economic, and ecological trade-offs among different management options	To constrain Stock assessment ACL outputs with real-world limits of total system production
To predict human behavior responses, especially fleet dynamics, with respect to ecosystem change	To produce multi-model ensembles and account for uncertainty associated with model structure
To conduct scoping and feasibility exercises with stakeholders, esp. with qualitative network modelling	To predict LMR species responses to a range of mgt options
To conduct quantitative testing aspects of IEAs	To predict LMR species responses to climate change, oceanography, esp. with respect to distribution

Most NMFS centers have simpler ecosystem models (e.g. multispecies surplus production), some have very complex models (e.g. Atlantis or other end-to-end models). Virtually every science center has used Ecopath for ecosystems within their purview. Many centers use EwE as one of suite of ecosystem models with the purpose of accounting for uncertainty associated with model structure. For example, the Alaska Fisheries Science Center uses EwE, along with other models of varying complexity, to evaluating fishing management strategies under different climate scenarios. The Northwest Fisheries Science Center has used Ecopath, along with an Atlantis Model and a Model of Intermediate Complexity, to evaluate effects of sardine fisheries on predators. These are just a few examples of the ways NMFS is beginning to include information from ecosystem models into living marine resource management.

Specifically, for Integrated Ecosystem Assessments (IEAs) within NMFS, ecosystem models can inform the IEA process (Figure 4.3.2.1) by:

1. Synthesizing available data to help us understand and assess system dynamics,
2. Scenario tests of the risk of key species to top-down or bottom-up mediated stressors, and
3. Scenario tests of the effectiveness and trade-offs of management strategy alternatives.

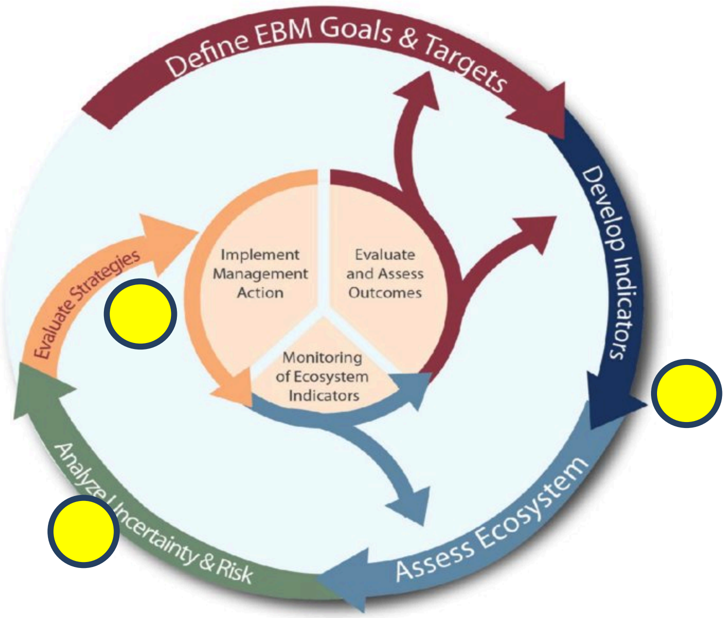


Figure 4.3.2.1. Integrated Ecosystem Assessments loop diagram (modified from www.noaa.gov/iea)

In addition to complex, data-driven ecosystem models, NMFS IEAs have been increasingly making use of qualitative, conceptual models to understand the driver, pressures and states of the ecosystem. The process for developing these conceptual models involves stakeholder input. The stakeholder involvement in model development process enables managers, stakeholders and scientists/modelers to develop a shared understanding of important social and biophysical processes in a n ecosystem. This approach has been useful in incorporating socio-economic aspects of ecosystems that often are not readily quantifiable, thus providing a more complete picture of the social-ecological system in NMFS regions.

4.3 Considerations and examples about the use of ecosystem models

4.3.1 Enhancing Europe's capability in marine ecosystems modelling for societal benefit

By Sheila Heymans (European Marine Board)

Marine ecosystem models are an important approach to: integrate knowledge, data, and information; improve understanding on ecosystem functioning; and complement monitoring and observation efforts. They also offer the potential to predict the response of marine ecosystems to future scenarios and to support the implementation of ecosystem-based management of our seas and ocean.

There are many marine ecosystem models, but there is no single model that can answer all policy questions, making it difficult to achieve a fully end-to-end (E2E) model. In each case the context, specific knowledge and scale need to be taken into account to design a model with the appropriate level of complexity. It is more practical to assemble several models in order to reach the full E2E spectrum. This requires a transdisciplinary approach and the inclusion of socio-economic drivers.

This Future Science Brief has identified the following research and development needs to improve model development as well as key recommendations to strengthen the marine ecosystem modelling capability:

- Collect and incorporate new data and information into marine ecosystem models;
- Model marine biodiversity and ecosystem services, based on critical understanding of marine ecosystems;
- Model changes in behaviour, based on understanding adaptive responses in marine organisms;
- Evaluate and reduce uncertainty in marine ecosystem forecasting; and
- Use new approaches in machine learning to enhance marine ecosystem models.
- Key recommendations to strengthen marine ecosystem modelling capability include:
- Enhance models by identifying crucial unavailable data, linking models to new and existing observations and data, and by strengthening links to data assimilation centers;
- Increase model predictability through coordinated model experiments and the ensemble approach;
- Develop a shared knowledge platform for marine models and support the development of next generation models;
- Make marine ecosystem models more relevant to management and policy by being more transparent about model limitations and the uncertainties in their predictions; including socio-economic drivers;
- Promoting co-design and dialogue between model developers and users; and
- Enhance trans-disciplinary connections and training opportunities.

4.3.2 Of Fish and Men: Integrated ecosystem assessments – Integrated fisheries management solutions

By Rudi Voss (Kiel University)

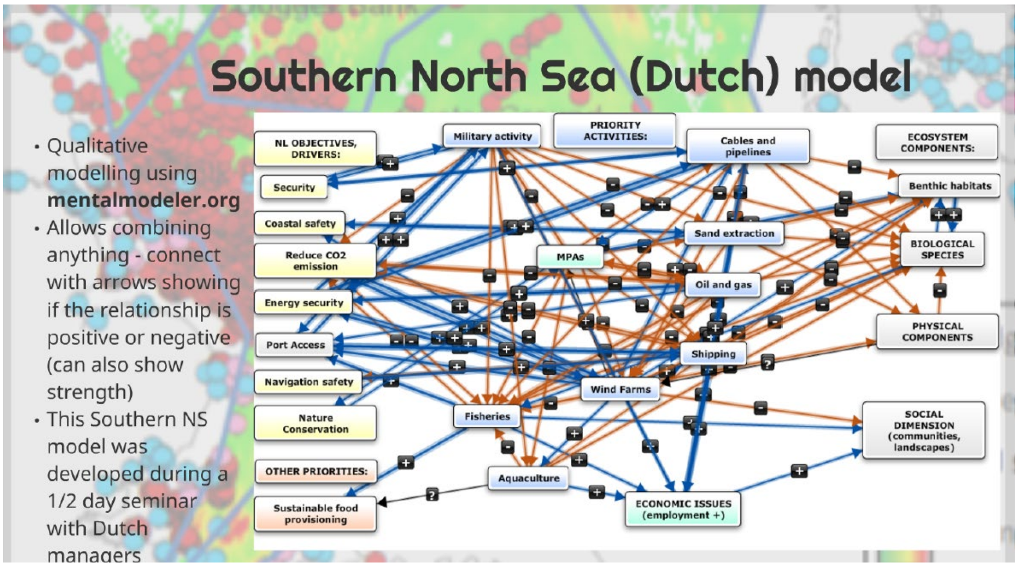
The world's fish stocks as well as the marine foodwebs they are embedded in, are increasingly under pressure, not only due to climate change effects, but also due to socio-economic development, leading to a worldwide increased demand for fish. One major reason is failing fisheries management, allowing for too generous catch opportunities, while disregarding ecological-economic feedback dynamics. New aspects of developing integrated, sustainable fisheries management solutions are needed. The work applies cutting-edge ecological-economic models based on newly available data that enable a necessary innovation in inter-and trans-disciplinary fisheries management. This research aims to improve 'on the ground' management applications in order to inform Integrated Ecosystem Assessments.

We use ecological-economic models of varying complexity to illustrate the importance of including socio-economic factors in Integrated Ecosystem Assessments – otherwise incomplete, or even simply false, conclusions might be reached. E.g. the application of a pure MSY strategy in a multispecies context (without any economic considerations) will result in economically AND ecologically disastrous outcomes (at least in the case study of the Baltic Sea).

Year-to-year management implicitly responds to short-term economic interests, and consequently, regularly resorts to tactical short-term rather than strategic long-term decisions. Using Baltic cod as a showcase, we introduce a new way of estimating management advice referred to as an 'ecologically-constrained Maximum Economic Yield' (eMEY) strategy, which takes into account ecological criteria as well as short- to medium-term economic costs. The eMEY approach aims at maximizing the economic benefits for the fishery as well as society (consumers), while safeguarding precautionary stock sizes. We find that application of eMEY advice results in less variable catches as compared to conventional management. Total allowable catches are dampened during high stock sizes, but importantly for the fishery, zero catch advice during phases of low stock size is avoided. Quantification and visualization of the costs of deviating from eMEY advice offers a transparent basis for evaluating decision-making outcomes. To foster the uptake of the eMEY approach, or other Integrated Advice, in current advice given by the International Council for the Exploration of the Sea (ICES) and the EU fishery management system, we suggest an easy-to-implement scheme of providing integrated advice, also accounting for economic considerations.

4.3.3 Qualitative modelling for assessing cumulative impacts on the North Sea ecosystem

The ICES North Sea IEA group (WGINOSE) is developing conceptual 'qualitative' models, using methods described by DePiper et al. (2017), for selected sub-regions of the North Sea. The strength of these modelling approaches is the ease with which they can be developed with stakeholders to identify the most important ecosystem components to assess from the perspective of the human dimension (e.g. types of activity, management objectives, target species and habitats) The direction and strength of ecosystem component interactions (or links) are again identified and agreed in consultation with stakeholders before running the models against an agreed set of scenarios or questions to be addressed. An example of a typical conceptual model structure and output in response to increasing fishing pressure from all fisheries, is shown in Figure 4.3.3.1 and 4.3.3.2.



Southern North Sea (Dutch) model

- Qualitative modelling using **mentalmodeler.org**
- Allows combining anything - connect with arrows showing if the relationship is positive or negative (can also show strength)
- This Southern NS model was developed during a 1/2 day seminar with Dutch managers

Figure 4.3.3.1. Conceptual ecosystem model developed in consultation with stakeholders for the Dutch sector of the Southern North Sea.

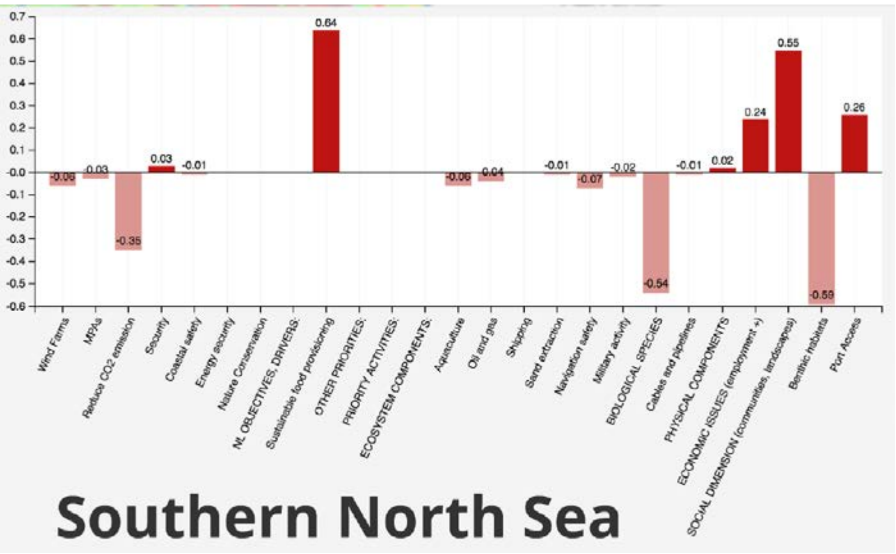


Figure 4.3.3.2. Model results for a scenario which increases fishing pressure for all types of fishing activity.

The consequences of different management scenarios can be readily evaluated with respect to non-target components of the ecosystem (Figure 4.3.3.2). However, confidence and reliability of the qualitative model outputs must be evaluated and supported through integration with quantitative modelling and assessment approaches. In this respect WGINOSE will couple its North Sea conceptual *MentalModels* with spatially comparable EwEs.

4.4 How could EwE models could inform next generations of Ecosystem Overviews – thoughts and examples

4.4.1 Natalia Serpetti: Western Coast of Scotland modelling in relation to Celtic Seas Ecosystem Overview

<u>By Natalia Serpetti (SAMS)</u>

This presentation was focused in three main topics:

1. **Why MSY? Context - West of Scotland fisheries**

This analysis was performed using two different modelling approaches. Ecopath with Ecosim (EwE NS and SH) and StrathE2E (by MH). Both models were used to assess the current state of MSY in this ecosystem: the major findings highlighted a strong reduction in fishing mortality from the 80's (when pelagic and demersal stocks were in overfishing) to an under fished ecosystem on 2000's.

This led to an increase of demersal biomass overall driven by a large increased of hake, saithe and flatfish, while other gadoids (cod, haddock and whiting) showed a continuous steady decline. Simulation from StratE2E showed that these trends caused a strong predation pressure on pelagic fish showing very low yields no related to fishing pressure. The yield curve for pelagic can be re-built only if the pelagic would be released by demersal predation pressure. EwE showed that also cod, whiting and haddock are crushed by predation pressure by saithe rather than fishing pressure.

Both models showed that to maximize the overall catches of pelagic domains we could fish twice as much the 2003-2013 baseline and up to ten times for the demersal domain, of course that will lead to a loss of biodiversity.

Currently the fishery has been managed under single stock assessment, however this approach does not take in consideration the predation pressure dictated by the food-web and the mix fishery issue. The demersal otter trawls catch all the main gadoids, so apply different fishing pressures for species caught by the same gear is not very applicable. For this reasons F at MSY were calculated across different methods (Surplus production model and EwE multispecies MSY plug-in) and compared with the baseline (F 2003-2013) and the fishing mortalities advised by stock assessment. Two more scenarios were also tested: one that look at the F MSY to maximize the catches of the demersal and pelagic overall domains (loosing biodiversity) and one scenario that represent a compromise which is taking in consideration an overall increase of fishing, but also an increase gear selectivity (reducing bycatches of juvenile gadoids by *Nephrops* trawler and spatially trying to avoid cod catches).

The overall comparison shows potential recovery of cod, whiting and haddock when a stronger fishing mortality for saithe was applied reducing the predation pressure of this predators over the other gadoids. Similar finding (no presented) have been found in the pelagic domain where an increasing fishing mortality for hake could lead to a reduction of predation pressure on pelagic group and an overall increase of their catches.

2. IPCC scenarios – Rising water temperature

This part of the presentation highlighted the importance of assessing the impact of ocean warming on sustainable fisheries management as warming water could have a strong impact on cold water species.

3. Impact of noise on harbour porpoise

Cetaceans groups was split into three sub-groups based on their sensitivity to noise sources: minke whales (low-frequency noise), harbour porpoise (high-frequency noise), dolphins (mid-frequency noise). Bottom-up and top-down spatial temporal data were coupled in Ecospace: top-predators data were supplied by Waggitt et al. (in prep) while depth integrated temperature and net primary were supplied by NEMO-ERSEM (Plymouth Marine Laboratory).

The new updated Ecospace model was used to assess the impact of noise on harbour porpoise.

4.4.2 Southern North Sea modelling in relation to North Sea Ecosystem Overview

By Moritz Stäbler (Leibniz Centre for Tropical Marine Research) and Miriam Püts (Thünen-Institute of Sea Fisheries)

1. Ecopath and Ecosim modelling of the southern North Sea

An Ecopath with Ecosim model was parameterized for areas IV b&c (WGSAM 2017; Stäbler et al. 2016; Stäbler et al. 2018). The model was fit to time-series of biomasses, catches and fishing efforts, and calibrated to stock–recruitment relationships of cod, plaice and sole. So far, applications of the model include a quantitative description of the structure and functioning of the foodweb in the model's base year, 1991 (Stäbler et al. 2018). The Ecosim model was used to check the feasibility of obtaining simultaneous 'pretty good yields' of cod, plaice, sole and brown shrimps. The compatibility of those multispecies MSYs with indicators of good environmental status was also addressed (Stäbler et al. 2016; Figure 1). A study investigating how multispecies MSYs of sole, plaice, cod and brown shrimp are affected by declines in system productivity, and by increasing populations of Grey seals and Harbour porpoises is under review (Figure 2).

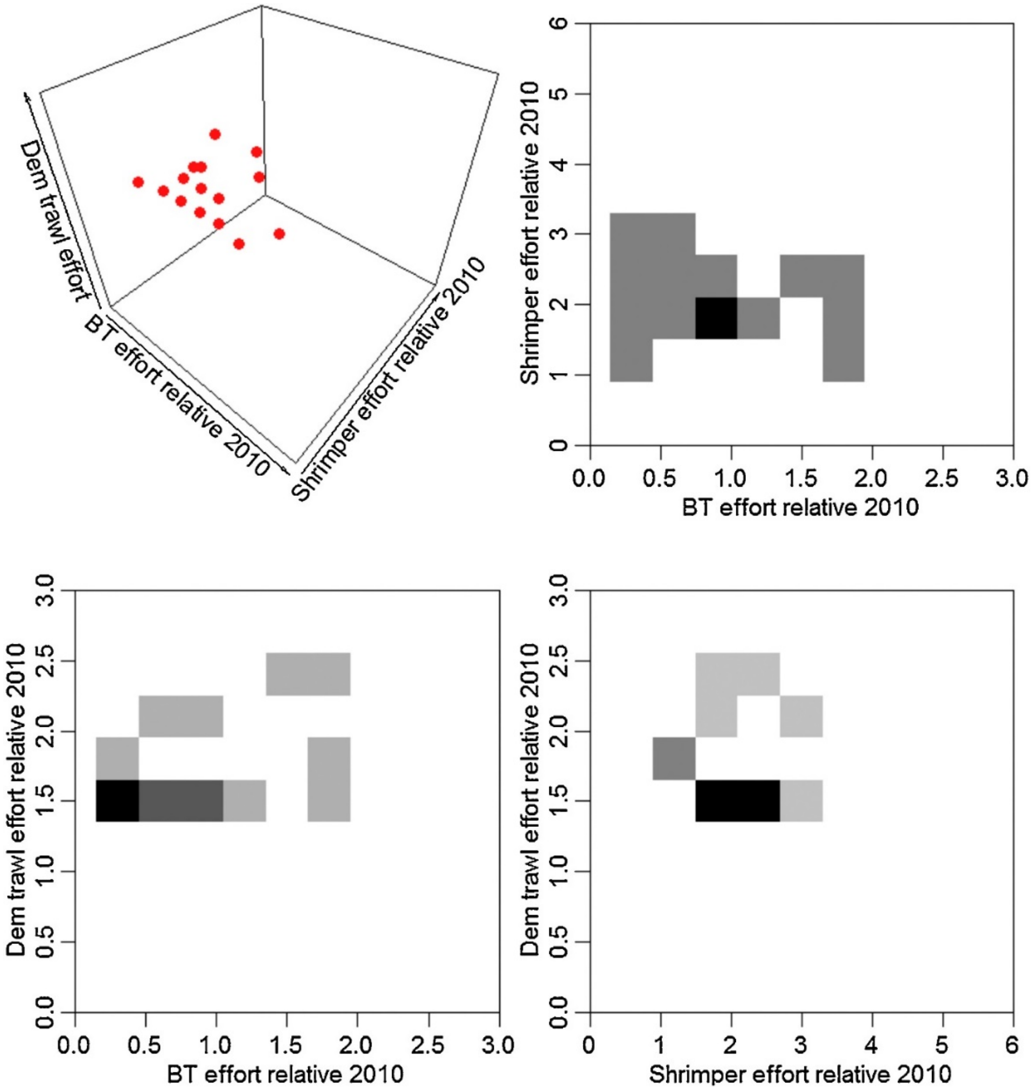


Figure 4.4.2.1: Fishing efforts of demersal, beam, and shrimp trawlers leading to simultaneous 'pretty good yields' of cod, plaice, sole and brown shrimp, while maintaining a proxy of Good Environmental Status. From Stäbler et al. 2016.

