Review article

Inclusion of jellyfish in 30+ years of Ecopath with Ecosim models

Philip D. Lamb ⓘ [1,2]*, Ewan Hunter[2,3], John K. Pinnegar[2,3], Thomas K. Doyle[4,5], Simon Creer[6], and Martin I. Taylor[1]

[1]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK
[2]Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft NR33 0HT, UK
[3]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK
[4]University College Cork, Distillery Fields, North Mall, Cork T23 N73K, Ireland
[5]MaREI Centre, Beaufort Building, Environmental Research Institute University, College Cork, Ringaskiddy, Cork P43 C573, Ireland
[6]School of Natural Sciences, Bangor University, Gwynedd LL57 2UW, UK

*Corresponding author: e-mail: philip.lamb@cefas.co.uk.

A review of the functional role of jellyfish in Ecopath with Ecosim (EwE) models by Pauly et al. [Pauly, D., Graham, W., Libralato, S., Morissette, L., and Deng Palomares, M. L. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia, 616: 67–85.] a decade ago concluded that recreation of jellyfish population dynamics in models required additional ecological research and the careful consideration of their unique biology during model construction. Here, amidst calls for ecosystem-based management and the growing recognition of jellyfishes' role in foodwebs, we investigate how jellyfish are implemented in EwE models and identify areas requiring improvement. Over time, an increasing percentage of models have included jellyfish. Jellyfish were often linked to the wider ecosystem, with many predators and prey included in models. However, ecotrophic efficiency, a measure of the extent to which they are used by higher trophic levels, was frequently set at low values, suggesting that jellyfish are still perceived as under-utilized components of the ecosystem. Moving forward, greater care should be taken to differentiate the functional roles played by ctenophores, cnidarians, and pelagic tunicates. Additionally, when feasible, early life stages should be incorporated as multi-stanza groups to more accurately depict jellyfishes' complex life cycle.

Keywords: Ecopath (EwE), ecosystem modelling, gelatinous zooplankton, jellyfish, predation

Introduction

Keeping marine ecosystems resilient and healthy is a conservation, economic development, and food security goal. The sustainability of fish stocks is not only dependant on careful management of catches, but also factors such as the preservation of foodweb linkages that underpin fish stocks and the ecologically-compatible implementation of other human activities in the marine environment (Pitcher et al., 2009). Ecosystem-based management (EBM) incorporates many of these considerations and is thought to be essential to the future health of fish stocks. Calls for EBM are widespread through academic and policy literature (Pauly et al., 2002; Murawski, 2007; Froese et al., 2016) and is a statutory requirement under the EU Common Fisheries Policy (Jennings and Rice, 2011).

Whole-ecosystem models can play an important role towards achieving EBM by providing a framework to quantify interspecific interactions. They can facilitate the exploration of alternative ecosystem states, improve our understanding of the ecosystem

network structure, and can identify knowledge gaps (Essington, 2007). Indeed, an inability to accurately parametrize a species in a model is often indicative of uncertainties in fundamental aspects of their ecology.

Jellyfish (here using the broadest definition of jellyfish including species belonging to the phyla Cnidaria and Ctenophora, in addition to pelagic tunicates), have been the focus of recent research, in part because of increases in the adverse economic and ecological effects they cause: such as overrunning aquaculture installations, stinging bathers, and physically blocking infrastructure such as cooling pipes (Purcell, 2012). However, there is uncertainty over the cause of these adverse effects: it has been suggested jellyfish populations are increasing globally (Brotz et al., 2012), conversely there is also evidence reporting bias and increased encounter rates may be responsible these apparent increases (Condon et al., 2012). Resolving the role of jellyfish in ecosystems is important for understanding potential mechanisms for their population growth, and managing their populations in a manner compatible with EBM (Roux et al., 2013).

Ecosystem modelling can play a role in understanding jellyfish population dynamics, as well as exposing knowledge gaps in their ecology. Previously, Pauly et al. (2009) used 23 Ecopath with Ecosim (EwE) models (Christensen and Pauly, 1992; the most frequently used whole-ecosystem approach for marine systems; Steenbeek et al., 2013), the FishBase database, and the SeaLifeBase database to summarize the modelling community's understanding of jellyfish ecology. Gelatinous biomass was higher in disturbed ecosystems where overfishing was thought to allow jellyfish population expansion by feeding on the zooplankton, which would otherwise be consumed by fish. Much variation in the parameterization of jellyfish was present in the EwE models. For example, in some models jellyfish were treated as trophic dead ends, whereas in others they were considered an integral part of the ecosystem. In some ecosystems (Lancaster Sound and Chesapeake Bay) jellyfish were considered to exert a large influence on other biota as a keystone species, whereas in others there appeared to be little influence. In the time since, knowledge of jellyfish ecology has improved, the tools available for analysis, and the number of published EwE models containing jellyfish have expanded considerably. Therefore, revisiting the Pauly et al. (2009) study is warranted to investigate whether the recommendations have been incorporated into common practice, and how the state of jellyfish in the ecosystem-modelling field has changed.

Ecobase is a database of more than 450 EwE models and metadata assembled by Colléter et al. (2015) that provides the basis for this study. The aim here is to characterize how jellyfish are incorporated into EwE models, with special attention being paid to the following objectives: (i) quantification of the extent and the manner in which jellyfish are incorporated in models (i.e. do the modelling community consider jellyfish to be important enough in foodwebs to warrant their inclusion in models?), (ii) assessment of the connectedness of jellyfish with the rest of the ecosystem (i.e. are jellyfish always treated as trophic dead ends? Is the trophic role of jellyfish groups in models changing as more evidence about their functional roles is gathered?), (iii) determination of the influence of key models (i.e. have parameters been copied between models? Do key publications strongly influence the field and if so, what is the rigour of "keystone" literature?), and (iv) to check if estimates of key parameters reflect the current state of jellyfish ecological knowledge.

Methods

Data collection
The primary literature (technical reports, publications, dissertations, and theses) and EwE models detailed in Ecobase were first examined to ascertain whether the models included a jellyfish group. The broadest definition of jellyfish was employed, and so all models that integrated pelagic tunicates, ctenophores, cnidarians, or some combination of all three were included in the analysis. In some instances, the primary literature could not be accessed, in which case the model was assessed by accessing the Ecobase database using R (R Core Team, 2017) or downloading and inspecting the model directly in EwE.

