

## Jellyfish in ecosystems, online databases, and ecosystem models

Daniel Pauly · William Graham ·  
Simone Libralato · Lyne Morissette ·  
M. L. Deng Palomares

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**Abstract** There are indications that pelagic cnidarians and ctenophores ('jellyfish') have increased in abundance throughout the world, or that outbreaks are more frequent, although much uncertainty surrounds the issue, due to the scarcity of reliable baseline data. Numerous hypotheses have been proposed for the individual increases or outbreaks that are better documented, but direct experimental or

manipulative studies at the ecosystem scale cannot be used for testing them. Thus, ecological modeling provides the best alternative to understand the role of jellyfish in large fisheries-based ecosystems; indeed, it is an approach consistent with new ecosystem-based fisheries management practices. Here, we provide an overview of online databases available to ecosystem modelers and discuss general aspects and shortcomings of the coverage of jellyfish in these databases. We then provide a summary of how jellyfish have been treated and parameterized by existing ecosystem models (specifically focusing on 'Ecopath with Ecosim' as a standard modeling toolset). Despite overall weaknesses in the parameterization of jellyfish in these models, interesting patterns emerge that suggest some systems, especially smaller and more structured ones, may be particularly vulnerable to long-term jellyfish biomass increase. Since jellyfish also feed on the eggs and larvae of commercially important food fish, outbreaks of jellyfish may ultimately imply a reduction in the fish biomass available to fisheries. On the other hand, jellyfish, which have been traditionally fished for human consumption in East and Southeast Asia, are now seen as a potential resource in other parts of the world, where pilot fisheries have emerged. It is also argued here that reduced predation on the benthic and pelagic stages of jellyfish, both a result of fishing, may be a strong contributing factor as well. For marine biologists specializing on jellyfish, this means that their research might become more applied. This

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Jellyfish Blooms: Causes, Consequences, and Recent Advances

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D. Pauly (✉) · M. L. Deng Palomares  
Sea Around Us Project, Fisheries Centre,  
University of British Columbia, 2202 Main Mall,  
Vancouver, BC, Canada V6T 1Z4  
e-mail: d.pauly@fisheries.ubc.ca

M. L. Deng Palomares  
e-mail: m.palomares@fisheries.ubc.ca

W. Graham  
Dauphin Island Sea Lab and University of South  
Alabama, 101 Bienville Blvd., Dauphin Island,  
AL 36528, USA  
e-mail: mgraham@disl.org

S. Libralato  
Istituto Nazionale di Oceanografia e di Geofisica  
Sperimentale—OGS, Borgo Grotta Gigante 42/c,  
Sgonico, Trieste 34010, Italy  
e-mail: slibralato@ogs.trieste.it

L. Morissette  
Institut des Sciences de la Mer de Rimouski, 310, Allée  
des Ursulines C.P. 3300, Rimouski, QC, Canada G5L 3A1

implies that they would benefit from adopting some concepts and methods from fisheries biology and ecosystem modeling, and thus from using (and contributing to) online databases, such as SeaLifeBase and FishBase, developed to support such research. This would remedy the situation, documented here, wherein jellyfish are either infrequently included in food web models, typically constructed using the Ecopath with Ecosim software, or included as a single functional group with the characteristic of an ‘average’ jellyfish. Thus, jellyfish specialists could readily improve the jellyfish-related components of such models, and we show how they could do this. Also, it is suggested that when such improvement is performed, the resulting models can lead to non-intuitive inferences and hence interesting hypotheses on the roles of jellyfish in ecosystems. This is illustrated here through (a) an investigation of whether jellyfish are keystone species and (b) the identification of conditions under which (simulated) jellyfish outbreaks may occur.