With reference to the 2016 ICES Greater North Sea Ecoregion Ecosystem Overview, the results found with the southern North Sea Ecosim model (sNoSe-EwE) can support coming rounds of the integrated ecosystem assessment as follows:

Table 1: Potential contributions to the ICES Greater North Sea Ecoregion Overview by Ecopath and Ecosim modelling of the southern North Sea (IV b&c) undertaken to date.

ICES Ecosystem Overview 2016	Potential contribution by southern North Sea EwE modelling
"Flatfish not included in multi-species models for the North Sea“ (pg. 3)	Plaice and sole are focal functional groups in the sNoSe-EwE. Their representation in the model has been calibrated to ICES single species stock assessment.
“Harbour porpoise moved southwards" and "grey seals increasing“ (pg. 3)	Implications of increased predation of marine mammals on target stocks is evaluated in Stäbler et al. (under review).

"Multispecies assessment models used to evaluate impact of fisheries and main predators on forage fish stocks" (pg. 5)	The sNoSe-EwE can serve as an additional tool to consider such multispecies interactions; and, other than SMS, includes Brown shrimp.
"Impacts on food-web" (pg. 6)	The 1991 representations of the total (Mackinson and Daskalov 2007) and the southern (Stäbler et al. 2018) North Sea deem the food-webs to be mature and resilient, compared to a global set of Ecopath models.
"Impacts on food-web" (pg. 6)	Safeguarding the Large Fish Indicator at levels above 0.3, and maintaining other, SSB based thresholds requires trade-offs in the multispecies MSYs (Stäbler et al. 2016).
"State of the Ecosystem: Food-webs" (pg. 12)	Flow from primary production through detritus into benthos is the dominant biomass flow in the (southern) North Sea (Stäbler et al. 2018).
"State of the Ecosystem: Productivity" (pg. 13)	Changes in system's productivity can have drastic effects on target stocks and yields (Stäbler et al., under review).

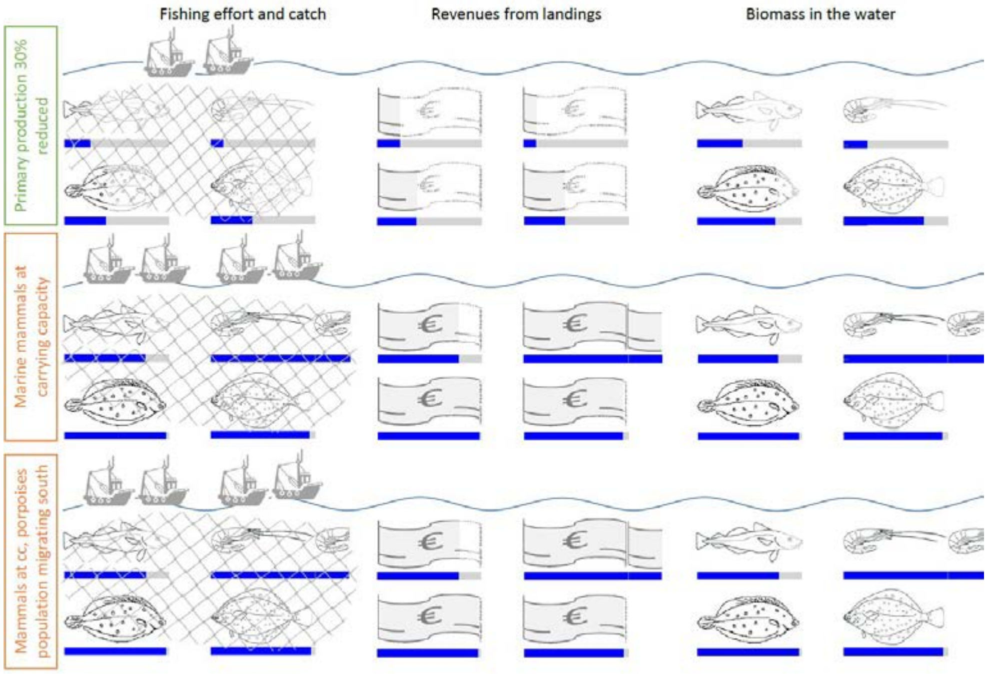


Figure 4.4.2.2: Southern North Sea Ecosim modelling results: Relative fishing efforts leading to multispecies MSY under changed ecosystem properties (30% reduced primary productivity, and marine mammal populations at carrying capacity); with respective catches, revenues from landings, and stock biomasses of cod, brown shrimp, plaice and sole (clockwise, starting top left) relative to baseline scenario. From Stäbler et al., under review.

1. Ecospace modelling of the southern North Sea

The Thünen Institute of Sea Fisheries is currently finalizing an Ecospace of the southern North Sea covering the ICES areas IV b and IV c. It is using the new spatial-temporal framework to dynamically implement habitat capacity maps for the majority of the functional groups. Studies on the effects of wind farms and designated marine protected areas are ongoing. This Ecospace has the potential to address several requirements for EOs, Advice and the MSFD. Consequences for the foodweb due to selective extraction of species will be analysed next to the identification of areas that are sensitive to change for commercial fish stocks and bycaught species. The effect of closed areas as alternative management measure to avoid the bycatch of certain species (i.e. choke species) under the landing obligation will be investigated. Additionally, the consequences of a reallocation of fishing effort due to windfarms and closed areas on indicators for e.g. biodiversity or abrasion can be evaluated. In the future IPPC scenarios will be implemented into the Ecospace model to test the effects of climate change on the ecosystem, the spatial distribution of fish stocks and the impact on spatial management.

Table 2: Potential contributions to the ICES Greater North Sea Ecoregion Overview by ongoing Ecospace modelling of the southern North Sea (IV b&c).

ICES Ecosystem Overview 2016	Potential contribution by southern North Sea EwE modelling
"Increase in the addition of new artificial hard substrate to the North Sea changed the biodiversity and productivity in local areas" (pg. 3)	Wind farms are implemented within sNoSe-Ecospace to test their effect on biodiversity within these areas
"Several of these elasmobranch species are now considered threatened or endangered by OSPAR and IUCN and are still caught as bycatch in fisheries" (pg. 3)	The effect of different spatial management options (e.g. closure of marine protected areas) on elasmobranch species are being tested
"Impact on foodwebs" (pg. 6)	Analysis of the effects of closed areas on the foodweb due to fishing effort reallocation
"Impact on foodwebs" (pg. 6)	Ongoing study of areas with high biodiversity that are sensitive to change
"Offshore wind farm development has started in the last decade with greater development planned for areas further offshore." (pg. 8) + "If the planned increase in power of wind farms … is established, the area occupied would be around 12 000 km^2, representing 1.6% of the total North Sea area" (pg. 9)	The effect of substrate loss due to artificial structures will be investigated as well as the impact of the non-fishing zones around these structures on commercially exploited species and their bycatch
"Over the last few decades, climate warming in the southern North Sea has been noticeably faster than in the northern North Sea" (pg. 14)	Different IPCC scenarios will be implemented to test the effect of climate change on the southern North Sea Ecosystem

4.4.3 Portuguese waters modelling in relation to Bay of Biscay and Iberian waters Ecosystem Overview

By Dorota Szalaj (University of Lisbon)

Modelling of Portuguese waters in the context of the Bay of Biscay and Iberian waters Ecosystem Overview, has been presented. Baseline static ecopath model, parameterized between 2006 and 2009 and developed by Veiga-Malta et al. (2018), was used to perform hindcast dynamic simulation between 1986 and 2017. Prior to the simulation, the ecopath model was adapted to year 1986. The model focuses mainly on pelagic component of the ecosystem because it was built with the objective to explain the drivers behind the Iberian sardine stock decline. The model was fitted to available time-series following the procedure proposed by Mackinson et al. (2009). It explained about 36% of variability in the data and the best fit model was achieved by including fishing, trophic effects and primary production anomaly as drivers. Because the analysis was focused on sardine, an improvement in the sardine fit, caused by each driver was quantified separately. The highest contributions for sardine fit improvement were obtained when fishing and trophic interactions were considered jointly, and here in contrary to the results related to the model treated as a whole, adding primary production anomaly did not improve the fit for sardine as it was a case for other species (e.g. rays, bogue, anchovy). These results aren't aligned with the literature that clearly linked sardine decline with environmental factors that affect sardine recruitment (Garrido et al. 2017; Malta et al. 2016). On the other hand, importance of trophic interactions and fishing as a drivers of sardine decline are also presented in the literature (Martins et al. 2013).

Considering the best fit model, few future projection scenarios, testing various levels of fishing mortality on sardine, have been performed. The results showed that by 2080 sardine biomass will recover up to the level from 1986 when fishing will maintain on current level or lower. Moreover, sardine biomass increase will be still observed even if fishing pressure will increase up to 50%. On the other hand, an increase of fishing mortality above 50% will impair sardine recovery and might even cause its collapse. The next step is a quantification of the impact that tested sardine fishing mortality scenarios might have on the ecosystem. Also, performing simultaneously the same simulation but with conventional stock assessment method will be an interesting avenue to explore, in order to see if ecosystem model results are aligned with the conventional stock assessment methods.

4.5 Other potential uses of EwE to inform ecosystem advice

4.5.1 Benefits of MPA networks in the Western Mediterranean Sea: a geographically-nested ecosystem modelling approach

By Marta Coll (ICM-CSIC)

In this presentation a geographically nested ecosystem modelling approach developed to assess the ecological and fisheries benefits of MPA networks in the Western Mediterranean Sea was shown. The study showed the implementation of the nested approach to quantify the benefits (to ecosystems and fisheries) of the establishment of MPA networks in the Western Mediterranean Sea. To develop the work, the Ecopath with Ecosim (EwE) foodweb modeling approach was used to develop spatial-temporal local, sub-regional and regional models representing areas with different levels of protection. For three Mediterranean MPAs, Cerbere-Banyuls, Cap de Creus and Medes Islands, nine models (three for each MPA) representing the three different management zones were developed: Fully Protected Area (FPA), Partial Protected Area, and Unprotected area. Then three models representing each MPA zone integrating the different management schemes were built. Afterwards, a sub-regional model including the three MPAs and their surroundings to describe the whole MPA network were constructed. Finally, a model covering the W Mediterranean included current general MPA dynamics. The nested modelling approach allowed to: (1) characterize the structure and functioning of MPA zones and identify differences between zones and between MPAs, (2) assess the regional effects of local MPAs, (3) quantify temporal changes, and (4) explore alternative MPA spatial configurations to promote fisheries sustainability in the region, accounting for stakeholders suggestions. Results highlighted the ecological importance of FPAs, although their benefits are local due to their small size. Current MPAs showed small differences with each other in terms of ecosystem structure and functioning. The study highlighted that a significant increase in the level of protection (and enforcement) is needed to get benefits on fisheries at the regional level. This study represents a baseline for the development of further management scenarios of MPA networks in the W Mediterranean and their assessment.

4.5.2 Incorporating fisher's knowledge AND uncertainty analyses into the development of ecosystem models

By Jacob Bentley (SAMS)

1. WKIrish: operationalizing ecosystem models for integrated ecosystem assessment of the Irish Sea

1.1. Ecopath

Under WKIrish, Ecopath with Ecosim (EwE) was used to construct a foodweb model of the Irish Sea Ecosystem representative of 1973, aiming to underpin the drivers of ecosystem change to inform integrated ecosystem assessment. The modelled foodweb includes 41 functional groups, ranging from detritus and plankton to seabirds and mammals, with a well-defined fish component. (Figure 4.5.2.1). 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. Diet information was also added based on knowledge provided during WKIrish4, where stakeholders designed individual foodwebs for cod, haddock, plaice, *Nephrops*, rays and whiting. We followed recommended best practice methods (Heymans et al., 2016) and ecological rules of thumb (Link, 2010) for ensuring 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, gillnets, pots, dredge, and longlines) which reflect those deemed most important by fishers during the WKIrish4 workshop. Landings and discards for 1973 were allocated to fleets using data from ICES and the Scientific, Technical and Economic Committee for Fisheries (STECF). For an in-depth description of the methods and parameters used to build the Irish Sea Ecopath model, see the published technical report (Bentley et al. 2018a).

1.2. Ecological indicators

The Ecopath model of the Irish Sea has been used to develop state indicators which reflect the structure and function of the foodweb (Bentley et al., 2018b). During this process we designed a new approach which incorporates diet uncertainty into the estimation of indicators, enabling stronger ecological inferences which are crucial to management (Figure 4.5.2.2).

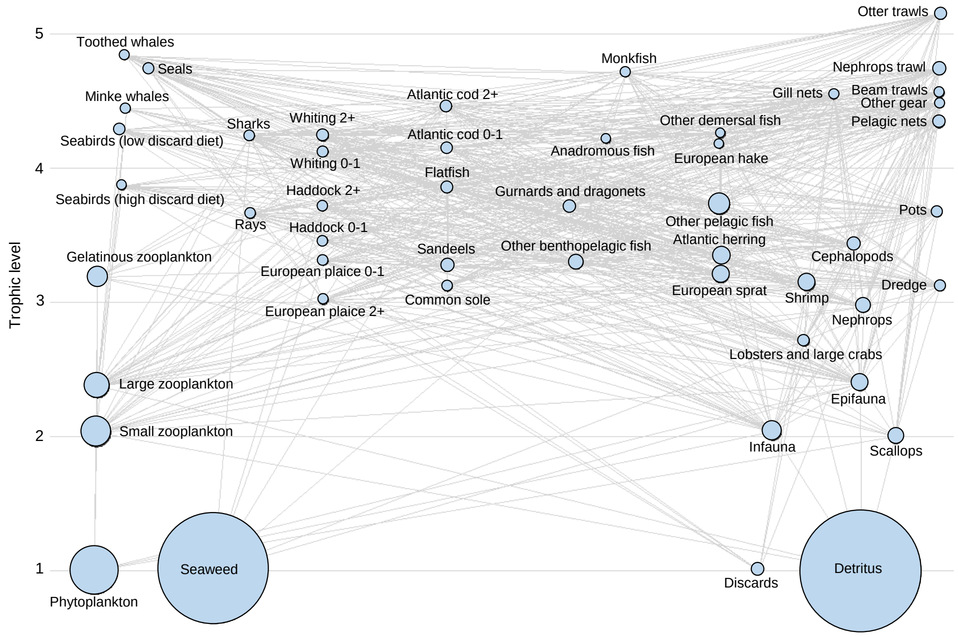


Figure 4.5.2.1. Energy flow and biomass diagram for the Irish Sea Ecopath foodweb model. Functional groups and fleets are represented by nodes, the relative size of which denotes their estimated biomass in the ecosystem in 1973. Lines represent the flow of energy and the y-axis denotes the trophic level.

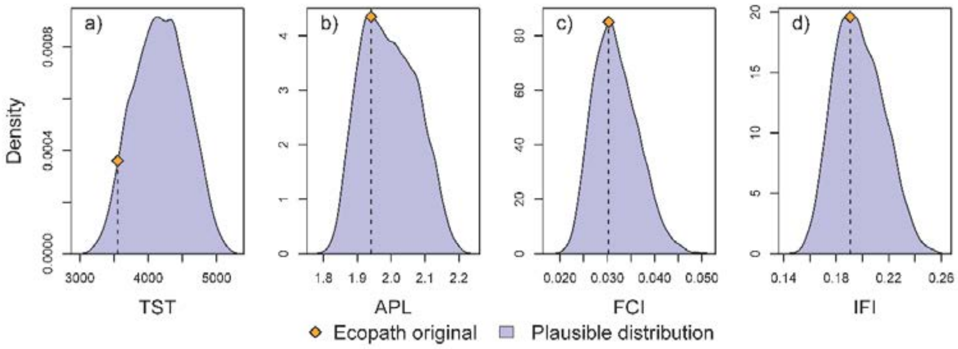


Figure 4.5.2.2. Probability density plots showing original estimates and distributions of foodweb indicators for the Irish Sea using data guided uncertainty: (a) Total system throughput (TST), (b) Average path length (APL), (c) Finns Cycling Index (FCI) and (d) Indirect Flow Intensity (IFI). Figure taken from Bentley et al., (2018b).

1.1. Ecosim

The Ecosim model of the Irish Sea runs from 1973 to 2016. 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 extent of the model were only available for three of the eight fleets: beam trawl, otter trawl, and *Nephrops* trawl. During WKIrish4 stakeholders provided effort trends for beam trawl, otter trawl, *Nephrops* trawl, pelagic net, gillnet, pot, dredge and longline fleets. 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 due to the magnitude of change they exerted on the system. Under the assumption that stakeholders' trends were more accurate than their suggested magnitude of change, trend magnitudes were adjusted using a Bayesian approach to find the magnitudes which led to better reconstructions of historic trends. Following this, the model performed best when driven by a combination of trends from data (beam, otter *Nephrops*) and stakeholders' knowledge (pots, pelagic. Gill, dredge, longline) (Figure 4.5.2.3).