Models that contained jellyfish were categorized as "plankton groups that included jellyfish" for those that represented jellyfish in the model as part of a broad zooplankton group, or "jellyfish groups" for those that had incorporated jellyfish as their own node (e.g. jellies, gelatinous zooplankton, or similar) or if they amounted to more than 75% of a zooplankton-subgroup such as carnivorous zooplankton. Hereafter, "jellyfish group" is used to refer to a mathematical representation of jellyfish in a model, whereas jellyfish refers to the organisms themselves. For all groups, the geographic location of the model was extracted from Ecobase using R where possible, or georeferenced in QGIS 3.2 (QGIS Development Team, 2018) using the map section of "Discovery Tools" on the Ecobase website (http://ecobase.ecopath.org/). For models with "jellyfish groups," the Biomass (B); consumption to biomass ratio (Q:B); production to biomass ratio (P:B), and ecotrophic efficiency (EE, a measure of the extent to which an organism is consumed and used by higher trophic level) were extracted. In addition, the input parameter estimated by EwE via mass-balance, prey items of jellyfish, predators of jellyfish, and the literature cited for parameterizing the "jellyfish group" were recorded for each jellyfish group within a model. In some instances, models had multiple jellyfish groups, or the same model was parameterized for different years: in these instances, all jellyfish groups and years were recorded.

Data visualization and statistical analysis
Many models with multiple EwE implementations for different years were created before the advent of Ecosim, and were used to conduct crude temporal analysis. To treat these models in a mode more analogous with contemporary models (that use a single Ecopath model) we used mean values of the input parameters across different periods to give a single set of values for each jellyfish group. For models with multiple jellyfish groups, all jellyfish groups were included for analysis.

It was hypothesized that EE would increase over time, as jellyfish were considered a more important component of the ecosystem—to this end EE and publication year were plotted, although non-independent data precluded formal analysis. To assess the relative influence of models within the literature, EwE models and the corresponding cited literature were used as nodes in a directed model in the R package "network" (Butts, 2008). Groups that jellyfish preyed upon, and groups that fed on jellyfish were visualized using "metacoder" (Foster et al., 2017). Because subtly different terminology (e.g. "macrozooplankton" and "zooplankton") was used to describe similar taxonomic groups, some functional groups were combined as detailed in Supplementary Tables S1 and Table S2.

Results

In total 329 models were examined: 211 contained no jellyfish groups, 32 included jellyfish as part of a zooplankton group, and 86 models incorporated jellyfish explicitly as their own separate group(s). The inclusion of jellyfish groups in EwE models has increased over time and is characterized by three periods: 1984–2000, 2000–2007, and 2007-present (Figure 1). Early models rarely featured jellyfish groups, but by the year 2000, six EwE models explicitly featured jellyfish groups, whereas 15.4% of models included jellyfish in some capacity. From 2000 to 2007 a rapid increase in the inclusion of jellyfish then occurred, with an approximate 50:50 split between models including jellyfish as part of a zooplankton group and those where jellyfish were included as an explicit group. Starting in 2007, representing jellyfish in EwE models as their own functional group became more prominent. During this time only four models included jellyfish as part of a wider plankton group, in contrast to 56 models that featured explicit jellyfish groups. Models that incorporate jellyfish now (2007-present) account for around 36% of models, 73% feature an explicit jellyfish group. Jellyfish groups are represented in a wide variety of ecosystem models around the world, although there is a concentration of research in North America and Europe, with fewer models seen in the other continents (Figure 2).

The network analysis of citations used to parameterize jellyfish components in the EwE models revealed that none of the published models are particularly influential, with the most-influential model used to parameterize only two other models (Figure 3). The cited literature tells a similar story; six manuscripts were used to parameterize more than three models. Models for the most part used locally derived independent sources of data.

The B, Q:B, P:B, and EE for models containing jellyfish groups are shown in Figure 4 (full details can be found in Supplementary Table S3). Figure 4a shows estimates of biomass used. Most estimates cluster between 0.1 and 10 tonnes km^{-2} (although note the log scale). Two clear outliers can be seen at $\sim$300 tonnes km^{-2}: these studies (Orek, 2000; Gucu, 2002) both model the outbreak of *Mnemiopsis leidyi* blooms in the Black Sea, which were responsible for fishery crashes and extirpation of some zooplankton and fish species (Finenko *et al.*, 2006).

Figure 4b and c shows a unimodal distribution of data is present in the Q:B and P:B ratio respectively, although there are outliers present in Q:B ratio. It is unclear why the Q:B is set so high for the most extreme outlier (Heymans and Baird, 2000). In this particular study, the model is the northern Benguela upwelling, a marine ecosystem now considered to be dominated by jellyfish after a fishery collapse (Lynam *et al.*, 2006). It is possible that the model has a high consumption to emulate strong top-down pressure from the jellyfish group on prey groups. The other outlier Q:B values belong to models of the Gulf of Maine, Mid-Atlantic Bight, Southern New England, and Georges Bank. The associated technical report (Link *et al.*, 2006) for all these models is unavailable and so again it is unclear why such high values were chosen.

Figure 4d shows the distribution of EE values. Unlike, B, P:B, and Q:B a unimodal distribution is not present, instead EE has no obvious central tendency with peaks at the zero (0) bin and just above the 0.75 bin. Although non-independent data preclude formal analysis no obvious EE trend appears present (Figure 5).
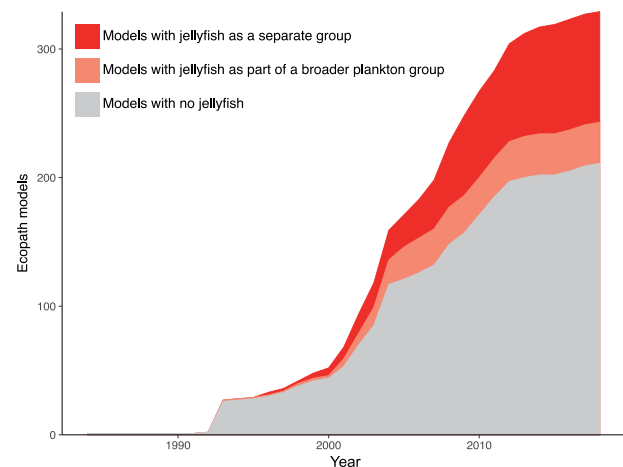

Figure 1. The accumulation of EwE models through time. Light grey are EwE models with no jellyfish functional group included at all. The mid-tone indicates models with jellyfish as part of a wider zooplankton group. The dark tone is those models with jellyfish included as their own group.