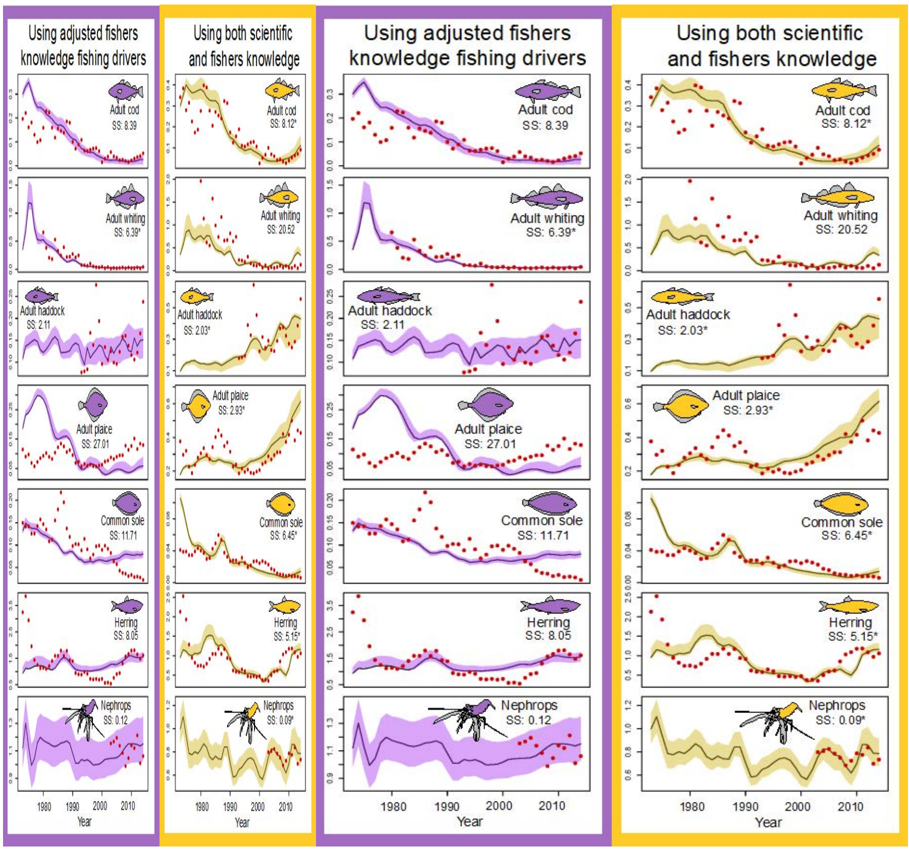


Figure 4.5.2.3. Biomass trends for the commercially important stocks in the Irish Sea EwE model. Solid lines indicate model predictions and dots represent observed data. Predictions are surrounded by 95% confidence intervals calculated using a Monte Carlo approach, generating 1,000 models within the range of plausible input estimates. Model predictions were generated using four sources of fishing effort data: 1) Scientific knowledge, 2) fishers' knowledge, 3) adjusted fishers' knowledge, 4) hybrid knowledge.

Through a fitting procedure the model estimates a primary production anomaly for phytoplankton to improve the statistical fit of simulated trends to observed data. The trend estimated for the Irish Sea model negatively correlates with the North Atlantic Oscillation Index (NAO).

1.1. Updates from WKIrish5

While the model in its current state is applying this environmental trend to phytoplankton to enact bottom-up change, hypotheses derived from environmental indicator analysis suggest the system is more likely driven by changes in secondary production. Work is therefore ongoing to ensure the direct impact of environmental change is applied in a realistic way. Through an external review of the models parameterization, recommendations were made for the alteration of a select few parameters (i.e. diets and production rates) prior to a key run assessment to be held in October 2019.

2. Ecosystem indicators to inform quota setting (stemming from WKIrish5-report in prep)

Ecosystem models quantify the cumulative impact of fishing and system productivity on stock trends, often concluding that it is a combination of both which drive stock dynamics. It would therefore be valuable to find ways to incorporate indicators of system productivity into the quota setting advice process. As discussed by WKIrish, ecosystem information could be used to suggest where to sit within the Fmsy range. For example, if the ecosystem indicator is in positive phase, and the ecosystem information suggests this will not have a negative impact on other stocks, the advice should be to remain in the upper limit of Fmsy. Whereas if the ecosystem indicator is in negative phase, the advice should be to remain in the lower limit of Fmsy as a precautionary approach (Figure 4.5.2.4).

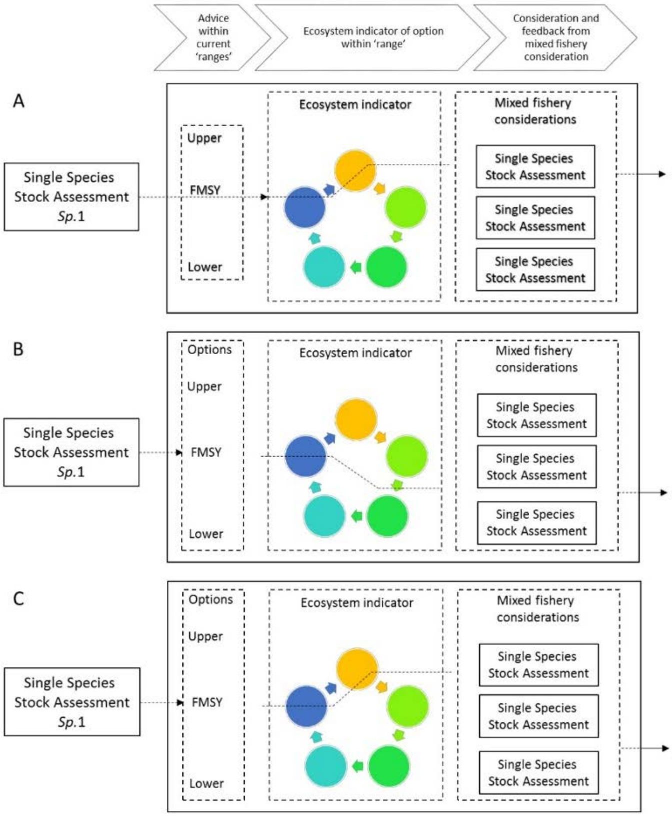


Figure 5.4.2.4. Ecosystem indicators to inform quota setting (figure credit: Mathieu Lundy, WKIrish): A: Ecosystem indicator suggests upper part of range and mixed fishery consideration supports that this with not have a negative impact on other stocks: keep advice in 'upper range'. B: Ecosystem indicator suggests lower part of range – should be used as a constraint in mixed fisheries assumptions: keep advice in 'lower range'. C: Ecosystem indicator suggests upper part of range but mixed fishery consideration suggest this would negatively impact other stocks: shift advice to 'lower range'.

4.5.3 Recent developments of EwE with special focus on Ecospace

By Jeroen Steenbeek

This presentation showed the most recent developments to the EwE software, with particular focus on spatial-temporal modelling with Ecospace. The recent introductions of the spatial-temporal data framework and the habitat foraging capacity model have turned Ecospace into an integrated, time-dynamic foodweb and species distribution model. Added flexibility in the consideration of Marine Protected Areas has improved the applicability of EwE for policy advice, as has the addition of consider system-wide impacts of parameter uncertainty through Ecosampler. Ecotracer, the contaminant tracing module of EwE, has been revamped and has seen a few new recent applications. Last, the addition of detailed discards management has enabled EwE to better address policy impacts, such as the common fisheries policy, onto marine foodwebs. Also presented was the recent integration of EwE into the Marine Spatial Planning Challenge 2050 serious game, where policy-makers become aware of possible ecological consequences of planned developments.

4.6 General remarks – current and further use of ecosystem models to support integrated advice

The focal point of the WK was the potential of using EwE models to inform ICES products such as the Ecosystem Overviews, as an integral part of the ecosystem advice. Several approaches and examples of using EwE were identified as useful to support IEA (see above), e.g. to inform quota setting (see WKIrish5), exploring trade-offs, MSFD indicators and supporting stakeholders' interactions. As agreed at the WK EwE allows quantification of links between activity-pressure and state relevant for (Figure 3) and interactive version of EO's. That could be done as a sensitivity analysis on external forcing on main pressures included in the model. In most cases main ecosystem pressures (relevant for foodweb dynamic) was identified at the existing EO's and bringing the EO's from fully descriptive to semi - quantitate. WKEWIEA identify that models, expert and required skills are available for most of ICES areas.

WGSAM could be a common platform, to develop models, on the other hand regional IEA group are the place where synthesis, analysis and model runs need to be performed and deliver information for EO's. However, at the operational level, EwE modelers does not establish yet thematic platform to work on specific EwE-EO's related issues i.e Expert Group' or series of WK, what would be required and recommended. It's possible to deliver quantification of links between activity-pressure and state within 3 years perspective but a number of conditions need to be fulfilled to accept model runs. WKEWIEA suggests that before using EwE models, the model quality protocol and key-runs need to be developed to implement Transparent Assessment Framework (TAF) and FAIR data principles in to publish models. Models for a number ICES ecoregions are already publish and described (in case of North Sea and Central Baltic ICES key runs exist). Right now, number of models exist as simulations of ecosystem dynamic, providing solid scientific results. Implementing model quality protocol and key-runs should improve reproducibility and transparency.

Because of EO's format …"will not include advice on management options and tradeoffs when meeting targets for state of the environment, as this would usually require a tailored, and often extensive, analysis in the main body of the advisory text" (WKECOVER), group supports progress towards the delivery of integrated advice as a next generation of integrated product ICES, not as a descriptive format of EO's, but in the direction where capacity of ecosystem models could be used to support IEA.

WKEWIEA identified and suggest steps to be done as follow:

1) Develop methods for using EwE as a modeling approach for Regional IEAs. Use existing ICES regional EwE models (as outline in the summaries by Serpetti, Stäbler,

Bentley, etc.) to inform Ecosystem Overviews. This work would be done by regional seas working groups/IEA groups.

2) Designate WGSAM as the review group for EwE models (and other ecosystem modeling approaches) for providing ecosystem information. WGSAM would ensure best practices for EwE models are being implemented and establish key runs.

3) Establish an EwE/Ecosystem Modeling workgroup that a) works with existing models and regional seas working groups/IEA groups to explore other options for informing ecosystem approaches to management and b)supports regional seas working groups/IEA groups in developing additional regional EwE/ecosystem models.

These recommendations are suggested for a long-term period. Recommendation 1 could take 2-3 years. After existing models had been refined and information from them tailored for Ecosystem Overviews, WGSAM would review these example cases to ensure the models were developed using best practices, best available science, and provide appropriate information for ecosystem overviews. When this has been established for existing models and the information taken up by appropriate ICES management bodies, WGSAM could then be designated as the review group for future models and updates to existing models (Recommendation 2). Once this process for using EwE models for informing Ecosystem Overviews is established, ICES could move forward with Recommendation 3.

Annex 1: List of participants

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Annex 2: Agenda

Final agenda for WKEWIEA

Monday 26th of November

13:00 Arrival of participants

13:15 Welcome word from Marta

13:30 Welcoming and presentation of the workshop, the agenda and the WK participants (Eider Andonegi)

14:00 Presentations of EOs by ICES secretariat (Iñigo Martinez): main goals and use for advice. Open discussion.

16:00 Coffee break

16:30 Presentation about idea of using EwE models for Advice - seating scene (Maciej Tomczak)

18:00 Closing the day

Tuesday 27th of November

09:00 Presentations on uses of modelling to inform ecosystem advice

- Villy Christensen: The use of EwE models for advice
- Chiara Piroddi: A modelling framework for the Mediterranean Sea ecosystem in support of EU policies
- Howard Townsend: Using EwE for management issues – the US example

11:00 Coffee break

11:30 Continuation of presentations

- Sheila Heymans: Enhancing Europe's capability in marine ecosystems modelling for societal benefit
- Rudi Voss: How to use using economic aspect for IEA/ICES advice
- Andrew Kenny: Qualitative modelling for assessing cumulative impacts on the North Sea

13:00 Lunch break

14:00 Discussions and report writing

16:00 Coffee break

18:00 Closing the day

Wednesday 28th of November

09:00 Presentations on uses of modelling to inform ecosystem advice

- Natalia Serpetti: Western Coast of Scotland modelling in relation to Celtic Seas

Ecosystem Overview

- Moritz Stäbler and Miriam Püts: Southern North Sea modelling in relation to

  North Sea Ecosystem Overview

- Dorota Szalaj: Portuguese waters modelling in relation to Bay of Biscay and Iberian

  waters Ecosystem Overview

11:00 Coffee break

11:30 Continuation of presentations

- Marta Coll: Benefits of MPA networks in the Western Mediterranean Sea: a geographically-nested ecosystem modelling approach
- Jacob Bentley: Incorporating Fisher's Knowledge and Uncertainty Analyses into the Development of Ecosystem Models
- Jeroen Steenbeek: A more generic overview of recent developments in Eco-space

13:00 Lunch break

14:00 Discussions and report writing

16:00 Coffee break

16:30 Discussions and report writing

18:00 Closing the day

19.30 Meeting dinner

Thursday 29th of November

09:00 Summary discussion and subgroup work

11:00 Coffee break

11:30 Subgroup work

13:00 Lunch break

14:00 Subgroup work and report writing

16:00 Coffee break

16:30 Report writing

18:00 Closing the day

Friday 30th of November

09:00 Wrap up and general conclusions

11:00 Coffee break

11:30 Wrap up and general conclusions

13:00 Meeting closure

Annex 3: WKEWIEA2 terms of reference for the next meeting (Draft)

The second **Workshop on operational EwE models to inform IEAs (WKEWIEA2)**, chaired by Maciej T. Tomczak (Sweden) and Eider Andonegi (Spain), Maria Angeles Torres (Spain) will meet in Stockholm. 2019 (data and time need to be agreed) to:

a) Perform practical examples of integrating information from existing EwE models from ICES areas for next generations of Ecosystem Overviews

b) Perform trial version of using EwE models at IEA framework to support EBFM

c) Discuss and shape quality protocol and key run requirements for EwE models used for policy exploration and advice frameworks.

Annex 4: Recommendations

RECOMMENDATION	ADRESSED TO
1. Develop key-run protocol for using EwE models for IEAs and advice	WGSAM (WGIPEM)
2. Review approach and provide feedback	ACOM/SCICOM + IEASG
3. IEA regional groups adopt EwE and equivalent models into their ToRs	ACOM/SCICOM + IEASG and IEA regional groups
4. Establish next workshop(s) for Intercomparability of EwE models for IEAs	ACOM/SCICOM
5. Provide advice about indicators from EwE modesl to be use in IEAs for the state of different ecosystem components	WGBIODIV
6. Guidelines about the visualization of the trade-offs	ICES secretariat

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Annex 6: Acknowledgements

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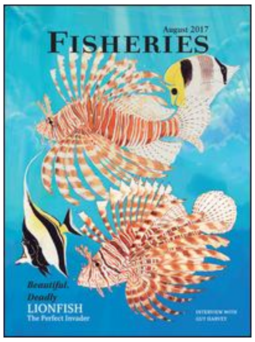

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FEATURE

An Ecosystem-Based Approach to Evaluating Impacts and Management of Invasive Lionfish

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Species invasions in marine ecosystems pose a threat to native fish communities and can disrupt the food webs that support valuable commercial and recreational fisheries. In the Gulf of Mexico, densities of invasive Indo-Pacific Lionfish, *Pterois volitans* and *P. miles*, are among the highest in their invaded range. In a workshop setting held over a 2-week period, we adapted an existing trophic dynamic model of the West Florida Shelf, located in the eastern Gulf of Mexico, to simulate the lionfish (both species) invasion and community effects over a range of harvest scenarios for both lionfish and native predators. Our results suggest small increases in lionfish harvest can reduce peak biomass by up to 25% and also that reduced harvest of native reef fish predators can lead to lower lionfish densities. This model can help managers identify target harvest and benefits of a lionfish fishery and inform the assessment and management of valuable reef fish fisheries.

INTRODUCTION

Red Lionfish *Pterois volitans* and Devil Firefish *P. miles* (hereafter, collectively referred to as "lionfish") are native to the Indo-Pacific and have become established on coral reefs, artificial reefs, mangroves, seagrasses, and hard-bottom habitats throughout the temperate and tropical western Atlantic, including the Caribbean Sea and Gulf of Mexico (GOM; Schofield 2010). Traits that may contribute to their invasive success (reviewed in Morris and Whitfield [2009] and Côté et al. [2013]) include fast growth, young age at maturity, high fecundity and egg survival, generalist diet, habitat versatility, unique feeding strategy, prey naïveté (Black et al. 2014; Anton et al. 2016), venomous spines, and defensive antipredator behavior. Where lionfish have become established, they have caused large reductions in the abundance and richness of native reef fish communities (Green et al. 2012; Albins 2015; Dahl et al. 2016a), with potential impacts to reef fishes over large geographic areas (Ballew et al. 2016), prompting national and regional strategies for their control.

Since invading the GOM in 2010, lionfish populations have grown exponentially through 2015 and in some areas are at the highest densities of their invaded range (Dahl and Patterson 2014; Switzer et al. 2015; U.S. Geological Survey 2015). In response, management agencies are supporting development of lionfish fisheries through marketing campaigns and by encouraging recreational and commercial fishers to harvest lionfish in an effort to reduce their population size and possibly mitigate local impacts to native species. Lionfish removal efforts have demonstrated localized benefits to small fishes at reef sites in the Caribbean (Frazer et al. 2012; De León et al. 2013; Green et al. 2014). However, the effects of invasive lionfish on regional food webs that also include exploited fish stocks have not been evaluated. Further, no previous studies have explored how changes in management of native reef fishes (e.g., reductions in fishing mortality) could potentially influence lionfish biomass and impacts to food webs.

A modeling workshop was held in July 2015 with the purpose of gaining a better understanding of the effects of invasive lionfish on native reef fish communities in the GOM and to evaluate strategies that mitigate those impacts. Workshop participants consisted of graduate students, scientists, and stakeholders from over a dozen different universities, government agencies, and nongovernmental organizations. During the 2-week workshop, we adapted an existing trophic dynamic model of the West Florida Shelf (WFS; Chagaris et al. 2015), located in the eastern GOM, to simulate the lionfish invasion and community effects over a range of harvest scenarios for lionfish and native reef predators. Our objectives were to (1) estimate the effects of lionfish on the native reef fish community of the WFS, (2) assess the efficacy of direct lionfish harvest to mitigate those impacts, and (3) evaluate whether management strategies for commercially and recreationally important reef fishes (e.g., groupers and snappers) have an effect on lionfish densities. A public seminar was given as part of the workshop to demonstrate our findings and understand stakeholder perceptions on lionfish and the development of fisheries for them.