Ecotrophic efficiency was the input parameter most frequently estimated by EwE (Figure 6) through mass-balance. Figure 7a shows EE values estimated via mass-balance calculation, Figure 7b shows EE when manually entered into the model. Because data are not independent, statistical testing is not possible. Anecdotally, it appears that the zero (0) bin is mainly favoured when manually inputting EE, whereas the 0.75 bin occurs with EwE-estimated EE.

In total, 44 prey items were extracted from the models (Figure 8). Because of the lack of consistency on how prey were described in models (e.g. taxonomic rank used) inferring common prey items from data proved challenging. However, once coerced into a network structure, common prey items within models became apparent including zooplankton, other invertebrates, and pelagic fish.

A diverse range of predators ($n = 69$) consuming jellyfish were reported within models (Figure 9). Much like prey items of jellyfish, predators required coercion into a network structure to illustrate inter-model commonalties. Predators frequently incorporated into models included deep-sea fish, pelagic fish, invertebrates, marine mammals, and plankton. Figure 9 details predators of jellyfish as reported in models.

Discussion

Prevalence of jellyfish in models

One of the most salient findings from this current review is that 64.1% of models do not include jellyfish (Figure 1). This situation appears most prevalent in older models (1984–2000, 84.6% contained no jellyfish) with an increase in the absolute and relative inclusion of jellyfish in EwE models identified in more recent times (2007–2018, 58.2% contained no jellyfish; Figure 1). Increased representation in models may be influenced by two factors. First, interest and research into jellyfish ecology has increased in recent years (Condon *et al.*, 2014) in part because of the frequency with which observed blooms interfere with human enterprise and cause economic losses (Purcell, 2012). Second, the Pauly *et al.* (2009) publication "Jellyfish in ecosystems, online
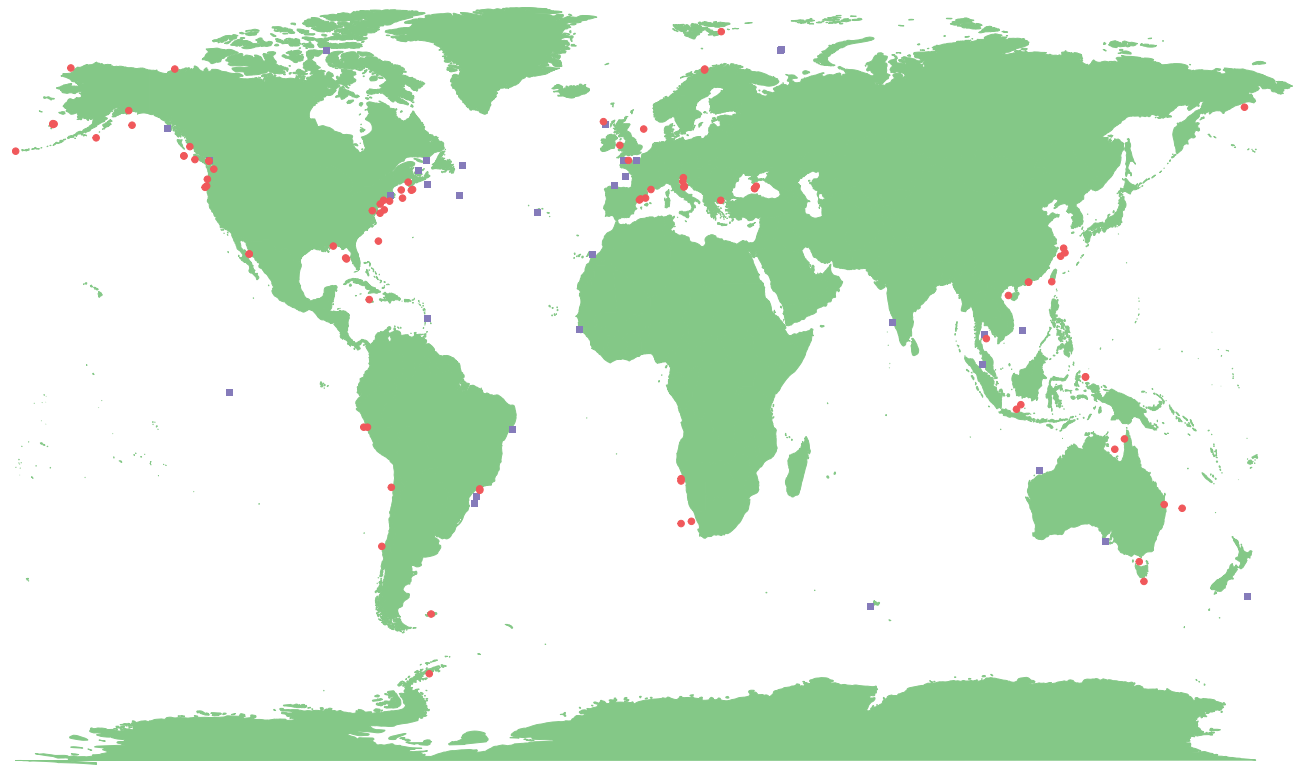
Figure 2. The global distribution of EwE models containing jellyfish. Groups containing jellyfish as part of a broad "zooplankton" group are denoted by squares. Models containing jellyfish as explicit functional groups are shown with circles. Models not containing jellyfish are not shown.
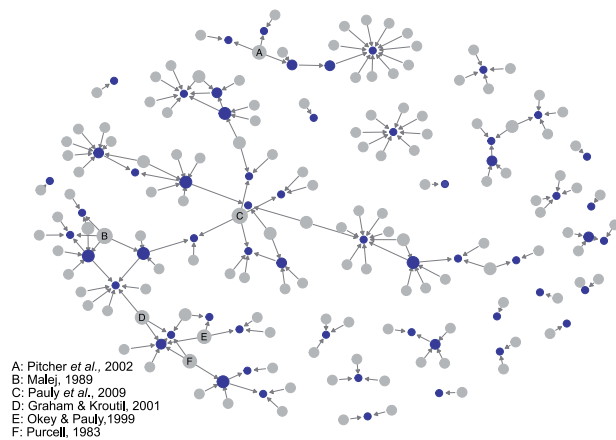

A: Pitcher *et al.*, 2002
B: Malej, 1989
C: Pauly *et al.*, 2009
D: Graham & Krouti, 2001
E: Okey & Pauly,1999
F: Purcell, 1983

Figure 3. A directed citation network of EwE jellyfish models (dark nodes) and cited literature (light nodes). The network only contains models with citations to other models or literature, models that used no other literature in parameterization of the jellyfish group are not included. Additionally, only citations within models are included, references between literatures are absent. The size of the nodes corresponds to the number of direct citations. Influential nodes, with more than three citations are labelled.

databases, and ecosystem models" may have elicited jellyfish group inclusion by explicitly highlighting the omission of jellyfish from EwE models and providing summaries of EwE parameters, thereby making the inclusion of jellyfish in new models much easier. Our directed citation network analysis of EwE jellyfish models

and cited literature (Figure 3) supports this idea, as Pauly *et al.* (2009) is the joint most-influential publication in the literature of direct citations. Whatever the underlying drivers for their inclusion, the fact that jellyfish are more frequently incorporated into EwE models should be lauded, as this improves the biological realism of the ecosystem models and helps dispel the notion that jellyfish are trophic dead ends.

The trophic ecology of jellyfish

Simply looking at the inclusion of jellyfish groups says nothing about how accurately jellyfish are incorporated into EwE models. The trophic ecology of jellyfish presented in the models presents a mixed picture: jellyfish prey (Figure 8) and predators (Figure 9) were broadly consistent with species included in the literature (Hansson *et al.*, 2005; Sullivan and Kremer, 2011; D'Ambra *et al.*, 2018; Hays *et al.*, 2018). However, shortcomings were present: notably EE was frequently set to zero even when predators of jellyfish were listed. When this occurs, jellyfish groups are treated as if no biomass is used by the next trophic level within the model. Low EE values are often associated with organisms that die-off following blooms (Christensen *et al.*, 2005). However, even taking this precedent into account, the values ascribed to jellyfish seem extreme. Older models may use very low EE values as this reflects the understanding of jellyfish ecology of the time. The archaic view that jellyfish are trophic dead ends is no longer widely held (Hays *et al.*, 2018), yet this contemporary understanding of jellyfish ecology is not reflected within EwE models, with EE values showing no change over time (Figure 5). Changing EE values to match the current state of jellyfish ecology should be a priority
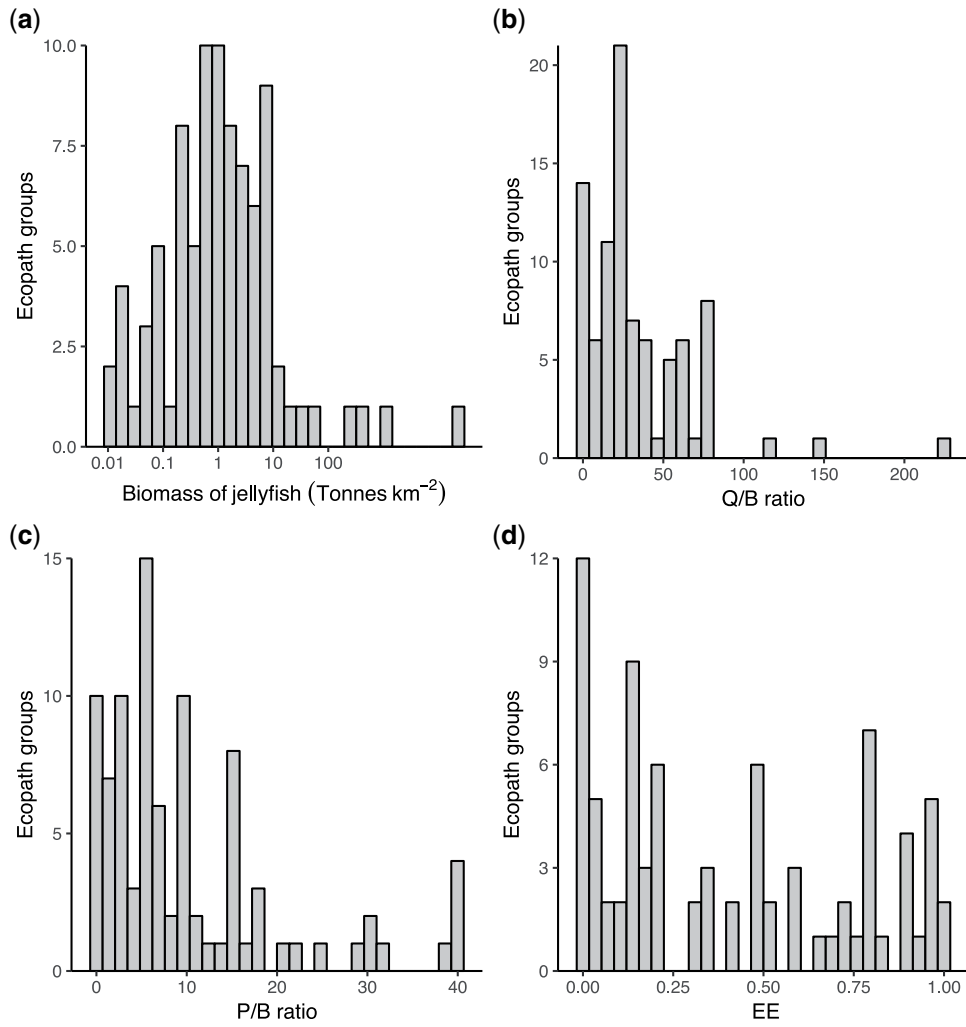
Figure 4. The (a) biomass, (b) Q:B (consumption:biomass) ratio, (c) P:B (production:biomass) ratio, and (d) EE (ecotrophic efficiency) of jellyfish groups included in EwE models.
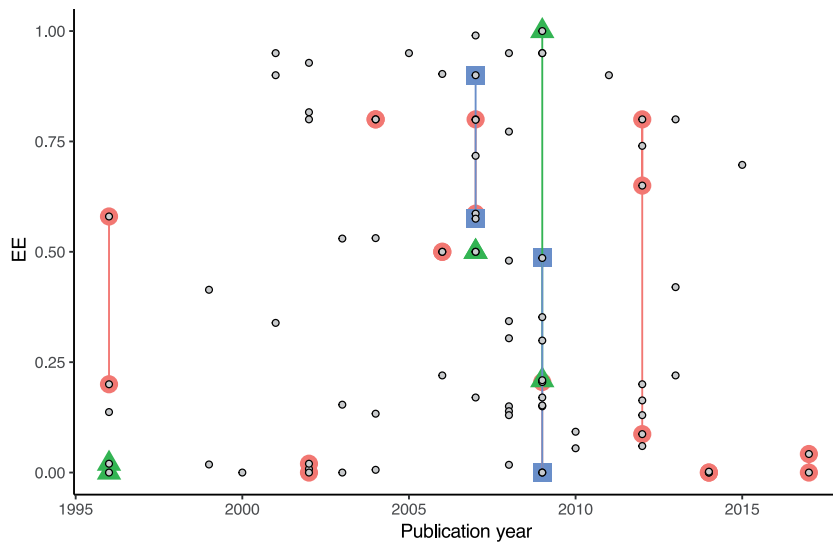