MATERIALS AND METHODS

Including Lionfish in the WFS Ecopath Model

We modified an existing Ecopath with Ecosim (EwE; Christensen and Walters 2004) model of the WFS (Chagaris et al. 2015) to include lionfish. The existing model consisted of 70 total biomass pools, 43 of which were fish, and focused on important predatory reef fishes (e.g., groupers and snappers) that were modeled as multiple age classes. The model also included mammals, birds, invertebrates, primary producers, and detritus, as well as 14 fishing fleets. The spatial domain of the model extends from the Florida Panhandle south to, but excluding, the Florida Keys and from shore to the 250-m isobath. This area covers approximately 170,000 km^2 and encompasses the entire eastern portion of the GOM. The model was calibrated to observed abundance and catch from 1950 to 2009 and driven by historical estimates of fishing effort, fishing mortality, and primary production. This WFS model was previously used to quantify the trophic impacts of reef fish harvest policies (Chagaris et al. 2015), identify tradeoffs in conflicting management objectives, and evaluate size and placement of marine protected areas on the WFS (Chagaris 2013). Additional details on model specifications and input parameterization are described in Chagaris et al. (2015).

Lionfish were added to the model as two age stanzas (juveniles 0–6 months and adults 6+ months) in order to accommodate ontogenetic shifts in diet and maturity that occur around 6 months or approximately 150 mm total length (Morris and Akins 2009; Munoz et al. 2011; Dahl and Patterson 2014) and also to coincide with the size at which they become vulnerable to harvest by spearfishing (Barbour et al. 2011). Adult lionfish density estimates were derived from a Southeast Area Monitoring and Assessment Program (SEAMAP) trawl survey on the WFS that targeted non-reef habitat (Switzer et al. 2015) and a remotely operated vehicle (ROV) survey of natural and artificial reef sites on the northern WFS and northern GOM (Dahl and Patterson 2014; Dahl et al. 2016b). A habitat-adjusted estimate of lionfish biomass (*B*; mt/km^2, Table 1) was developed by averaging the values from both surveys, each weighted by the proportion of the shelf area classified as reef (7% based on a U.S. Geological Survey rugosity map; Robbins et al. 2010) and non-reef. Lionfish were first detected in 2010, but we initialized their biomass in Ecopath using 2011 densities (the first year of the ROV study) under the assumption that lionfish were still in the early establishment phase of the invasion. A biomass accumulation rate for lionfish (*BA*) was calculated as $(B2012 - B2011)/B2012$ to account for the change in biomass that occurred during the Ecopath base year of 2011 and averaged for the trawl and natural reef habitat types (Table 1).

Lionfish consumption (*Q*) was derived from a bioenergetics model that estimated daily consumption rates (g/g/day) as a func-

Table 1. Biomass density estimates (g/m^2) from SEAMAP trawls conducted on the West Florida Shelf and an ROV study on natural reefs in the Northern Gulf of Mexico. Habitat-adjusted biomass was calculated by averaging the densities from the trawl and natural reef ROV surveys and weighting by the percentage coverage of each habitat type, 93% non-reef (i.e., trawl) and 7% natural reef. Biomass accumulation (BA) was calculated as $(B_{2012} - B_{2011})/B_{2012}$ and averaged for the trawl and natural reef surveys.

Year	SEAMAP trawl density	Northern Gulf of Mexico ROV natural reef	Habitat-adjusted biomass	Average *BA*
2010	8.01227E−07			
2011	0.0001	0.0183	0.0014	0.80
2012	0.0004	0.2529	0.0181	0.83
2013	0.0064	0.9631	0.0734	0.44
2014	0.0149	1.4124	0.1127	

Table 2. Consumption and mortality rates across size classes observed in the SEAMAP trawl survey. Consumption, Q, was calculated as a function of body mass and assuming an ambient temperature of 24°C using the equations in Cerino et al. (2013). Natural mortality, M, was estimated using the Lorenzen (1996) equation based on body mass. Estimates of Q and M for juveniles (≤150 mm TL) and adults (>150 mm TL) were calculated by averaging across size bins weighted by the biomass (Numbers × Weight) in each size bin. The daily consumption rate estimates were multiplied by 365 and input to the model as annual rates.

Length bin (mm TL)	Bin mid (mm TL)	Total *n*	Body weight (g)	Biomass (g)	Q ($g\ g^{-1}\ d^{-1}$)	M (y^{-1})
50–75	62.5	8	4	36	0.15	2.34
76–100	87.5	13	12	153	0.10	1.74
101–125	112.5	24	24	585	0.07	1.39
126–150	137.5	50	43	2,175	0.05	1.17
151–175	162.5	107	70	7,541	0.04	1.01
176–200	187.5	124	107	13,214	0.04	0.89
201–225	212.5	112	153	17,134	0.03	0.80
226–250	237.5	93	211	19,619	0.03	0.72
251–275	262.5	98	282	27,605	0.02	0.66
276–300	287.5	90	366	32,972	0.02	0.61
301–325	312.5	55	466	25,638	0.02	0.57
326–350	337.5	26	582	15,137	0.02	0.53
351–375	362.5	12	716	8,589	0.01	0.50
376–400	387.5	2	868	1,736	0.01	0.47
401–425	412.5	4	1,040	4,158	0.01	0.44
Juveniles					21.90	1.26
Adults					8.41	0.66

tion of body mass and temperature (Cerino et al. 2013). Using the bioenergetics model applied to size structure from the SEAMAP trawl survey and assuming a constant ambient temperature of 24°C (water column average over the WFS predicted by the Hybrid Coordinate Ocean Model [Chassignet et al. 2007] Gulf of Mexico 1/25° analysis), we estimated a population-wide annual consumption rate for adult and juvenile stanzas (Q/B; Table 2). Instantaneous natural mortality of lionfish (M) was estimated using the Lorenzen (1996) function based on body mass. Consumption and mortality were averaged across size bins for juveniles (<150 mm total length [TL]) and adults weighted by the biomass in each size bin (Table 2). Growth and maturity parameters (the von Bertalanffy growth coefficient K and the ratio of weight at maturity to maximum weight) were available from life history studies of lionfish from the southeast United States (Barbour et al. 2011). Preliminary estimates suggested that these parameters are comparable on the WFS (Dahl and Patterson, unpublished data).

Diet compositions for adult and juvenile lionfish were assimilated from eight different assessments conducted throughout their invaded range (Tables 3 and 4). Cannibalism by adults on juveniles has been documented in multiple systems, including the northern GOM (Valdez-Moreno et al. 2012; Côté et al. 2013; Dahl et al. 2017); therefore, juvenile lionfish was included as a prey item of adult lionfish. To generate the diet composition input for Ecopath, lionfish prey items were assigned to model groups in Table 4, summed, and converted to proportion diet (see supplemental information for full list of species groupings). The diet compositions were then averaged across studies and weighted by the number of non-empty stomachs in each study. The remaining portion of unidentified prey was distributed proportionately to other model groups within taxonomic hierarchy for input into the model (Table 4).

Simulating the Lionfish Invasion and Harvest Scenarios in Ecosim

There are several approaches to simulating species invasions with EwE (see Langseth et al. 2012). In this study, the invasion was modeled with Ecopath base lionfish biomass at low levels and an artificial fishery that is set to 0 in Ecosim to initiate the invasion. In Ecopath, landings of adult lionfish were entered such that fishing mortality (F) was equal to adult M of 0.66/year. The Ecopath production rate (P/B), also the total mortality (Z), was then doubled ($Z = 2 * M$). The model was configured in this way to elicit a biomass increase of lionfish in Ecosim at the beginning of the simulation period, so that when fishing was removed the population was changing according to M ($Z = M$ when $F = 0$). This method initializes the model with a realistic starting biomass of lionfish that does not create mass imbalance and facilitates simple exploration of harvest strategies by adjusting fishing effort, which functions as a multiplier on fishing mortality.

We explored multiple Ecosim scenarios to investigate how lionfish removals and reef fish management strategies might influence lionfish densities and their effects on native fishes. All scenarios were run for 30 years beginning in 2011. In Ecosim, the predator–prey functional response is modeled based on foraging theory, which states that predator–prey interactions are restricted to spatial and temporal arenas (Ahrens et al. 2012). The most sensitive parameters in Ecosim models are the vulnerability parameters, v_{ij}, which describe the exchange rates of prey i from not vulnerable states into vulnerable foraging "arenas," where they can be consumed by predator j. The v_{ij} parameters control the amount of prey biomass available for consumption and are input in Ecosim as multipliers on Ecopath base predation mortality rates ($M2_{ij}$) to represent the maximum possible predation mortality rate ($M2_{max}$) that can be exerted on a prey item at high predator biomasses. For this reason, we also refer to the v_{ij} parameters as "predation rate limits" in the invasion scenarios. The v_{ij} parameters must be greater than or equal to 1, with low values restricting flow into the vulnerable state, which thereby

Table 3. Summary of diet studies of lionfish used to develop the diet composition input into the Ecopath model. TL = total length, SL = standard length, V = volume, *N* = number, *M* = mass.

Location	Habitat type	Size	*N*	Units	Top 10 prey items	Study
Gulf of Mexico–north central	Natural and artificial reefs	67–377 mm TL	1,224	M	Synodontidae, *Centropristis ocyurus*, Pomacentridae, *Chromis scotti, Rhomboplites aurorubens, Halichoeres bathyphilus, Apogon pseudomaculatus, Stegastes fuscus, Trachurus lathami,* Blenniidae	Dahl and Patterson (2014)
Bahamas	Reefs, mangroves, man-made canals	62–424 mm TL	699	V	Unidentified fish, unidentified shrimp, *Pseudupeneus maculatus, Gramma loreto, Chromis multilineata, Apogonidae, Clepticus parrae, Halichoeres garnoti, Stegastes variabilis, Coryphopterus personatus/hyalinus*	Morris and Akins (2009)
Southeast United States–North Carolina	Hard-bottom reef	150–350 mm TL	183	V	Haemulidae, Serranidae, Scaridae, Crustacea, Carangidae, Blenniidae, Labridae, Pomacentridae, Bothidae, Monacanthidae	Munoz et al. (2011)
Caribbean–Mexico	Coral reef	20–330 mm TL	157	N	Decapoda, *Halichoeres garnoti, Thalassoma bifasciatum, Pterois volitans, Stomatopoda, Coryphopterus venezuelae, C. tortugae,* Lythrypnus, *Sparisoma aurofrenatum,* Euphasiacea	Valdez-Moreno et al. (2012)
Bahamas–New Providence	Reef	122–372 mm TL	130	N	*Coryphopterus personatus, Coryphopterus eidolon, Chromis cyanea, Thalassoma bifasciatum, Stegastes partitus, Coryphopterus glaucofraenum, Synodus synodusa, Clepticus parrae, Apogon townsendi, Coryphopterus bol*	Côté et al. (2013)
Bahamas–Abaco Island	Back reef	60–208 mm SL	122	V	*Stegastes leucostictus, Halichoeres bivittatus,* Scaridae, Haemulidae*, Malacoctenus macropus, Thalassoma lucasanum, Abudefduf saxatilis, Bodianus rufus, Mithrax spp.,* Alpheidae	Layman and Allgeier (2012)
Gulf of Mexico–West Florida	Non-reef habitat	74–156 mm SL	52	V	Actinopterygii, Penaeidae, *Metapenaeopsis* sp., *Sicyonia* sp., *Processa* sp., Callianassidae, shrimp, *Tozeuma serratum, Periclimenes pedersoni*, Squilloidea	FWC unpublished data
Southeast United States–Florida Bay	Hard-bottom	95–330 mm TL	32	N	Unidentified teleost, Gobiidae, Palaemonidae, Haemulon, Lutjanidae, Hippolytidae, *Lysmata* spp., unidentified shrimp, *Coryphopterus glaucophraenum*	Faletti and Ellis (2013)

limits consumption and prevents any biomass gains in the predator. High v_{ij} values imply strong top-down effects and can lead to dynamic instability in Ecosim models. To simulate a population increase of an overexploited or invasive species with a low initial biomass and low $M2_{ij}$ on their prey, the v_{ij} parameters must be quite high in order for consumption, and therefore biomass, of the predator to increase.

In the first scenario, we simulated biomass dynamics without the lionfish invasion (the no invasion scenario). In this scenario, lionfish are still present in the model but are held at the early establishment phase (i.e., at Ecopath base 2011 biomass) by applying a combination of high lionfish F and low vulnerability parameters. During the no invasion simulation, lionfish fishing mortality remained at Ecopath base ($F = M$) and the vulnerability parameters of their prey were set to a minimum of 1.0 in order to prevent any increases in consumption that in turn prevents any gains in biomass thereby suppressing the invasion. Because groups are increasing and decreasing in the no invasion simulation, this scenario was used as the point of reference to compare community effects of the lionfish invasion scenarios.

Next, we established a baseline invasion scenario in which fishing mortality of lionfish was equal to 0, and lionfish vulnerability parameters were set so that the maximum possible predation mortality rate by lionfish on each of their prey at maximum lionfish biomass does not exceed half of M for each prey ($M2_{max} = 0.5M$). For example, when lionfish reach carrying capacity in the invasion scenarios the maximum possible predation mortality rate by lionfish on a prey item with $M = 0.8$/year would be 0.4/year. We arrived at the $M2_{max} = 0.5M$ baseline setting by comparing the predicted lionfish biomass with observed relative abundance trends from 2011 to 2014. Sensitivity runs were conducted for all lionfish harvest scenarios where $M2_{max}$ by lionfish ranged from $0.25M$ to M of each prey item.

We then simulated the effect of various harvest scenarios on lionfish biomass by modifying fishing effort for the lionfish fleet, beginning in 2015. In Ecosim, fishing effort is relative and functions as a multiplier on the Ecopath fishing mortality rates so that a doubling of effort results in a doubling in Ecopath F for all species captured by the fleet. Therefore, we refer to the relative effort parameter as a fishing mortality multiplier (F_{mult}) that was used to simulate the lionfish harvest scenarios. For lionfish, F_{mult} was increased from 0 (the baseline invasion scenario) to 2.0 in increments of 0.1, leading to fishing mortality rates of lionfish ranging from $F = 0$ to $F = 1.32$/year. For all other species, fishing mortality remained at Ecopath base levels ($F_{mult} = 1$), which are representative of the 2009–2011 time period and validated against stock assessments where available (Chagaris et al. 2015).

Lastly, we simulated the lionfish invasion under alternative harvest scenarios of native predator reef fishes, beginning in 2015. This was done by manipulating the F_{mult} (i.e., the fleet ef-

Table 4. Ecopath input parameters for lionfish and their prey items. *B* = biomass (mt/km²), *Z* = instantaneous total mortality, *F* = instantaneous fishing mortality, *M* = instantaneous natural mortality, *Q/B* = consumption rate, *DC* = proportion of diet, *M2* = predation mortality rate by lionfish, *V* = vulnerability parameters that controls predation rate limits ($M2_{max}$) where base input value is equal to 0.5 * *M/M2* of each prey.

Group name	*B*	*Z*	*F*	*M*	*Q/B*	DC_{juv}	DC_{adult}	$M2_{juv}$	$M2_{adult}$	V_{juv}	V_{adult}
Red Snapper age 0–1	1.0E−03	2.00	0.04	1.96	21.63		<0.01		6.2E−03		1.6E+02
Vermilion Snapper	9.0E−03	0.86	0.46	0.36	6.29		0.07		9.5E−02		1.9E+00
Other snapper	1.9E−01	0.63	0.30	0.31	5.77		0.02		9.4E−04		1.6E+02
Triggerfish	5.5E−03	0.89	0.42	0.42	5.50	<0.01		3.2E−05		6.6E+03	
Black Sea Bass	1.2E−02	1.12	0.08	1.03	4.75	0.03	0.06	4.0E−03	6.4E−02	1.3E+02	8.0E+00
Reef carnivores	9.0E−01	1.32	0.01	1.31	5.89	0.25	0.27	4.3E−04	3.5E−03	1.5E+03	1.8E+02
Reef omnivores	4.0E−01	1.98	<0.01	1.98	8.26	0.26	0.29	9.8E−04	8.6E−03	1.0E+03	1.1E+02
Coastal piscivores	1.0E−01	0.71	0.21	0.48	4.40	0.01	0.01	7.7E−05	9.2E−04	3.1E+03	2.6E+02
Large coastal carnivores	4.3E−01	0.92	0.07	0.84	5.66	<0.01	<0.01	6.2E−06	9.1E−06	6.8E+04	4.6E+04
Small coastal carnivores	5.8E−01	1.76	0.01	1.76	7.61	0.03	0.11	7.6E−05	2.4E−03	1.2E+04	3.7E+02
Coastal omnivores	7.0E−01	2.10	0.01	2.09	10.39		<0.01		1.4E−05		7.4E+04
Sardine/herring/scad	1.7E+00	2.20	0.03	2.20	9.25	0.14	0.05	1.2E−04	3.6E−04	9.1E+03	3.0E+03
Anchovies/silversides	4.8E−01	3.20	<0.01	3.25	13.81		<0.01		7.0E−05		2.3E+04
Squid	3.2E−01	2.67	<0.01	2.80	16.64		0.01		2.6E−04		5.5E+03
Shrimp	9.1E−01	2.66	0.02	2.64	19.20	0.23	0.09	3.9E−04	1.2E−03	3.4E+03	1.1E+03
Lobsters	3.5E−02	1.00	0.11	0.87	8.20	<0.01	<0.01	2.1E−04	5.0E−04	2.1E+03	8.7E+02
Crabs	5.1E−01	1.80	0.04	1.75	9.35	0.01	0.01	3.0E−05	1.4E−04	2.9E+04	6.3E+03
Octopods	1.0E−01	3.10	<0.01	3.09	11.97		<0.01		6.7E−05		2.3E+04
Stomatopods	9.9E−01	1.34		1.34	11.15	0.01	<0.01	1.5E−05	3.8E−05	4.6E+04	1.8E+04
Echinoderms/gastropods	1.9E+01	2.60		2.58	9.89	<0.01	<0.01	9.7E−08	4.1E−07	1.3E+07	3.1E+06
Small mobile epifauna	1.2E+01	4.76		4.76	27.14	0.02	<0.01	2.9E−06	3.9E−06	8.1E+05	6.2E+05
Mesozooplankton	6.7E+00	10.60		10.62	57.67		<0.01		1.1E−08		4.8E+08
Carnivorous zooplankton	1.1E+01	8.70		8.73	34.80	<0.01		1.6E−07		2.7E+07	
Juvenile lionfish	5.8E−05	1.26	0.00	1.26	26.35		<0.01		1.0E−01		6.3E+00
Adult lionfish	1.4E−03	1.32	0.66	0.66	8.45						

forts) of the recreational private boats, recreational charter boats, recreational head boats, commercial vertical lines, and commercial bottom longline fleets, which have catch largely composed of native reef fishes. Using the baseline invasion scenario ($M2_{max}$ = 0.5*M* and lionfish F_{mult} = 0), we simulated lionfish biomass under scenarios ranging from no fishing (F_{mult} = 0) on reef predators to a doubling of Ecopath base 2009–2011 fishing mortality rates on reef predators (F_{mult} = 2.0) by increments of 0.25. In total, we conducted 176 invasion scenarios to cover a range of lionfish harvest efforts, native predator abundances, and predation rate limits (i.e., 21 lionfish harvest scenarios × 8 $M2_{max}$ scenarios + 8 reef fish harvest scenarios).