Figure 5. The ecotrophic efficiency (EE) reported in jellyfish groups over time. Within each year separate jellyfish groups (e.g. small jellyfish and large jellyfish) that feature within the same model are highlighted (shape) and connected to indicate non-independence.
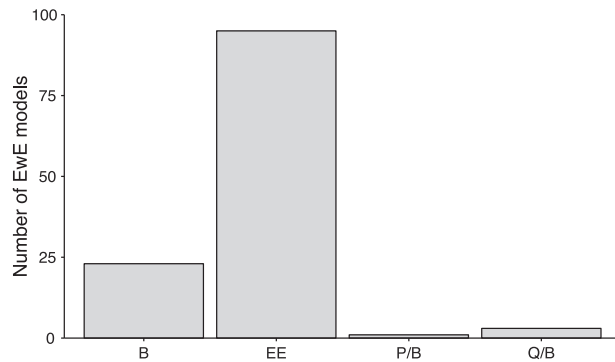
Figure 6. EwE requires four main inputs when parameterizing a group: biomass (B), ecotrophic efficiency (EE), production to biomass ratio (P:B), and consumption to biomass ratio (Q:B). Three inputs must be entered manually, whereas the fourth (usually the parameter with most uncertainty) can be calculated within EwE. Here, the EwE-estimated input parameters for jellyfish groups ($n = 122$) are shown.
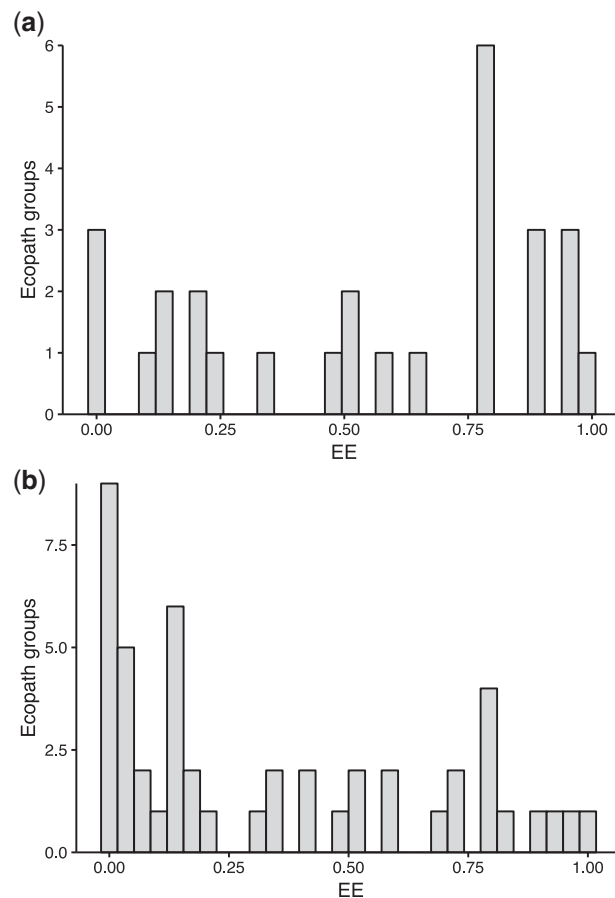

Figure 7. Distribution of EE values when (a) it is estimated by the EwE software via mass-balance, and (b) when it is directly input into the model.

for ecosystem modellers as poorly optimized models will give erroneous predictions. Quantitative diet assessment techniques such as stable isotope analysis (Cardona *et al.*, 2012) could be employed to generate accurate EE values. Alternatively, EE could

be estimated within EwE by using B, Q:B, and P:B estimates derived from high-quality sources.

Input parameters and the ecology of jellyfish

Accurate input parameters for jellyfish groups are important, not just to ensure the ecosystem model accurately portrays the relative biomasses of species found in the environment, but also because these values (B, P:B, Q:B) are used to infer the trophic ecology (EE) of jellyfish groups. Issues can arise as EwE was principally developed with the physiology and development of fish functional groups in mind, where energetic content of biomass is assumed to be the same across all functional groups (Plagányi and Butterworth, 2004). However, jellyfish have a much lower energy density than fish (Doyle *et al.*, 2007). Therefore, modellers must decide if biomass should be adjusted to represent relative energy flows or remain closer to values seen in the ecosystem. Furthermore, in some instances, the paucity of jellyfish biomass data (Lucas *et al.*, 2014) makes it such that it is difficult to assess what a biologically accurate portrayal of jellyfish within an ecosystem model may entail. Generating novel jellyfish biomass estimates [e.g. Bastian *et al.*, 2014; estimated that the average biomass of jellyfish in the Irish sea was more than seven times that of the herring biomass (39.7×10^6 kg vs. 292×10^6 kg)] and the ongoing curation of jellyfish databases such as JeDI (Lucas *et al.*, 2014) should aid modellers in incorporating jellyfish groups within ecosystem models.

If locally derived data are not available, a frequently used approach is to borrow model input parameters from another EwE model. However, this approach can propagate bias and erroneous findings throughout the literature. Previously, Sanz-Martín *et al.* (2016) used network analysis to demonstrate that the common perception that jellyfish populations were increasing was propagated mainly as a result of inappropriate citation practices. Using a similar concept, Figure 3 shows a citation network of EwE models containing jellyfish groups. A loose network is formed, however, the references used for parameterizing jellyfish groups appear to be largely independent from one another; 84.7% of nodes are cited only once, 11.3% cited twice. Papers with more than two citations are labelled: four papers were cited three times, and only Pauly *et al.* (2009) and Malej (1989) were cited four times. In some instances, citations appear appropriate, for instance, the Barausse *et al.* (2009), Coll *et al.* (2006), and Libralato *et al.* (2010) models of the Adriatic Sea borrowed jellyfish parameters of Malej's (1989) study of the same ecosystem. However, elsewhere more questionable use of published data was observed, notably where the input parameters for jellyfish were borrowed or derived from contrasting ecosystems. For example a jellyfish group from the Falkland Islands (Cheung and Pitcher, 2005) was parameterized with data obtained from Hong Kong harbour (Pitcher *et al.*, 2002). Similarly, jellyfish data from Alaska (Okey and Pauly, 1999) were used to parameterize a jellyfish group in the Gulf of Carpentaria, Australia. Fortunately, the constructed citation network suggests that only a loose network exists and so any hypothetically unfounded parametrization of jellyfish does not proliferate throughout the entire field, but instead remains in the original model for the most part. However, our approach only investigated direct references of models (shared citations between references was not included) and so the extent to which jellyfish data are shared (indirectly) may be greater than that suggested by the network presented here.
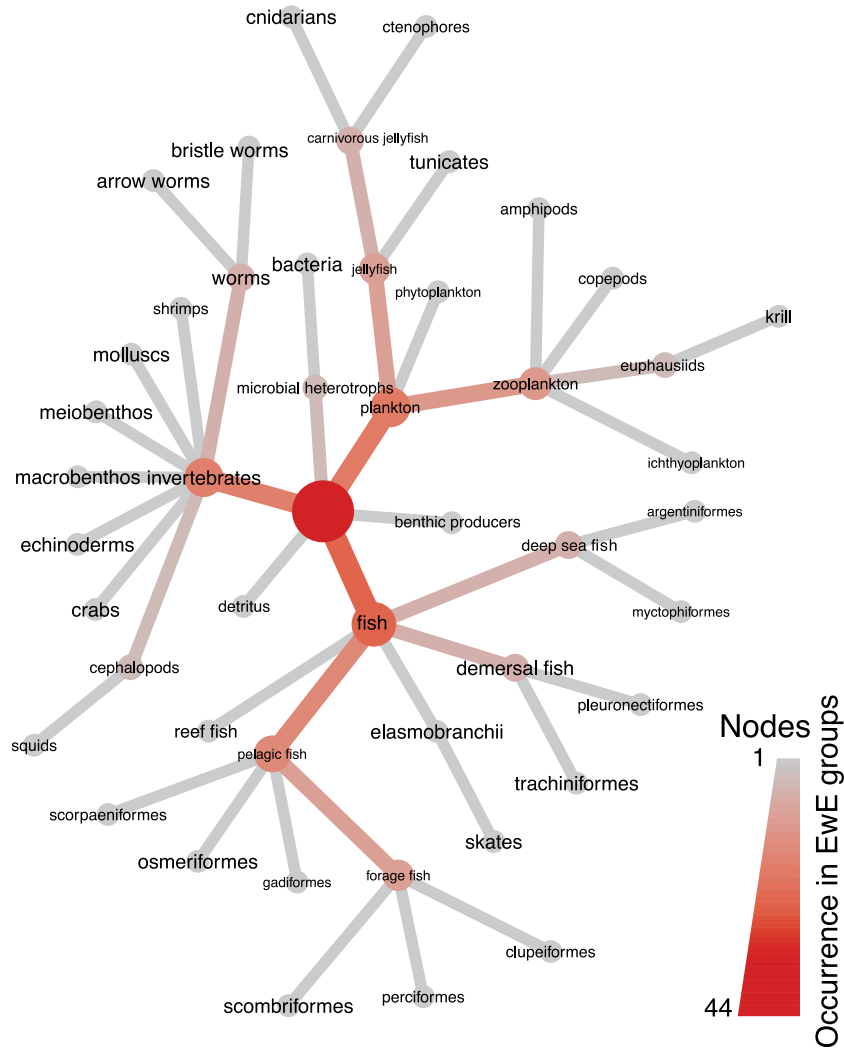
Figure 8. Reported prey items of jellyfish. Large nodes, and dark tones, indicate prey is frequently reported in models. Smaller nodes, and light tones, show that prey are infrequently listed in models. Note that the hierarchy is split into functional groups, to match the nomenclature found in models, rather than taxonomic classifications.

Regardless of whether the input parameters were sourced directly from the research, or borrowed from another EwE model, due diligence to assess the quality of the original source of the data from a model must be undertaken and explicitly stated in model documentation. To this end, we strongly encourage modellers to use Heymans *et al.* (2016) guidance: particularly the use of EwE's pedigree functionality (a score to show the confidence in the underlying assumptions of a modelled group; Christensen and Walters, 2004) as this facilitates the appropriate interpretation of EwE model predictions in light of the quality of the underlying data.

The life cycle of jellyfish

Most (but not all) cnidarian jellyfish share a metagenetic life cycle. The timing of the life cycle can vary between years within a population, between populations of the same species, and between different species (Ceh *et al.*, 2015). However, a general pattern emerges in which sessile polyps reproduce asexually on hard substrata (typically overwinter), until conditions favour