RESULTS

Simulated Lionfish Biomass Trajectories

Simulated lionfish biomass followed the typical stages of a biological invasion and with good agreement to observed relative indices of abundance over the first 4 years (Figure 1). An establishment period occurred during the first 2 years (2011–2012) followed by several years of exponential growth (2013–2018) before reaching equilibrium around 2025. Terminal adult lionfish biomass was 0.305 mt/km², which is 2.7 times higher than 2015 prediction of 0.114 mt/km² and 218 times higher than the initial 2011 input estimate (Figure 1). Biomass trajectories were sensitive to the assumptions about predation rate limits. When maximum possible predation mortality by lionfish ($M2_{max}$) was capped at low levels, relative to each prey's own natural mortality rate, lionfish consumption was limited and biomass increases were far lower than observed. With high predation rate limits, lionfish biomass was predicted to increase more sharply but then overshoot carrying capacity and decline slightly. The fits to observed relative indices of abundance suggest moderate predation rate limits, in which lionfish predation could account for up to 50% of the natural mortality of its prey (Figure 1).

To maintain lionfish at projected 2015 biomass, a fishing mortality rate equal to *M* of 0.66/year (F_{mult} = 1) would need to be exerted on the adult population each year (Figure 2). Increasing lionfish *F* from 0 to 0.066/year (F_{mult} = 0.1) resulted in a terminal biomass of 0.261 mt/km², a 14% decline from the baseline inva-

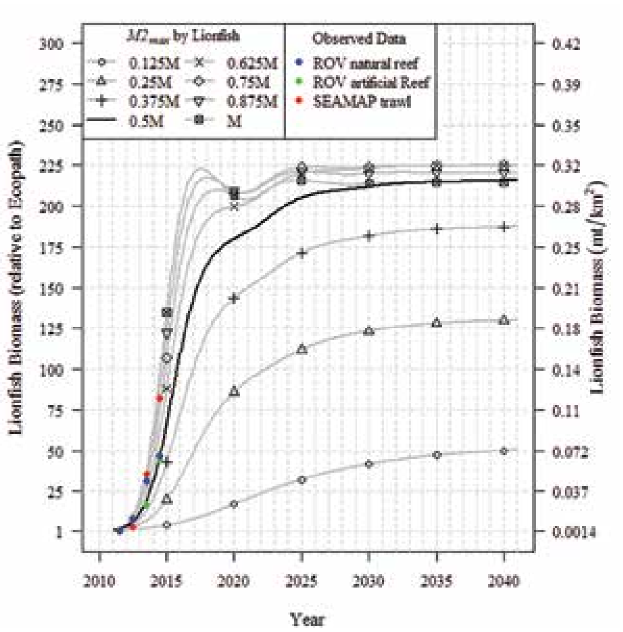

Figure 1. Simulated biomass of adult lionfish from 2011 to 2040 under alternative assumptions about maximum predation mortality rate limits ($M2_{max}$) relative to each prey's own natural mortality rate (M). The baseline invasion scenario is indicated by the solid black line where $M2_{max}$ is equal to half M for each prey. Observed abundance estimates were rescaled to the 2011 Ecopath base biomass for adult lionfish.

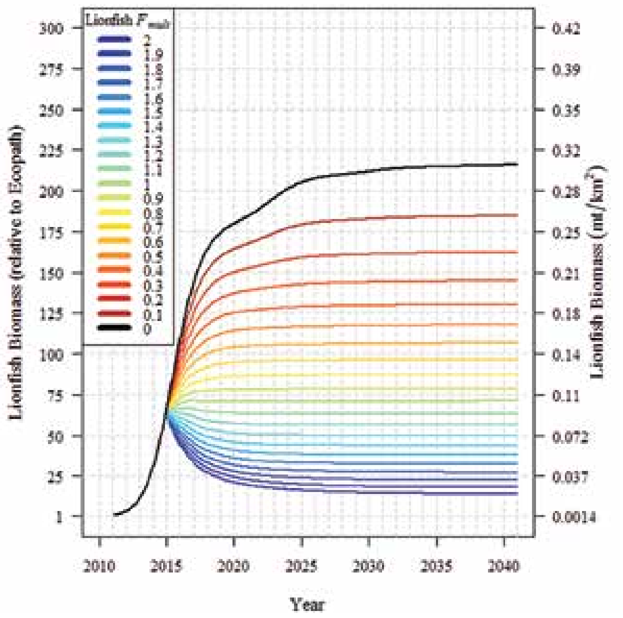

Figure 2. Simulated lionfish biomass from 2011 to 2040 under various levels of fishing mortality (F) on adult lionfish beginning in 2015. Fishing mortality is expressed as a multiplier (F_{mult}) on the Ecopath F value that was set equal to lionfish M of 0.66. The baseline invasion scenario (with $M2_{max}$ = 0.5M) is the black line where F = 0.

sion scenario that had no lionfish harvest. Increasing F further to 0.132/year (F_{mult} = 0.2) led to a terminal biomass of 0.229 mt/km^2, which is 25% lower than the no-harvest baseline scenario. This indicates that even relatively small increases in fishing mortality can lead to rather large declines in lionfish densities. Harvest of native predators also had an effect on the simulated lionfish biomass (Figure 3). At one extreme, shutting down fishing on native species (F_{mult} = 0) resulted in a terminal lionfish biomass of 0.242 mt/km^2, a 20% decrease from the baseline scenario with Ecopath reef fish harvest rates and $M2_{max}$ = 0.5M. Conversely, doubling the fishing pressure on native species (F_{mult} = 2) led to a terminal biomass of 0.359 mt/km^2 that is 17% higher than the baseline scenario. In reality, if any changes to future reef fish harvest occur, they are likely to be very modest (i.e., no more than ±25%) and could lead to lionfish biomass densities between 0.297 and 0.319 mt/km^2 at F_{mult} of 0.75 and 1.25, respectively, or approximately ±5% of baseline terminal biomass.

Community Effects of Lionfish

The most common prey of adult and juvenile lionfish were small-bodied reef omnivores (e.g., Acanthuridae, Pomacanthidae, and Pomacentridae), reef carnivores (e.g., Haemulidae, Holocentridae, Labridae, and Sparidae), and shrimp (Tables 3 and 4). Strong negative effects were predicted for these groups when there was no harvest of lionfish, and this effect was magnified when predation rate limits ($M2_{max}$) were high (Figure 4). Black Seabass *Centropristis striata* was strongly affected by lionfish (Figures 4 and 5) despite contributing to just 3% and 6% of juvenile and adult lionfish diets, respectively (Table 4). Because biomass of Black Sea Bass is low compared to other lionfish prey items, these small contributions to the diet of lionfish result in rather high predation mortality rates in Ecopath (Table 4). Impacts were negative and more modest for other key fishery species including Red Snapper *Lutjanus campechanus*, Gag Grouper *Mycteroperca microlepis*, Red Grouper *Epinephelus morio*, Black Grouper *Mycteroperca bonaci*, and Greater Amberjack *Seriola dumerili* (Figure 4).

The lionfish invasion was predicted to have cascading effects on the benthic invertebrate community. Declines in biomass of reef carnivores and reef omnivores led to increases in squid, crabs, octopods, stomatopods, echinoderms and gastropods, sessile epibenthos, small infauna, and small mobile epifauna (Figure 4). As a result, respective biomass increases of 7% and 11% were predicted for Gray Triggerfish *Balistes capriscus* and tilefishes (*Lopholatilus chamaeleonticeps*, *Caulolatilus chrysops*, *C. cyanops*, and *C. intermedius*; Figure 4) that feed predominately on invertebrates.

Vermilion Snapper *Rhomboplites aurorubens* displayed contrasting patterns of biomass change compared to the other lionfish prey groups. As lionfish harvest rates increased, Vermilion Snapper declined, especially when predation rate limits were high (Figure 5). Most species/groups exhibited positive responses to lionfish harvest under all predation rate limit scenarios (Figures 5 and 6). Commercially and recreationally important reef fishes responded positively to increased lionfish harvest (Figure 6). In the baseline invasion scenario ($M2_{max}$ = 0.5M), increasing fishing mortality on lionfish from 0 to 0.66/year (F_{mult} going from 0 to 1) yielded increases in terminal biomasses of Greater Amberjack, Red Snapper, Red Grouper, and Gag Grouper by 16, 21, 11, and 9%, respectively (Figure 6).

DISCUSSION

Modeling the Lionfish Invasion

Using an Ecosim model of the WFS, we predicted that lionfish biomass would increase exponentially through 2018 and eventually reach densities that are about 200 times higher than the early establishment period (2011–2012), when biomass was near 0. From 2013 to 2015, lionfish biomass was predicted to increase by about fivefold, which is similar to the relative increases observed in other parts of their invaded range at similar stages of the invasion. For instance, lionfish were first sighted off southwest New Providence, Bahamas, in 2004 and their densities increased by about 4.5 times over the period of 2006 to 2008 (Green et al. 2012). In coastal North Carolina, where lionfish were first detected in 2002, densities at depths of 38–46 m increased four- to fivefold from 2004 to 2006 (Whitfield et al. 2014). However, both of these studies indicate that lionfish densities did not continue to increase much further or even declined slightly after the first 3 years of exponential increase. Whether or not the lionfish invasion will follow a similar pattern on the WFS or continue to increase for another 3–5 years as predicted is not yet known. It is equally likely that the protracted period of exponential increase in the Ecosim simulations is a result of model parameterization, particularly for the vulnerability parameters (discussed further below) and cannibalism rates, the latter of which may have strong density-dependent effects on lionfish biomass.

Our EwE model revealed complex trophic interactions that have implications for mitigating lionfish effects and managing fishery stocks at an ecosystem scale. The strongest effects were predicted for the reef omnivore, reef carnivore, and shrimp groups. These functional groups contribute the most to lionfish diet and were thus directly impacted by the invasion, with predicted biomass declines ranging from 5% to 75% depending on vulnerability settings. Albins (2015) observed a 32% loss in biomass, and studies by Green et al. (2012, 2014) reported reductions of 65% and 40–60%, respectively, in abundance of small reef fishes at invaded sites in the Bahamas. Thus, the magnitude of decline in lionfish prey predicted by Ecosim is within the range of what has been observed at sites throughout the invaded range. Future increases in ocean temperatures on the WFS (above the 24°C used here to calculate consumption rates for lionfish) could cause up to a 20% increase in daily consumption rates (Cerino et al. 2013) and potentially stronger effects to their prey.

Potential mechanisms for indirect effects caused by lionfish may include trophic cascades, competitive release, and predation release. In this simulation study, a trophic cascade was predicted to occur as a result of the lionfish invasion, where declines in mesopredators (i.e., reef carnivores and reef omnivores) due to lionfish predation led to increases in their benthic invertebrate prey (excluding shrimp). Trophic cascades have been observed in reef ecosystems when predator abundances increase (Stallings 2008). A lionfish-induced trophic cascade occurred at an invaded site in the Bahamas, where declines of herbivorous fish led to increases in foliose algae and declines in percent cover of coral (Lesser and Slattery 2011). Therefore, a trophic cascade involving the invertebrate community, like that predicted by the Ecosim model, is plausible. To test this prediction, comprehensive monitoring of fish, benthic, and algal communities (Kindinger and Albins 2016) associated with lionfish removal experiments is needed.

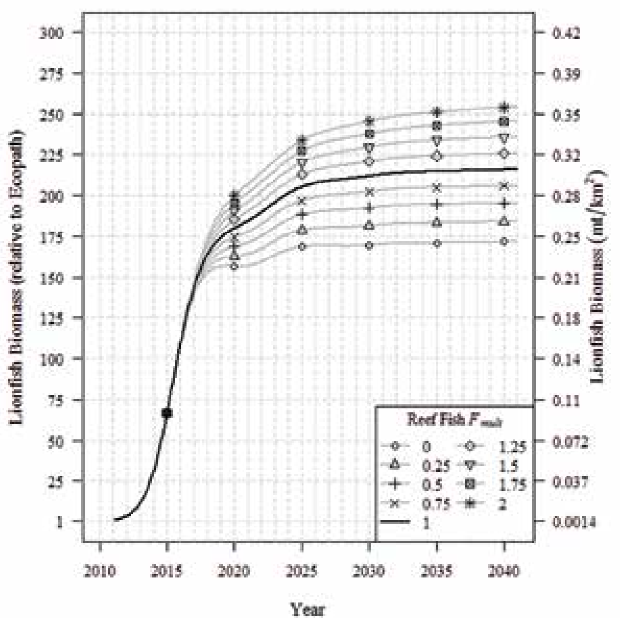

Figure 3. Simulated lionfish biomass from 2011 to 2040 under a range of fishing mortality rates on native reef fish species. In these scenarios, fishing mortality is expressed as a multiplier (F_{mult}) on the 2010 Ecopath *F* values (see Chagaris et al. 2015).

The simulated declines in mesopredators also led to competitive release for a few species that consume mostly invertebrates, including Gray Triggerfish, tilefishes, and Vermilion Snapper. In the case of Vermilion Snapper, both direct and indirect effects were at play. During the early part of the baseline simulation, Vermilion Snapper biomass initially declined due to the direct effect of predation by lionfish. Later in the simulation, Vermilion Snapper biomass begins to increase due to release from competition with reef carnivores and, to a lesser extent, release from predation by Gag Grouper and Black Grouper. In Chagaris et al. (2015), Vermilion Snapper were predicted to be negatively influenced by large reef fish, which was also observed by Dance et al. (2011) on artificial reefs in the GOM; therefore, it is not surprising the model predicted a net increase in biomass when meso- and top predators declined in the invasion scenarios.

The strong effect by lionfish on other predators in the system, especially Greater Amberjack and groupers (Figures 4 and 6) was somewhat unexpected given that lionfish do not prey directly on these species. This suggests that the negative effects caused by the invasion on these species can be attributed to competition for food with lionfish. However, the level of taxonomic aggregation in the small reef fish groups (i.e., reef carnivores and reef omnivores) that both lionfish and native predators consume could cause petitive effects predicted by the model to be exaggerated. For instance, these groups may share a common food source in the model, but in reality they feed on different species within that group. Higher resolution in these prey groups is required to better represent trophic niches and disentangle the interactions between lionfish and large predators. This work is ongoing for a lionfish-centric model that is currently under development for the northern GOM.

The Ecosim vulnerability parameters that control the predation rate limits were found to substantially alter the predicted influence of lionfish on other components of the food web. We evaluated lionfish biomass and community effects over a range of scenarios where each prey item of lionfish was assigned the same $M2_{max}$ relative to its own natural mortality rate. However, it is likely that differential predation rate limits occur across lionfish prey items. For instance, Green and Côté (2014) found that body size and shape, position in water column, schooling behavior, and foraging strategies were all important determinants of diet selec-

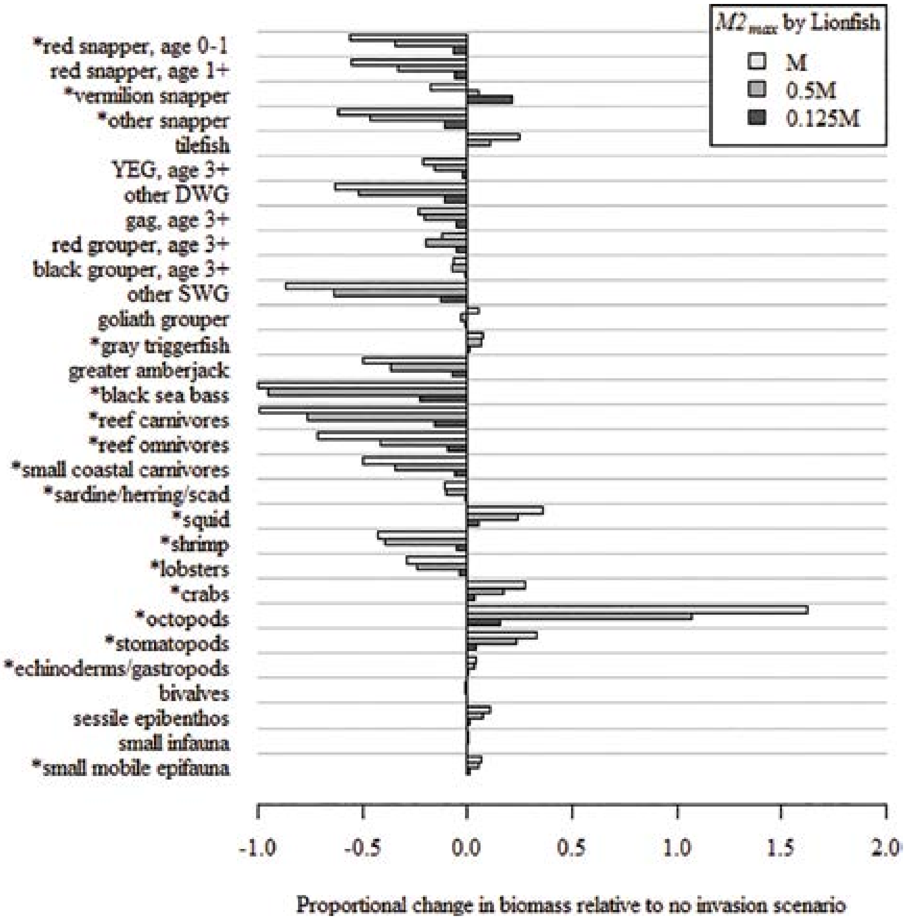

Figure 4. Proportional change in terminal biomass of species and functional groups, relative to the no invasion simulation, under three different vulnerability settings expressed as a proportion of *M* for each prey (low = 0.125*M*, baseline = 0.5*M*, and high = *M*) and assuming no harvest of lionfish. Asterisks indicate lionfish prey items. YEG = Yellowedge Grouper, DWG = deep water grouper, and SWG = shallow water grouper.

tion by lionfish. Additionally, prey fishes that are more active during crepuscular periods on and around patch reefs, when lionfish are actively hunting, are likely more vulnerable to lionfish predation (Benkwitt 2016). One option for estimating predation rate limits empirically is to experimentally manipulate abundances of lionfish and their prey at several sites and closely monitor diet compositions and prey communities over time. In one such experiment, lionfish were found to cause high per capita loss rates of a prey fish (Ingeman 2016), suggesting that predation rate limits in Ecosim should also be high. This is a much needed area of research for trophic dynamic modeling in order to address a major source of uncertainty in model predictions.