strobilation and production of planktonic jellyfish known as ephyrae (Lucas *et al.*, 2012). Ephyrae develop into large free-swimming jellyfish known as medusae (about 2–4 months in *Aurelia aurita*; Lucas, 2001). Medusae reproduce sexually to create planula, a small planktonic form that spends a few days in the water column, before settling onto hard substrata and developing into polyps. Recent evidence suggests that predators consume jellyfish life stages differently: medusae appear to be targeted less frequently than ephyrae or polyps (Lamb *et al.*, 2019). Large, free-swimming medusae are also likely to play a different trophic role to small sessile polyps both as predators and prey. EwE features a "multi-stanza" approach to model species with a changing role within the ecosystem. This is achieved by representing different ontogenetic life stages with linked groups within the model (such that population growth of adult groups depends on the success of juvenile life stages; Christensen and Walters, 2004). However, none of the reviewed models used the "multi-stanza" functionality with jellyfish groups. The lack of the incorporation of different jellyfish ontogenetic stages in models is troubling and may be a function
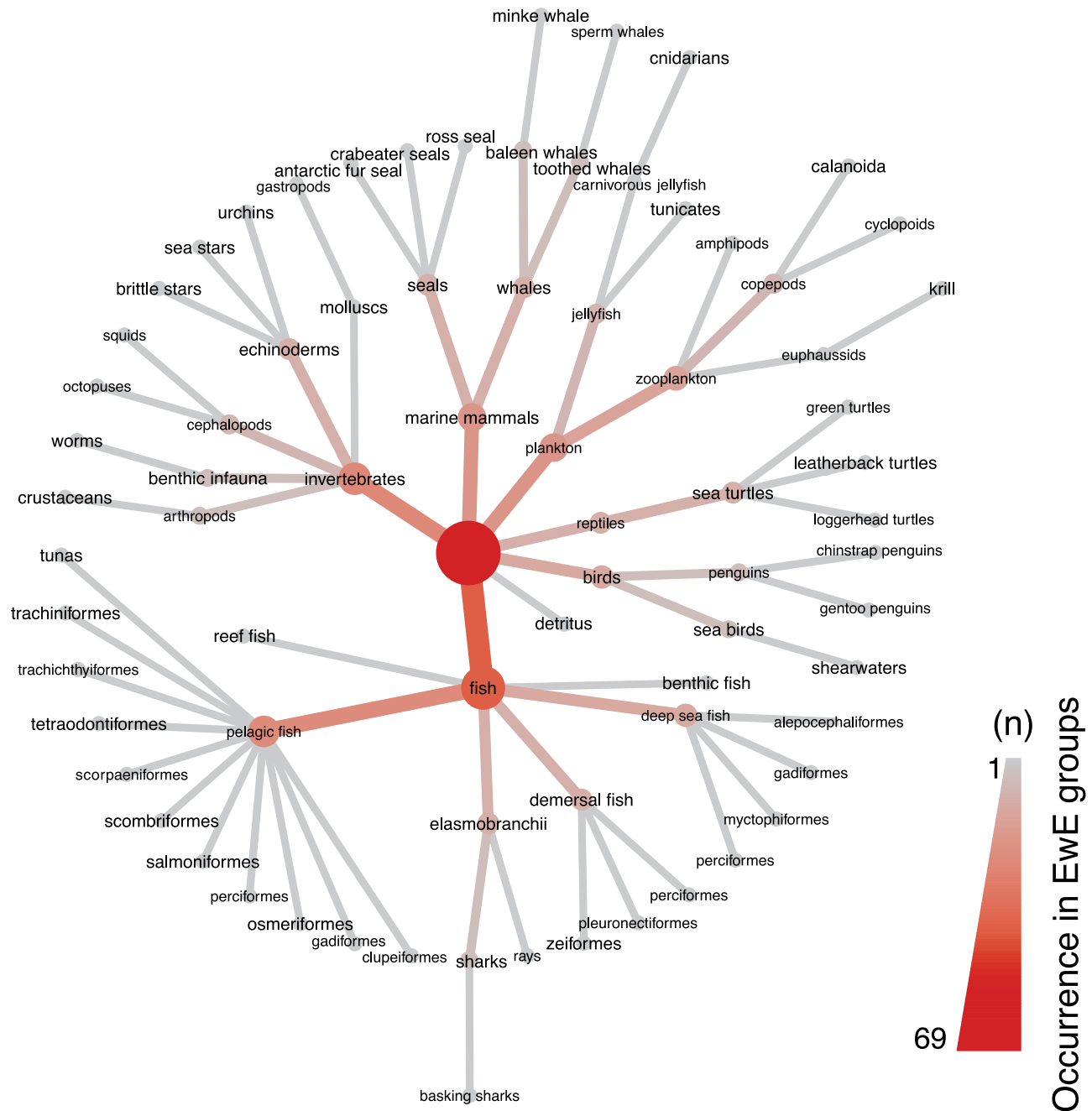
Figure 9. Predators of jellyfish. Large nodes, and dark hues, indicate a predator is frequently reported in models. Smaller nodes, and light tones, show that the predators are infrequently listed in models. Note that the hierarchy is split into functional groups, to match the nomenclature found in models, rather than taxonomic classifications.

of the rarity of quantitative data on polyp populations; reviewed by Lucas *et al.*, 2012). Additional field research into the ecology of polyps is required to generate the requisite input parameters needed for a multi-stanza approach. It should be noted that additional complexity in EwE models inherently increases the uncertainty in the output (Plagányi and Butterworth, 2004). Therefore, explicitly considering the trade-off between biological realism and model simplicity should be made when deciding if a multi-stanza approach may yield better model performance.

Conclusion

Jellyfish are recognized as an important part of marine ecosystems around the world, and feature in a growing array of EwE models. Analysis of 329 models uncovered the current state of jellyfish in EwE models, as well as future data needs. Here, we focused on areas that were addressable with the metadata held in Ecobase. However, there are other parameters within EwE (especially those pertaining to Ecosim modules) that may affect model performance: vulnerability, time spent in the foraging arena, and speed splitting settings for jellyfish groups could be further explored

(ideally with time-series data) to improve biological realism. Outside the modelling environment, other measures could take place to improve the biological realism of modellers. Historically, jellyfish have been overlooked or ignored in many monitoring programmes (Hamilton, 2016). Moving forward, including jellyfish in monitoring programmes and making data available either through publication or the use of databases is warranted: at present, modellers may lack the biological details required to accurately parameterize jellyfish groups. Research should also be directed towards quantifying the interspecific interactions between jellyfish and the rest of the ecosystem. Furthermore, documenting the ecology of wild polyps and less studied jellyfish life stages are also recommended. These steps should facilitate the accurate parametrization of jellyfish groups in EwE models and may, ultimately, improve our knowledge of the role of jellyfish in marine ecosystems and our ability to manage jellyfish populations.

Supplementary data

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

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References

Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., and Friday, N. 2007. A Comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands Large Marine Ecosystems Through Food Web Modeling. 298 pp. http://www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-178.pdf (last accessed 31 July 2018).

Aydin, K. Y., Lapko, V. V., Radchenko, V, I., and Livingston, P. A. 2002. A Comparison of the Eastern Bering and Western Bering Sea Shelf and Slope Ecosystems Through the Use of Mass-Balance Food Web Models. NOAA Technical Memorandum NMFS-AFSC-130: 78. http://www.afsc.noaa.gov/ Publications/AFSC-TM/NOAA-TM-AFSC-130.pdf (last accessed 1 August 2018).

Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., and Palmeri, L. 2009. Trophic network model of the northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. Estuarine, Coastal and Shelf Science, 83: 577–590.

Bastian, T., Lilley, M. K. S., Beggs, S. E., Hays, G. C., and Doyle, T. K. 2014. Ecosystem relevance of variable jellyfish biomass in the Irish Sea between years, regions and water types. Estuarine, Coastal and Shelf Science, 149: 302–312.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., and Pauly, D. 2012. Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia, 690: 3–20.

Butts, C. T. 2008. network: a package for managing relational data in R. Journal of Statistical Software, 24: 1–36.

Cardona, L., de Quevedo, I. Á., Borrell, A., and Aguilar, A. 2012. Massive consumption of gelatinous plankton by Mediterranean apex predators. PLoS One, 7: e31329.

Ceh, J., Gonzalez, J., Pacheco, A. S., and Riascos, J. M. 2015. The elusive life cycle of scyphozoan jellyfish—metagenesis revisited. Scientific Reports, 5: 12037.

Cheung, W. W. L., and Pitcher, T. J. 2005. A mass-balance model of the Falkland Islands fisheries and ecosystems. Fisheries Centre Research Reports, 13: 6584.

Christensen, V., and Pauly, D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109–139.