Biotic resistance to the lionfish invasion by native predators has been suggested but remains debatable due to confounding factors at different study sites (Mumby et al. 2011; Hackerott et al. 2013; Anton et al. 2014). In our simulations, reducing fishing mortality on recreationally and commercially important reef species (e.g., groupers and snappers) resulted in lower lionfish biomasses. This was predicted despite the assumption in our model that lionfish are not preyed upon by other species, implying that competition for food between lionfish and native species is strong. Native predators have the potential to alter lionfish foraging behavior, causing them to switch from fish to crustacean prey (Ellis and Faletti 2016). Whether or not native predators have begun to consume lionfish is not known but is expected to have implications on simulated invasion dynamics. The only confirmed indication of natural predation on lionfish in their invaded range was by two large groupers, Nassau Grouper *Epinephelus striatus* and Tiger Grouper *Mycteroperca tigris* (Maljkovic et al. 2008). Despite anecdotal reports from the GOM, predation on lionfish by native species has not yet been observed on the WFS in ongoing surveys of fish stomach contents. Without any data to inform parameterization, we can only infer the effects of possible predation by native species on lionfish. Had we assumed that it was occurring, the model would have predicted lower biomass of lionfish and stronger response in the reef fish harvest scenarios.

Because lionfish have only recently invaded the WFS, there are still several aspects of the invasion and effects on the ecosystem that are poorly understood. First, lionfish densities on the WFS were exponentially increasing during 2014, making it difficult to determine carrying capacity. Continued monitoring of lionfish densities will improve our ability to model their impacts as the population stabilizes. Second, no information has been collected on lionfish deeper than about 100 m (Dahl and Patterson 2014; Switzer et al. 2015), but lionfish are known to exist to depths up to 300 m (Kimball et al. 2004; Schofield 2010; Nuttall et al. 2014). It is likely that deep reefs would offer a refuge to lionfish spawning stock biomass even if efforts were successful to clear lionfish from shallow reefs. There is a need to survey outer shelf and upper slope environments for lionfish to gain understanding of their ecology, density, and size/age structure in these habitats. Third, we recognize that lionfish diets from the mid- and

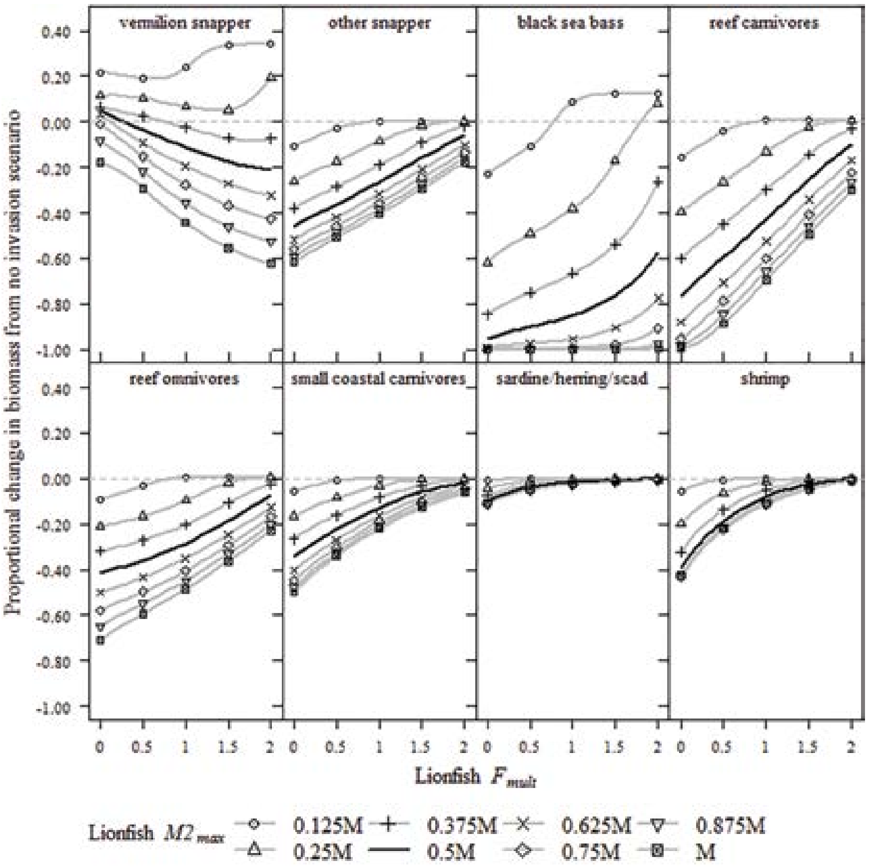

Figure 5. Proportional change in terminal (year-30) biomass relative to the no invasion scenario for species or functional groups contributing to at least 2% of the diets of juvenile or adult lionfish. Lines show the terminal biomass under alternative $M2_{max}$ assumptions and across a range of lionfish fishing mortality rates expressed as a multiplier (F_{mult}) on the Ecopath *F* value of 0.66. The baseline $M2_{max}$ configuration scenario is indicated by the solid black line where $M2_{max}$ is equal to half *M* for each prey.

southern WFS have not been reported. In the absence of a comprehensive survey of lionfish feeding habits, future adjustments to the diet matrix could be based on trait-based prey selection and prey availability (Green and Côté 2014). Lastly, the lack of observations of lionfish in conventional diet studies of native predators could be due to inadequate sampling of some species in recent years (namely, large groupers and snappers), stomach eversion when fish are brought up from depth, and difficulty in identifying juvenile fish in stomach contents. Expanded collection of diet data for reef predators using methods that prevent loss of stomach contents due to barotrauma (e.g., by spearing and bagging whole fish at depth) along with DNA barcoding of unidentified prey are needed to determine whether native predators are actually consuming lionfish and in what proportion to other available prey.

Management Implications

This study has important implications for promoting lionfish harvest and managing native reef fish fisheries. Increasing lionfish harvest improved the abundance of most mid-level consumers in the food web, indicating that targeted lionfish removals can at least partially mitigate the negative effects caused by the invasion. Harvest of lionfish, even at relatively low levels (e.g., less than 0.33/year or half of *M*), translated into increases (large ones in some cases) of the biomass of the rest of the community. Using single-species models, recruitment overfishing of lionfish was estimated to occur at annual exploitation estimates around 0.2 to 0.6/year (Barbour et al. 2011; Morris et al. 2011), and our model also predicted declines to occur at rates in this range ($F_{mult} = 0.3$ to 1.0) indicating that the biomass dynamics in Ecosim are in agreement with other modeling approaches.

In 2015, the total removals of lionfish on the WFS by commercial and recreational fishers were estimated to be 10 metric tons (Personal communication from the National Marine Fisheries Service, Fisheries Statistics Division, May 1, 2016). Adult lionfish biomass on the WFS in 2015 was predicted by Ecosim to be approximately 19,350 mt (0.114 mt/km^2 over a modeled area of 170,000 km^2). Thus, to achieve a fishing mortality rate of 0.05/year (where Ecosim predicted likely benefits), landings of lionfish will need to increase by at least 100-fold, to around 1,000 mt. Public education on safe handling of lionfish, deregulation of lionfish harvest, and more frequent lionfish tournaments are aimed at attracting recreational effort on lionfish. Highly selective fish traps have been approved for testing in order to harvest lionfish more efficiently and in deeper water (NOAA 2016). At the same time, lionfish are being marketed for human consumption and the number of restaurants and retail markets offering lionfish to the general public is increasing. The lionfish fishery is currently at virgin levels; therefore, increasing harvest from 10 mt/year to at least 1,000 mt/year is not inconceivable, especially if novel harvest techniques are successful at improving efficiency in the commercial fishery and a steady supply–demand of lionfish in retail markets can be established.

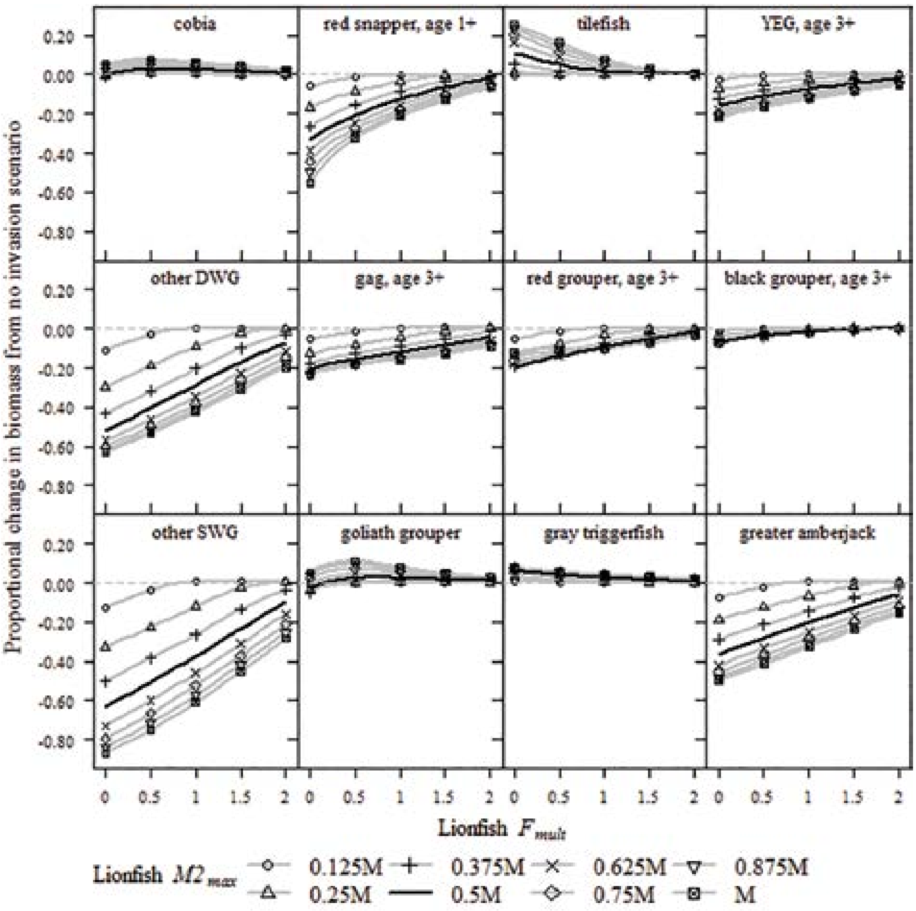

Figure 6. Proportional change in terminal (year-30) biomass relative to the no invasion scenario for commercially and recreationally important reef fish species or functional groups. Lines show the terminal biomass under alternative $M2_{max}$ assumptions and across a range of lionfish fishing mortality rates expressed as a multiplier (F_{mult}) on the Ecopath F value of 0.66. The baseline $M2_{max}$ configuration scenario is indicated by the solid black line where $M2_{max}$ is equal to half M for each prey.

At the end of the workshop, we presented our findings in a public forum to learn citizen's concerns about lionfish and understand their perspectives on control efforts and development of commercial fisheries for lionfish. The attendees consisted largely of recreational divers and spearfishers who were concerned about lionfish and willing to engage in their control efforts. It was recognized at the forum that it will be difficult, if not impossible, to remove lionfish by spearfishing at rates high enough to cause recruitment overfishing and declines in lionfish populations over a large geographic area. However, the effect of frequent lionfish removals at smaller spatial scales could have localized benefits (Frazer et al. 2012; De León et al. 2013; Green et al. 2014). In response, a spatially explicit model is currently being developed to explore the effects of site-specific lionfish removal strategies that could be adopted by local municipalities.

Lastly, the effect of invasive lionfish on productivity of native reef fishes has been identified as a research priority by the Gulf of Mexico Fisheries Management Council (2014). Our model predicts modest declines in biomass of valuable commercial and recreational species, including Gag Grouper, Black Grouper, Red Grouper, Red Snapper, and Greater Amberjack. Lionfish impacts have yet to be incorporated into stock assessments for these species, and management decisions are based on projections from single-species models that assume a constant environment. If competition between lionfish and these native species does exist, as our model suggests, then growth, mortality, average weight, and spatial distributions might be affected. Therefore, stock assessments should attempt to incorporate changes to vital rates caused by lionfish, and managers should be cognizant of potential lionfish impacts. Our model can be used, at least qualitatively, to inform ecosystem-based approaches to assessing and managing WFS reef fish fisheries in the face of this unprecedented species invasion.

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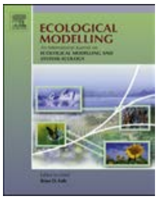

Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model

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ABSTRACT

The formation of an extensive hypoxic area off the Louisiana coast has been well publicized. However, determining the effects of this hypoxic zone on fish and fisheries has proven to be more difficult. The dual effect of nutrient loading on secondary production (positive effects of bottom-up fueling, and negative effects of reduced oxygen levels) impedes the quantification of hypoxia effects on fish and fisheries. The objective of this study was to develop an ecosystem model that is able to separate the two effects, and to evaluate net effects of hypoxia on fish biomass and fisheries landings. An Ecospace model was developed using Ecopath with Ecosim software with an added plug-in to include spatially and temporally dynamic Chlorophyll *a* (Chl *a*) and dissolved oxygen (DO) values derived from a coupled physical–biological hypoxia model. Effects of hypoxia were determined by simulating scenarios with DO and Chl *a* included separately and combined, and a scenario without fish response to Chl *a* or DO. Fishing fleets were included in the model as well; fleets move to cells with highest revenue following a gravitational model. Results of this model suggest that the increases in total fish biomass and fisheries landings as a result of an increase in primary production outweigh the decreases as a result of hypoxic conditions. However, the results also demonstrated that responses were species-specific, and some species such as red snapper (*Lutjanus campechanus*) did suffer a net loss in biomass. Scenario-analyses with this model could be used to determine the optimal nutrient load reduction from a fisheries perspective.

1. Introduction

Nutrient rich waters flowing from the Mississippi River into the Gulf of Mexico result in high primary productivity in this coastal area (Turner et al., 2006). Bacterial decomposition of this organic matter in combination with summer stratification has led to the occurrence of an extensive area of low bottom oxygen since at least the early 1970s (Rabalais and Turner, 2006). While often referred to as the 'dead zone', the effect on living marine resources of this annually reoccurring area of hypoxic bottom waters off the coast of Louisiana is not necessarily lethal.

Hypoxia refers to oxygen levels of 2 mg/l or lower, which can lead to decreased feeding and growth rates, changes in activity level, avoidance behavior, and death in fish and shellfish (Bell and Eggleston, 2005; Robert et al., 2011; Goodman and Campbell, 2007). The exact level of dissolved oxygen that results in effects on physiology or behavior is species-specific, which can results in community structure shifts and changes in species interactions (Essington and Paulsen, 2010). Indirect effects occur through predator–prey relationships; fish could be affected not by hypoxia, but by the response of their prey or predators to hypoxia, and the effects could be either positive or negative (Altieri, 2008; Pierson et al., 2009; Eby et al., 2005). Effects on fisheries may be even more complicated, as catch per unit effort (CPUE) could decrease when the abundance of target species is reduced by hypoxia, or could increase due to aggregation of target species at the edge of the hypoxic zone, which may enhance their susceptibility to be caught (Craig, 2012).

A significantly obscuring mechanism is the fact that the same nutrient enriched waters that are the main cause of bottom hypoxia (Rabalais and Turner, 2001), are responsible for the high primary

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and secondary production in this region (Gunter, 1963; Nixon and Buckley, 2002; Chesney et al., 2000). It is likely due to these complications, that holistic effects of hypoxia on the fisheries ecosystem of the northern Gulf of Mexico have remained elusive (Rose, 2000; Rose et al., 2009).

The purpose of this study is to analyze effects of hypoxia on fish and fisheries through ecosystem model simulations, and to provide a tool that can be used in management scenario analyses pertaining to Mississippi River nutrient load reductions and coastal fisheries management. To this purpose an Ecospace model was developed using Ecopath with Ecosim (EwE) software that was enabled to receive spatio-temporal primary productivity and dissolved oxygen output from a coupled physical–biological hypoxia model developed by Fennel et al. (2011). Since a reduction in hypoxia would entail a reduction in nutrients that enter the Gulf of Mexico, it is important to incorporate the effects of nutrient enrichment on phytoplankton (and changes therein) in an ecosystem model that studies effects of hypoxia and scenarios that may reduce this hypoxia. Output of the Fennel et al. (2011) model of dissolved oxygen (DO) as well as Chl *a* was used as forcing functions in the Ecospace model to account for both effects. Similar approaches to incorporate effects of biogeochemistry on foodweb models, often referred to as End-to-End modeling, have been used in other studies (see e.g. Libralato and Solidoro, 2009).

The ecosystem model developed for this study takes a holistic approach by simulating species interactions, while accounting for changes in biomass as well as spatial distribution changes, and by explicitly simulating fisheries with dynamic fleets. The model allows for simulations of all direct and indirect effects on fish and fisheries, in an environment where hypoxia and primary productivity fueling can be evaluated together and separately. While this ecosystem model contains sixty groups to provide a representative simulation of the ecosystem, the main focus of this paper is on a select group of species that are of economic or ecological significance. These species are Gulf menhaden (*Brevoortia patronus*), which is largest fishery in Louisiana by weight; brown, white and pink shrimp (*Farfantepenaeus aztecus*, *Litopenaeus setiferus*, and *Farfantepenaeus duorarum*), together comprising the largest fishery by value; red snapper (*Lutjanus campechanus*), a popular sportfish; Atlantic Croaker (*Micropogonias undulatus*), the most dominant forage fish in the model area; and jellyfish, a group of organisms of interest because of previous documented responses to hypoxia in other areas.

2. Methods

2.1. Data preparation

Fisheries independent survey data from the SEAMAP program of the Gulf States Marine Fisheries Commission (seamap.gsmfc.org) was used to determine which species were representative of the area, and to determine the biomass of each species present in the model area. Initial biomass in the base model was based on the average biomass of each group (species or functional group) from 2005 to 2008. Fishing was represented by including shrimp trawls, recreational fishing, snapper/grouper fishery, crab pots, menhaden fishery, squid fishery, and longlines as ‘fleets’ in the model. Annual landings of model groups by these fleets were based on NOAA Fisheries Annual Commercial Landings Statistics (st.nmfs.noaa.gov), and trip ticket data from the Louisiana Department of Wildlife and Fisheries. These data were used to develop the Ecopath model.

Landings data from 1950 to 2010, and SEAMAP data collected in the model area from 1982 to 2010 were used to calculate annual landings and biomass (t/km^2) respectively for each group in the model for which these data were available. In addition, an oxygen forcing function was developed from data collected during Lumcon cruises from 1998 to 2007 (D. Obenauer, personal communication), and a nutrient forcing function from NO$_x$ data collected in the Mississippi River by USGS from 1950 to 2010 (toxics.usgs.gov) to simulate nitrogen load into the coastal area from the Mississippi River. These time series and forcing functions were used for model calibration in Ecosim.

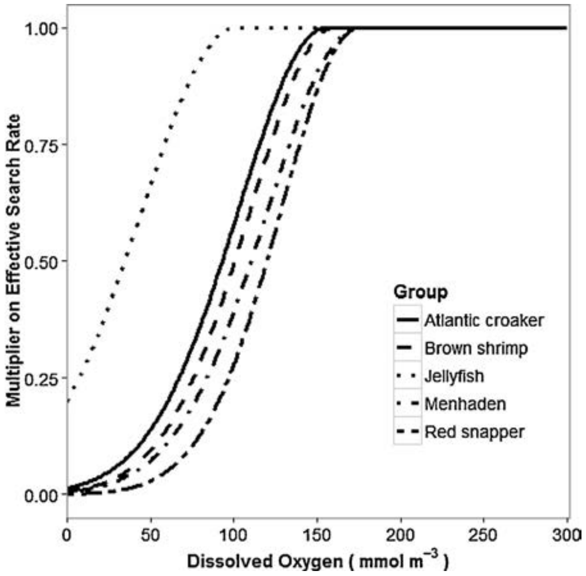

Fig. 1. Oxygen response curves of selected species.

In EwE, a nutrient forcing function serves as a multiplier on primary production. In order for groups to respond to the level of dissolved oxygen, empirically derived sigmoidal oxygen response curves were developed. These curves were developed by determining catch rates at each level of dissolved oxygen, using all SEAMAP data where dissolved oxygen was measured during collections. The tolerance curves were then used as a multiplier on effective search rate in Ecosim (and Ecospace, using a plug-in described in Section 2.5) as described in Christensen et al. (2008) and de Mutsert et al. (2012), to affect biomass of each specific group (Fig. 1).

2.2. Model preparation

The EwE modeling suite was used to build the model (www.ecopath.org). The virtual representation of the ecosystem was developed in Ecopath, the static model of the EwE modeling suite. Groups in the model represent single species as well as species aggregated in functional groups. Where deemed necessary to represent ontogenetic diet changes or size-selective fisheries, species were split into multiple life stages. For those species, the initial biomass of only one life stage was derived from empirical data, and the biomass of other stages were determined using a *von Bertalanffy* growth model. Some functional groups were represented with multiple life stages as well. This resulted in 60 groups (Table 1). Parameters included for each group to develop a mass-balanced Ecopath model in addition to biomass (B), were the P/B (production/biomass) ratio, Q/B (consumption/biomass) ratio, and the total fisheries catch rate (Y) for the groups that are fished. Parameters were derived from other Gulf of Mexico food web models (Walters et al., 2008; de Mutsert et al., 2012) or fishbase (fishbase.org).

Two master equations must be satisfied to correctly parameterize the Ecopath model. The first equation describes the production of each functional group as a set of n linear equations for n groups:

$$\left(\frac{P_i}{B_i}\right) \cdot B_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \qquad (1)$$

Table 1
Initial conditions of mass-balanced Ecopath model. B = biomass, Z = total mortality, P/B = production to biomass ratio, Q/B = consumption to biomass ratio, EE = ecotrophic efficiency.

Nr.	Group name	B (t km^{-2})	Z (yr^{-1})	P/B	Q/B	EE
1	marine mammals	0.069		0.02	11.97	0.623
2	tunas	0.024		0.9	13.00	0.811
3	jacks	0.018		0.8	3.30	0.693
4	birds	0.011		0.25	35.00	0.722
5	juv Atlantic cutlassfish	0.003	2		8.48	0.011
6	Atlantic cutlassfish	0.228	0.41		2.05	0.745
7	lizardfish	0.384		0.6	5.00	0.806
8	juv coastal sharks	1.2E−04	2		5.52	0.625
9	coastal sharks	0.148	0.08		1.00	0.646
10	mackerel	0.300		0.7	2.00	0.591
11	0–3 seatrout	2.5E−04	6		23.96	0.056
12	3–18 seatrout	0.072	1.4		4.11	0.279
13	18+ seatrout	0.647	0.7		1.60	0.478
14	0–6 red snapper	0.001	3		9.20	0.065
15	6–24 red snapper	0.032	2		2.91	0.659
16	24+ red snapper	0.090	0.6		1.20	0.222
17	0–1 groupers	0.008	2		5.13	0.011
18	1–3 groupers	0.090	0.6		2.07	0.027
19	3+ groupers	0.226	0.45		1.30	0.452
20	other snappers	0.141		1.3	13.70	0.405
21	0–3 red drum	4.4E−06	2		30.83	0.065
22	3–8 red drum	1.2E−04	3.5		11.16	0.451
23	8–18 red drum	0.001	1.1		5.10	0.298
24	18–36 red drum	0.003	0.6		3.03	0.810
25	36+ red drum	0.029	0.15		1.86	0.084
26	juv rays & skates	0.001	2		4.49	0.577
27	rays & skates	0.082	0.3		1.00	0.319
28	flounders	0.202		0.42	6.36	0.274
29	pompano	0.002		1	8.00	0.450
30	Atlantic bumper	0.434		1.2	6.00	0.632
31	scad	0.182		1.65	5.00	0.526
32	juv Atlantic croaker	1.303	2		4.01	0.014
33	Atlantic croaker	4.344	1.5		2.00	0.263
34	catfish	0.582		0.8	7.60	0.340
35	spot	0.690		1.1	12.00	0.909
36	squid	0.168		1	3.90	0.986
37	pinfish	0.094		2	5.00	0.744
38	porgies	1.223		2.52	8.00	0.468
39	anchovy	2.032		2.53	14.00	0.322
40	juv menhaden	1.891	2.3		14.53	0.008
41	menhaden	6.240	1.9		6.00	0.614
42	clupeids	4.448		1.8	12.11	0.219
43	mullets	0.100		0.8	8.00	0.309
44	sea turtles	0.030		0.11	6.76	0.082
45	small forage fish	3.715		2.53	12.00	0.851
46	jellyfish	0.360		22	67.00	0.727
47	blue crab	0.244		2.4	8.50	0.960
48	juv brown shrimp	0.007	3		17.36	0.027
49	brown shrimp	0.558	2.4		5.00	0.680
50	juv white shrimp	0.004	3		17.36	0.019
51	white shrimp	0.300	2.4		5.00	0.236
52	juv pink shrimp	2.6E−04	3		17.36	0.037
53	pink shrimp	0.020	2.4		5.00	0.208
54	other shrimp	0.369		2.4	19.20	0.551
55	benthic crabs	0.045		2	7.00	0.948
56	benthic invertebrates	12.08		4.5	22.00	0.800
57	zooplankton	7.642		36	89.00	0.387
58	benthic algae/weeds	29.8		25		0.072
59	phytoplankton	25		182		0.203
60	Detritus	100				0.046

where (P_i/B_i) is the production to biomass ratio for group i, EE_i is the ecotrophic efficiency (the proportion of production used in the system), B_i and B_j are the biomasses of the prey and predators respectively, (Q_j/B_j) is the consumption to biomass ratio, DC_{ji} is the fraction of prey i in predator j's diet, Y_i is catch rate for the fishery for group i, E_i is the net migration rate, and BA_i is the biomass accumulation for group i.

The Ecopath model assumes conservation of mass over a year. Energy balance within each group is ensured with the second master equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated energy} \tag{2}$$

where production can be described as:

$$\text{Production} = \text{predation mortality} + \text{catches} + \text{net migration} + \text{biomass accumulation} + \text{other mortality} \tag{3}$$

More succinctly, production can be described by the following equation:

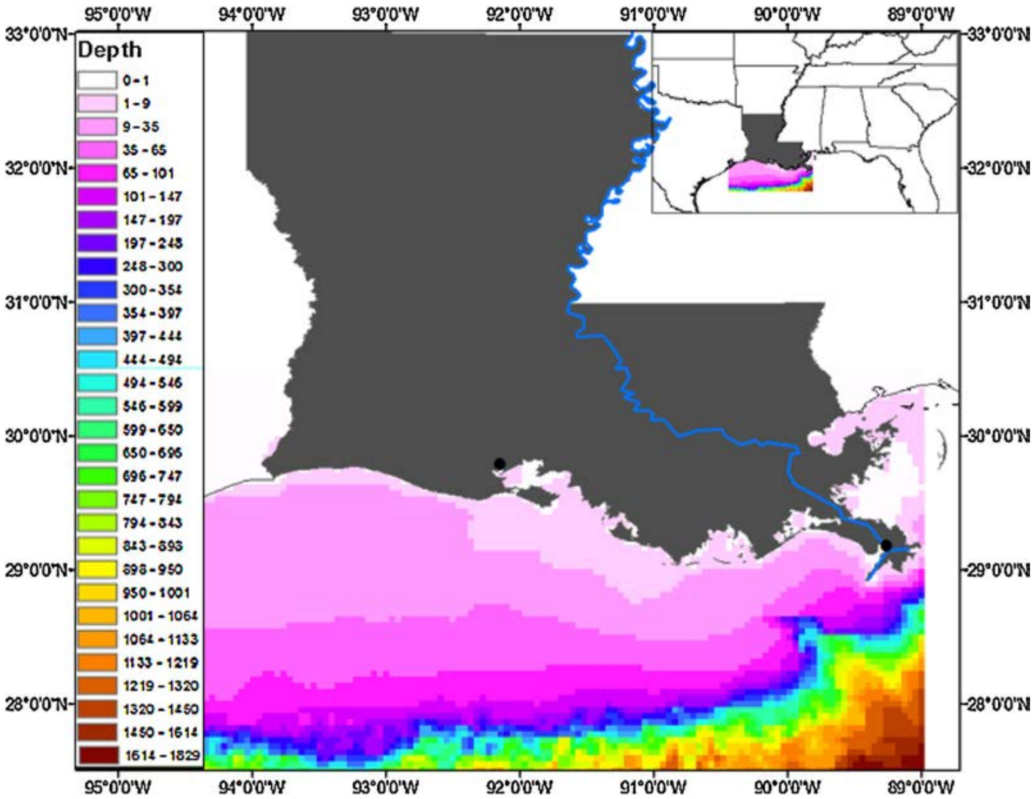

Fig. 2. Model area of the NGOMEX (Northern Gulf of Mexico) Ecosystem model. Louisiana (USA) is indicated in gray, and the Mississippi River in blue. The coloration in the northern Gulf of Mexico indicates the bathymetry (source of bathymetry data: The Fish and Wildlife Research Institute).

$$P_i = \sum_j Q_j \cdot DC_{ji} + (F_i + NM_i + BA_i + M0_i) \cdot B_i \tag{4}$$

where P_i is the production of prey group i, Q_j is the consumption of predator j, DC_{ji} is the diet composition contribution of i to j's diet, F_i is the instantaneous rate of fishing mortality, NM_i is the net migration rate of prey group i, BA_i is the biomass accumulation rate for i, $M0_i$ is the other mortality rate for i (non-predation, non-fishery), and B_i is the biomass of i.

In addition, a diet matrix was constructed based on diet information from stomach content analysis from nekton collected in the model area (A. Adamack, unpublished data), supplemented by information available in the literature. To achieve mass balance, the diet matrix was adjusted to attain a plausible solution of the flow of biomass through the foodweb. The available diet information usually did not provide exact proportions of each diet item, which made the diet matrix the most suitable component to adjust in order to achieve mass-balance. For example, when previous studies indicated that a specific species was the dominant prey species for a predator, the exact proportion of this prey item was adjusted during the mass-balancing procedure while still maintaining its status as dominant prey item. The diet matrix is provides as supplemental material 1.

During the mass balancing procedure in Ecopath, the model calculates Ecoptrophic Efficiency (EE) of each group, which represents the amount of biomass of that group used in the system (Christensen et al., 2008). A mass-balanced solution of the model is presented in Table 1.

2.3. Spatial components

A model area of 44,890 km^2 was chosen, which encompasses the Louisiana coastal zone and the annually recurring hypoxic zone. This area was represented in Ecospace with 5 km^2 grid cells, and is the model area of our Ecospace model, which we have called the NGOMEX (Northern Gulf of Mexico) ecosystem model (Fig. 2).

For the spatial and temporal model simulations, dissolved oxygen and Chl *a* output from 1990 to 2004 of a coupled physical–biological hypoxia model (Fennel et al., 2011) was used as forcing functions. Chl *a* levels in Fennel et al. (2011) are affected by the nutrients entering the coastal zone from the Missisippi River and other freshwater sources. This output was averaged by month and matched to the Ecospace grid map so that one value of bottom dissolved oxygen and one of Chl *a* could be read into Ecospace per month per grid cell during a model simulation. In the few occasions where the model area of Fennel et al. (2011) did not overlap with our model, DO and Chl *a* output was extrapolated from nearby cells. This was done for the estuaries, while the focus area for our modeling effort had 100% overlap. Example DO output from Fennel et al. (2011) that is used as a spatial–temporal forcing function is shown in Fig. 3. A plug-in to Ecospace was used to read in this spatial–temporal forcing function (see Section 2.5 for more details). Dissolved oxygen affected the groups in the model as stipulated by the response curves, while Chl *a* was used as a driver of phytoplankton biomass, assuming a linear relationship.

Two non-dynamic habitat features were included in the spatial model, depth and salinity area. Depth was based on the bathymetry of the model area; depth ranges were included to ensure (adult) offshore species would not enter shallow estuarine areas if they are not known to do that. While salinity is not modeled dynamically in this model, a 'marine', 'estuarine' and 'freshwater' zone is described loosely based on existing salinity gradients in the model area. While the focus of this model is on the marine coastal zone, these habitat features prevented species to escape coastal hypoxia by fleeing to areas that are too shallow or too fresh for them to enter in real life. A conceptual model of the NGOMEX ecosystem model is presented in Fig. 4.

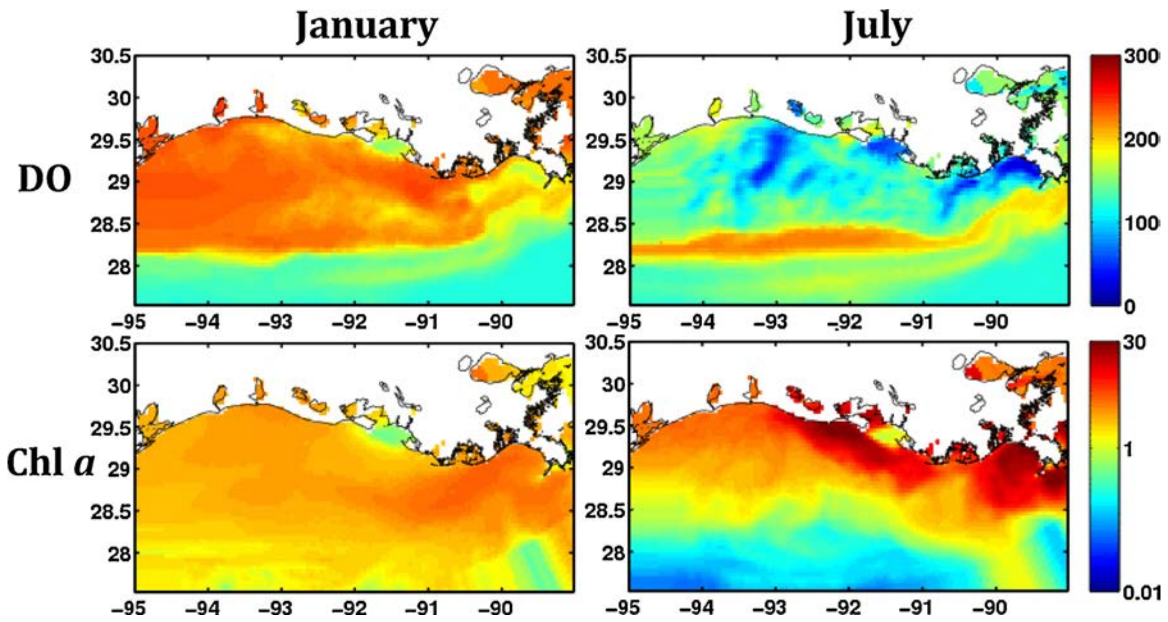

Fig. 3. Example output of dissolved oxygen in mmol m^{-3} (top) and Chl a in mg m^{-3} (bottom) from Fennel et al. (2011) in a month without hypoxia (January) and a month with hypoxia (July). Monthly "maps" of this output are used as spatial–temporal forcing functions in the NGOMEX ecosystem model. Output was extrapolated in the estuaries as shown in the figure.

2.4. Model calibration

Temporal dynamic simulations were performed in Ecosim, the time-dynamic module of EwE, to calibrate the model. DO and NO_x were included in the calibration runs as environmental forcing functions based on data described in Section 2.1. The level of dissolved oxygen affects the effective search rate of species in the model as described by the response curves in the same manner as salinity affected species in de Mutsert et al. (2012). The model was calibrated against biomass time series and landings data as described in Section 2.1. During calibration, the model was iteratively fitted to landings and biomass time series data by making vulnerability exchange rate adjustments until the smallest sum of squares (SS) was found using the fit-to-time-series feature in

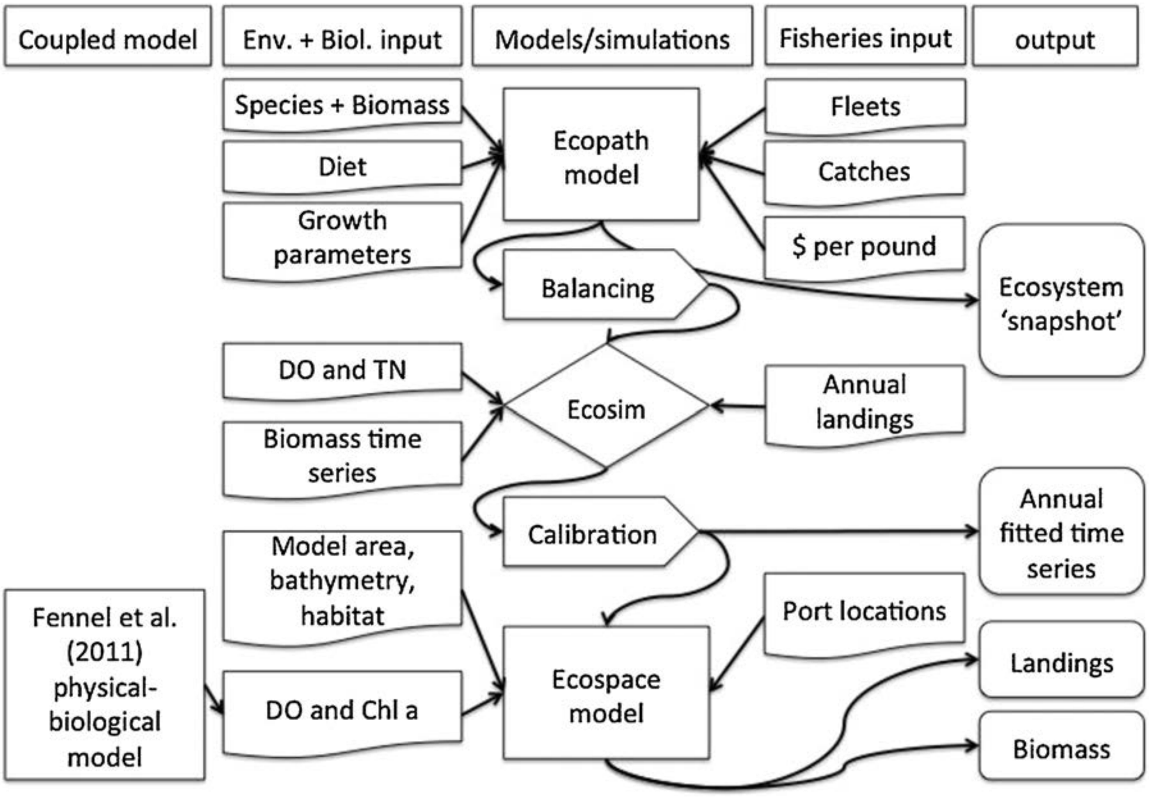

Fig. 4. Conceptual diagram of the NGOMEX ecosystem model. DO = dissolved oxygen, TN = total nitrogen.