Christensen, V., Walters, C. J., and Pauly, D. 2005. Ecopath with Ecosim: A User's Guide. http://www.ecopath.org/modules/ Support/Helpfile/EweUserGuide51.pdf (last accessed 31 July 2018).

Coll, M., Palomera, I., Tudela, S., and Sardà, F. 2006. Trophic flows, ecosystem structure and fishing impacts in the south Catalan Sea, northwestern Mediterranean. Journal of Marine Systems, 59: 63–96.

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., and Christensen, V. 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecological Modelling, 302: 42–53.

Condon, R., Lukas, C., Pitt, K., and Uye, S. 2014. Jellyfish blooms and ecological interactions. Marine Ecology Progress Series, 510: 109–110.

Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., and Sutherland, K. R. 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience, 62: 160–169.

D'Ambra, I., Graham, W., Carmichael, R., and Hernandez, F. 2018. Dietary overlap between jellyfish and forage fish in the northern Gulf of Mexico. Marine Ecology Progress Series, 587: 31–40.

Doyle, T. K., Houghton, J. D. R., McDevitt, R., Davenport, J., and Hays, G. C. 2007. The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. Journal of Experimental Marine Biology and Ecology, 343: 239–252.

Essington, T. E. 2007. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Canadian Journal of Fisheries and Aquatic Sciences, 64: 628–637.

Finenko, G. A., Kideys, A. E., Anninsky, B. E., Shiganova, T. A., Roohi, A., Tabari, M. R., Rostami, H. *et al.* 2006. Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. Marine Ecology Progress Series, 314: 171–185.

Foster, Z. S. L., Sharpton, T., and Grunwald, N. J. 2017. MetacodeR: an R package for manipulation and heat tree visualization of community taxonomic data from metabarcoding. PLoS Computational Biology, 13: e1005404.

Froese, R., Winker, H., Gascuel, D., Sumaila, U. R., and Pauly, D. 2016. Minimizing the impact of fishing. Fish and Fisheries, 17: 785–802.

Gucu, A. C. 2002. Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuarine, Coastal and Shelf Science, 54: 439–451.

Hamilton, G. 2016. The secret lives of jellyfish. Nature, 531: 432–434.

Hansson, L., Moeslund, O., Kiørboe, T., and Riisgård, H. 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Marine Ecology Progress Series, 304: 117–131.

Hays, G. C., Doyle, T. K., and Houghton, J. D. R. 2018. A paradigm shift in the trophic importance of jellyfish? Trends in Ecology & Evolution, 33: 874–884.

Heymans, J. J., and Baird, D. 2000. Network analysis of the northern Benguela ecosystem by means of network and Ecopath. Ecological Modelling, 131: 97–119.

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., and Christensen, V. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecological Modelling, 331: 173–184.

Jennings, S., and Rice, J. 2011. Towards an ecosystem approach to fisheries in Europe: a perspective on existing progress and future directions. Fish and Fisheries, 12: 125–137.

Lamb, P. D., Hunter, E., Pinnegar, J. K., Creer, S., and Taylor, M. I. 2019. Cryptic diets of forage fish: jellyfish consumption observed in the Celtic Sea and Western English Channel. Journal of Fish Biology, 94: 1026–1032.

Libralato, S., Coll, M., Tempesta, M., Santojanni, A., Spoto, M., Palomera, I., Arneri, E. *et al*. 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. Biological Conservation, 143: 2182–2194.

Link, J. S., Griswold, C. A., Methratta, E. T., and Gunnard, J. 2006. Documentation for the Energy Modeling and Analysic eXercise (EMAX). Northeast Fisheries Science Center reference document: 06-15.

Lucas, C. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita* in relation to its ambient environment. Hydrobiologia, 451: 229–246.

Lucas, C. H., Graham, W. M., and Widmer, C. 2012. Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Advances in Marine Biology, 63: 133–196.

Lucas, C. H., Jones, D. O. B., Hollyhead, C. J., Condon, R. H., Duarte, C. M., Graham, W. M., Robinson, K. L. *et al*. 2014. Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Global Ecology and Biogeography, 23: 701–714.

Lynam, C., Gibbons, M., Axelsen, B., Sparks, C., Coetzee, J., Heywood, B., and Brierley, A. S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. Current Biology, 16: R492–R493.

Malej, A. 1989. Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskål, 1775). Journal of Experimental Marine Biology and Ecology, 126: 259–270.

Murawski, S. A. 2007. Ten myths concerning ecosystem approaches to marine resource management. Marine Policy, 31: 681–690.

Okey, T. A., and Pauly, D. 1999. Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post-spill period 1994–1996. Fisheries Centre Research Reports, 7: 1–137.

Orek, H. 2000. An application of mass-balance Ecopath model to the trophic structure in the Black Sea after anchovy collapse. 119 pp.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Rashid, S. U., Walters, C. J., Watson, R. *et al*. 2002. Towards sustainability in world fisheries. Nature, 418: 689–695.

Pauly, D., Graham, W., Libralato, S., Morissette, L., and Deng Palomares, M. L. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia, 616: 67–85.

Pitcher, T., Buchary, E., and Trujillo, P. 2002. Spatial simulations of Hong Kong's marine ecosystem: forecasting with MPAs and human-made reef. Fisheries Centre Research Reports, 10: 1–168.

Pitcher, T. J., Kalikoski, D., Short, K., Varkey, D., and Pramod, G. 2009. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. Marine Policy, 33: 223–232.

Plagányi, É. E., and Butterworth, D. S. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. African Journal of Marine Science, 26: 261–287.

Purcell, J. E. 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annual Review of Marine Science, 4: 209–235.

QGIS Development Team. 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. https://www.qgis.org/ (last accessed 13 August 2018).

R Core Team. 2017. R: A Language and Environment for Statistical Computing. https://www.R-project.org/ (last accessed 12 August 2018).

Roux, J. P., Van Der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D. M., and Cury, P. M. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: lessons from the Benguela. Bulletin of Marine Science, 89: 249–284.

Sanz-Martín, M., Pitt, K. A., Condon, R. H., Lucas, C. H., Novaes de Santana, C., and Duarte, C. M. 2016. Flawed citation practices facilitates the unsubstantiated perception of a global trend toward increased jellyfish blooms. Global Ecology and Biogeography, 25: 1039–1049.

Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., and Christensen, V. 2013. Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial-temporal data. Ecological Modelling, 263: 139–151.

Sullivan, L. J., and Kremer, P. 2011. Gelatinous zooplankton and their trophic roles. *In* Treatise on Estuarine and Coastal Science, pp. 127–172. Ed. by D. McLusky and E. Wolanski. Elsevier, London.

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