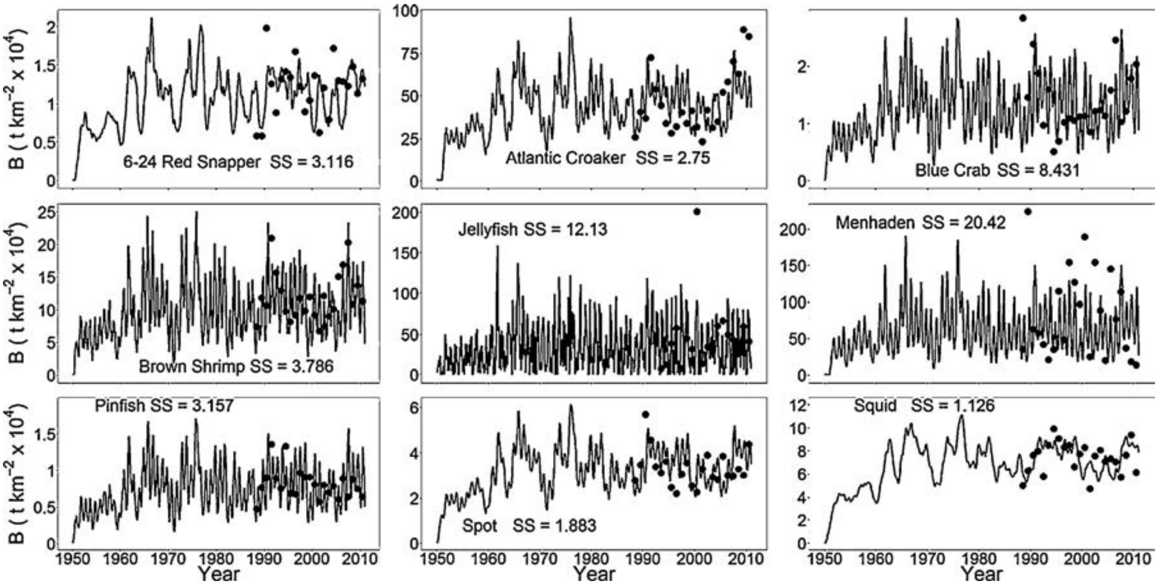

Fig. 5. Model fits to observed biomass of selected groups/species in the model. The SS of the fit is indicated in each panel.

EwE (Christensen et al., 2008). Following the Foraging Arena Theory described in Walters and Martell (2004), each group is present in the model in a vulnerable (to predation) and invulnerable state. The vulnerability exchange rate determines how quickly the mass of a group can switch between those states, where high numbers (around 100) indicate Lotka–Volterra predator–prey interactions (all prey is vulnerable to predation because of the high exchange rate between the vulnerable and invulnerable portion), and low numbers (around 2) indicate a significant portion of the group is unavailable to predation. We used the fit-to-time series procedure to determine the vulnerability exchange rates that resulted in the best fit of model predictions to biomass and landings data. The metric used to determine model fit was the following:

$$SS = \sum_{i}^{nts} \left(\sum_{i}^{nobs_i} w_i \log \left(\frac{o_{it}}{p_{it}} \right)^2 \right) \quad (5)$$

where SS is sum of squares, nts is the number of time series loaded, $nobs_i$ the number of observations in time series i, w_i is the weight of the time series i (all time series weighted equal in our model), o_{it} is the observed value in time series i at time step t and p_{it} is the Ecosim predicted value for variable i at time step t.

Including DO and nutrient loading (in the form of NO_x) as environmental forcing functions in Ecosim improved the fit of the model to time series, and decreased the total SS for all fits. Fig. 5 shows fits to time series (with SS) of a selection of species that are highly abundant in the area and/or have economic or ecological significance. The vulnerability exchange rates that were altered during this calibration procedure were carried over to Ecospace.

2.5. Model simulations

After calibration, spatial simulations were performed in Ecospace, the spatial–temporal module of EwE. In the new habitat foraging capacity model of Ecospace, dispersal rates of groups into a cell are affected by the cell suitability/capacity (Christensen et al., 2014). If the neighboring cell has a lower capacity then the dispersal rate to the cell will be proportional to the capacity difference. For example, if the capacity of a cell is 0.5 for a specific group, the maximum movement rate into this (in this model set to 300 km/yr for all groups) was adjusted by this proportion. The capacity of a cell was based on DO and habitat (depth and salinity area as described in Section 2.3). Fleets are dispersed by a gravitational model based on profitability per cell. Profitability per cell is based on the biomass of the target group(s) of a fleet, the price per pound of each target group in 2010, and the distance from port (fuel cost). Two ports with the highest landings in Louisiana were included in the model, Empire-Venice and Intracoastal City (www.oceanomics.org; Fig. 6).

To loosely link the physical–biological hypoxia model from Fennel et al. (2011) to Ecospace, a plug-in was added to the EwE source code. The plug-in reads in a DO and Chl *a* value per grid cell per time step (5 km^{-2} month^{-1}). This provides for spatial and temporal variation in the effective search rate and primary production. The DO values are fed into the environmental response functions defined in Ecosim. The values returned by the environmental response functions act as a forcing multiplier on the rate of effective search. This facility, provided by the plugin, works in the same manner as an Ecosim forcing function that has been applied to search rate (Christensen et al., 2008). The Chl *a* data is used to update the Ecospace Relative PP spatial layer, which allows for spatial shifts in primary production over time. The Ecospace Relative PP layer is a multiplier that is used to scale the primary production relative to the base productivity of the Ecopath model. During initialization the values in the Relative PP layer are normalized to scale the spatially averaged Ecospace productivity to the Ecopath base productivity rate (Christensen et al., 2008). The values read by the plug-in can shift from this baseline value to increase or decrease the spatially averaged productivity over time.

Scenarios simulated were ‘no forcing’, which simulated a coastal environment without nutrient fueling from the Mississippi River (or any other source of added nutrients) but also no formation of a hypoxic zone; ‘enrichment only’, which simulated nutrient loading effects on primary productivity, but where hypoxia had no effect on any organism; and ‘enrichment + hypoxia’, which included primary productivity forcing, and effects of DO (and thus hypoxia for part of the year) on fish biomass. Each scenario was run from 1950 to 2010; results presented reflect the output from simulation year 2010. While sixty groups were simulated, results are presented of a select group of species that are of economic or ecological interest.

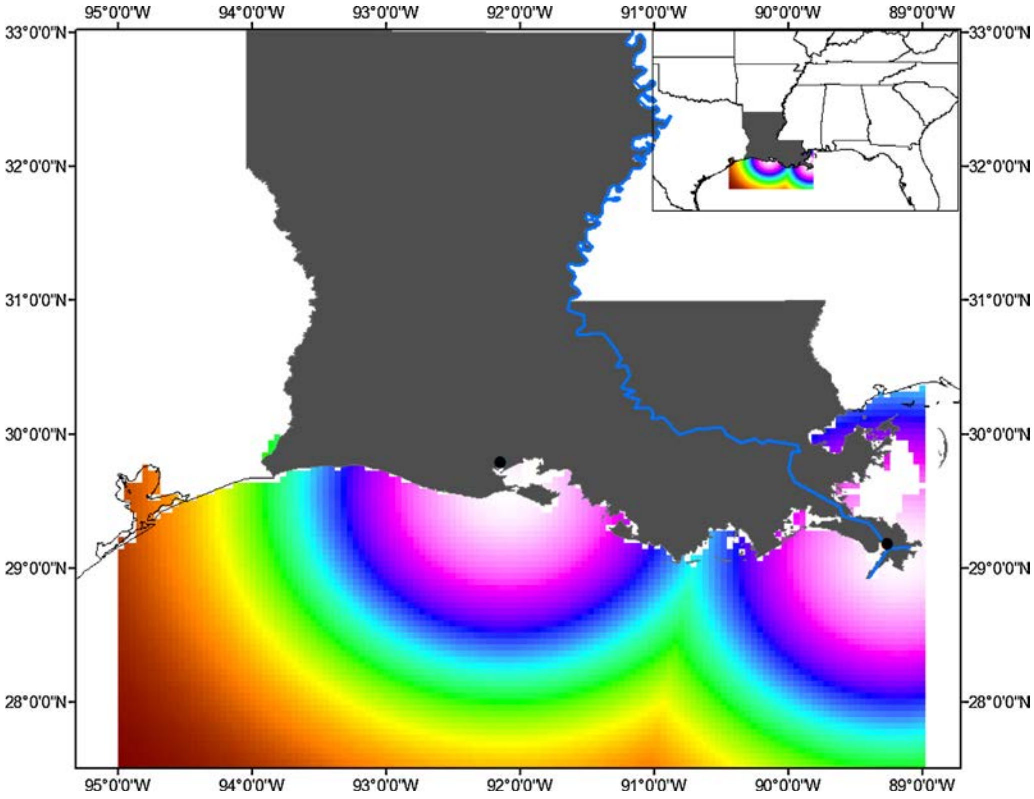

Fig. 6. Location of ports in the NGOMEX ecosystem model, representing Intracoastal City on the left, and Empire-Venice on the right (black dots). The coloration indicates distance from port, which is included in the calculation of fisheries revenue.

3. Results

Biomass and landings output of the scenarios 'no forcing', 'enrichment only', and 'enrichment + hypoxia' was compared. The scenario 'enrichment + hypoxia' simulates the real world scenario of Chl *a* concentration fueled by nutrient loading, and seasonal hypoxia in the coastal zone. The scenarios were run from 1950 to 2010, and output is presented as relative change, which is the change in biomass or landings of each group from the initial biomass or landings. The initial biomass and landings were the same for each scenario, so the scenario outcomes can be compared to each other. When looking at total landings and biomass, results indicate that the seasonal presence of hypoxia reduces both landings and biomass as compared to the 'enrichment only' scenario (Fig. 7). However, both 'enrichment only' and 'enrichment + hypoxia' had much higher increases from initial biomass and landings than the 'no forcing' scenario; the latter even showed a small decrease. The difference between 'enrichment only' and 'enrichment + hypoxia' is comparatively so small that these simulations suggest that the decrease in secondary production due to

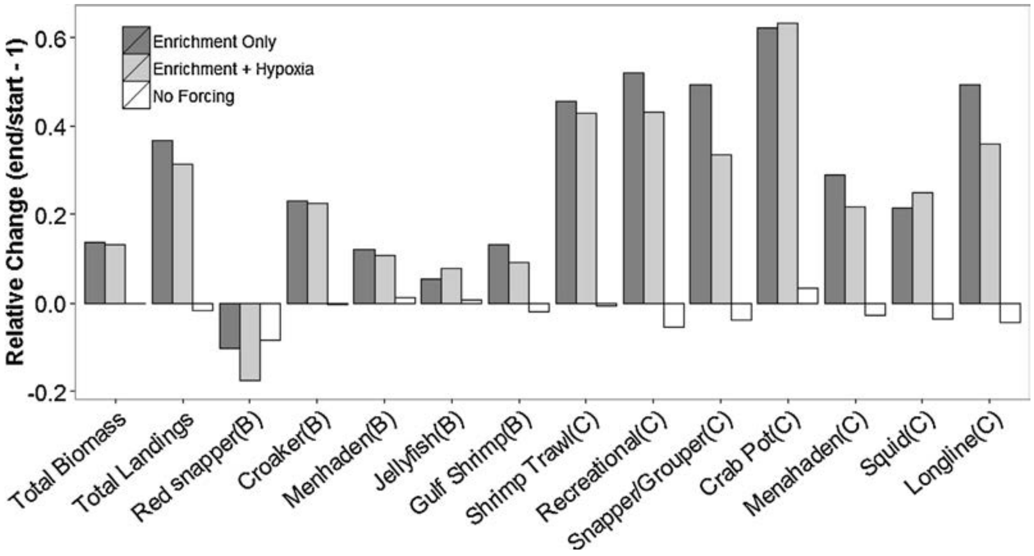

Fig. 7. Total landings and total biomass results of three scenarios (no forcing, enrichment only, and enrichment + hypoxia) that ran from 1950 to 2010. The relative change from the same initial conditions is presented of total biomass and total landings, species-specific biomass of selected species (B), and catch from all fleets (C).

hypoxia (in indirect effect of nutrient loading) is trivial in comparison to the increase in secondary production due to the bottom up effect of nutrient loading. Overall, there was a 33% increase in total landings in the 'enrichment + hypoxia' scenario as compared to the 'no forcing' scenario, and a 13% increase in total biomass. Removing hypoxia only increased that amount by an extra 5% and 0.6% respectively.

While total landings and biomass show the concurring trend of a small decrease in the 'no forcing' scenario, and large increases in 'enrichment only' and 'enrichment + hypoxia', individual groups vary in their response (Fig. 7). The biomass of common species in Louisiana; Gulf menhaden (*Brevoortia patronus*), Atlantic croaker (*Micropogonias undulatus*), and shrimp (brown shrimp – *Farfantepenaeus aztecus*, white shrimp – *Litopenaeus setiferus*, and pink shrimp – *Farfantepenaeus duorarum*) showed a response similar to what was seen in total biomass. Red snapper (*Lutjanus campechanus*) biomass however, decreased in all three scenarios, and decreased most in the 'enrichment + hypoxia' scenario (17.6%), followed by 'enrichment only' (10.4%) and 'no forcing' (8.3%). An opposite effect was seen in jellyfish, which displayed increases in all three scenarios, and the highest increase in the scenario with hypoxia (7.8%). Changes in landings do follow this pattern for almost all fleets, except for crab and squid fisheries, which see a small increase in landings when hypoxia is added as compared to enrichment alone.

4. Discussion and conclusion

Our simulations suggest that reductions in landings and biomass due to hypoxia are an order of magnitude lower than increases seen due to the nutrient enrichment (which is the main cause of hypoxia). Some fisheries in the model even experience an increase in landings in the scenario that includes hypoxia, namely blue crab and squid landings. The crab pots are not set in areas affected by hypoxia, which could explain this pattern, while the increase in squid landings is likely an indirect effect, since squid had a slightly higher tolerance for low oxygen as most of its predators, and slightly higher biomass in the scenario with hypoxia as a result. In general, current simulations do not suggest that natural resource managers should take the hypoxic zone into account in fisheries management plans (e.g. by restricting effort during hypoxic events), as the occurrence of seasonal hypoxia in combination with fishing does not lead to unsustainable biomass reductions.

This study emphasizes the importance of the positive bottom-up effect of nutrient enrichment on secondary productivity (Nixon and Buckley, 2002). Some notable species that follow the pattern of large increases in biomass as a result of nutrient enrichment, and only a slight reduction in biomass as a result of hypoxia, include Atlantic croaker, which is the most abundant species in this area and knows to have a high tolerance for hypoxia (Bell and Eggleston, 2005), Gulf menhaden, which is the largest fishery in Louisiana, and gulf shrimp (brown, white, and pink shrimp), which is the fishery with the highest revenue in Louisiana.

Still, from these results cannot be inferred that nutrient load reduction is not an important restoration measure, and that it would necessarily reduce secondary productivity. Our scenario of 'no forcing' is not a real-world scenario, and no nutrient reduction plan would conceivably remove all nutrients from the freshwater sources flowing into the Gulf of Mexico. Therefore, the corresponding low secondary production seen in the 'no forcing' scenario would never be attained. In addition, the relationship between nutrient loading, primary productivity, and hypoxia is non-linear and complex (Fennel et al., 2011); a reduction in nutrient load would not necessarily reduce bottom up fueling of the foodweb and hypoxia to the same extent. Momentarily disregarding the 'no forcing' scenario, a consistent small decrease in biomass from the nutrient enrichment scenario to the nutrient enrichment scenario with summer hypoxia can be seen. This small reduction could be ecologically significant for some species.

One species that seems affected by nutrient loading as well as hypoxia in our simulations is red snapper. An increase in mortality due to higher shrimp landings – and thereby higher bycatch of juvenile red snapper – in the scenarios that include nutrient enrichment is a likely cause of a decrease in red snapper biomass in those scenarios. The model reflects the impact shrimp trawling has on red snapper, which has been reported in studies related to red snapper stock status (Cowan, 2011). The additional decrease in biomass when hypoxia is present does indicate a negative effect of hypoxia on red snapper. Weaker recruitment of red snapper in years of severe hypoxia has been observed in a previous study (Switzer et al., 2015).

Another interesting result is the increase in jellyfish biomass in the scenario with hypoxia. Jellyfish, often regarded as nuisance species, likely find refuge from predation in hypoxic areas due to their high tolerance of low oxygen conditions. Increases in jellyfish in response to hypoxia in coastal ecosystems has been predicted or observed in other studies (Breitburg et al., 2003; D'Elia et al., 2003; Miller and Graham, 2012), and could exacerbate hypoxia effects on zooplankton by adding increased predation pressure.

This study concurs with some previous publications that hypoxia typically does not reduce overall fisheries landings or biomass, but that hypoxia should still be addressed in restoration plans (Breitburg et al., 2009). The use of novel spatial–temporal forcing functions in Ecospace allows for more realistic simulations of effects on fish and fisheries of environmental drivers that vary in space and time. Ecosystem models with this capability have only recently been described (Steenbeek et al., 2013; Christensen et al., 2014), but are expected to increase in numbers rapidly. Their usefulness in developing restoration and/or natural resource management strategies, especially when linked to physical/chemical models seems evident, and has already been recognized (de Mutsert et al., 2014a, 2014b). The model presented in this paper would be useful in restoration planning, and development of management strategies to reduce hypoxia without unacceptable losses to fisheries productivity. Models such as the physical–biological model of Fennel et al. (2011) could be used to simulate effects of nutrient load reductions on hypoxia and primary productivity in the coastal zone. The NGOMEX Ecospace model could then use those results to simulate effects of nutrient reductions on fish and fisheries in a scenario analysis. These loosely coupled models could thereby be used as a tool in nutrient reduction analyses to inform management decisions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.10.013.

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