**Keywords** Ecopath with Ecosim · FishBase · SeaLifeBase · Keystone species · Fishing down marine food webs · Jellyfish outbreaks

## Introduction

There are a number of examples of what appear to be recent (i.e., past few decades) increases, if not only longer-term climate-driven cycles, of jellyfish populations (reviewed by Mills, 2001; Graham, 2001; Brodeur et al., 2002; Purcell, 2005; Kawahara et al., 2006; Purcell et al., 2007). Since the majority of the world’s oceans are under some level of fishing pressure (Pauly et al., 1998a, b; 2002), it is reasonable to say that jellyfish predators, at a minimum, contribute additionally through predation on eggs and larvae of fishes to a multitude of human-induced pressures (Halpern et al., 2008). It only makes sense, therefore, that fisheries, by either contributing directly to increased jellyfish populations or by being impacted by jellyfish (or both), should incorporate jellyfish populations into newly emerging ecosystem-based fisheries management schemes (Ruckelshaus et al., 2008).

Historically, the relationship between jellyfish scientists and fisheries scientists has been obscured. We may attribute this to differences between applied and basic science approaches, and thus where our respective work is ultimately published. It is likely, though, a difference in scientific language, tools, and data requirements contributes as much as simply not reading each other’s publications. Therefore, it is of greatest priority that fisheries scientists understand the truly special nature of arguably the most important predators of the sea, the jellyfish, and that jellyfish scientists understand what tools are being used in fisheries research and, consequently, how best to supply good data to, and/or collaborate with, fisheries scientists.

In this contribution, we highlight established toolsets currently in use by fisheries sciences to describe the functioning of the ecosystems upon which fisheries are based, notably the modeling architecture of Ecopath with Ecosim (EwE; [www.ecopath.org](http://www.ecopath.org)). More precisely, the three specific aims of this contribution are:

The first is to review the coverage of jellyfishes in two online databases, FishBase and SeaLifeBase. We also seek to review and examine the role of jellyfish in published trophic models of ecosystems, constructed using the ‘EwE’ software and, in part at least, parameterized with the aid of these databases. We pay special attention to important parameterization features of EwE so that future modeling efforts may correctly incorporate jellyfish.

Our second aim is to provide examples of the kind of hypotheses concerning the ecological role of jellyfish that can be tested using such trophic models. This concerns hypotheses based on the structure (relative biomasses, food web linkages, etc.) of such (Ecopath) models, as well as hypotheses resulting from an examination of their population dynamics (as run by Ecosim).

Our third aim, finally, is to reframe these hypotheses, all eminently testable, around the ubiquitously observed pattern of ‘fishing down marine food webs’ (Pauly et al., 1998a, b), to explain why jellyfish outbreaks, worldwide, should occur more frequently than hitherto—notwithstanding the fact that the compelling evidence that they do is dubious, owing to the nature of available datasets (Purcell, 2005). We then conclude by outlining what we believe would be fruitful avenues for further research.

## Jellyfish in FishBase

FishBase ([www.fishbase.org](http://www.fishbase.org)) is an online database of fish, containing information about all (>30,000) fish species described so far. It provides information on nomenclature and taxonomy, as well as quantitative and qualitative information on biological and ecological aspects of fish (e.g., distribution, food and feeding, growth, and reproduction, all of which can be combined to yield new insights), extracted from the scientific literature and fully referenced (Froese & Pauly, 2000). FishBase is a hugely successful online resource to scientists and laypersons alike, with about 25 millions ‘hits’ and over 2 million visitors per month.

Initially conceived for the purposes of (single-species) fisheries management, FishBase now increasingly includes data which link fish to their ecosystem, paralleling the move of fisheries science toward ecosystem-based consideration (Pikitch et al., 2006). FishBase thus includes much information on the prey of fishes, including jellyfish, both as reports on individual food items and as components of detailed diet composition studies. Also, FishBase incorporates information on fish predators, including jellyfish. This information, extracted from Arai (1987) and Purcell (1985) and other sources, is summarized in Fig. 1 (top). A total of 124 species of fish are reported as feeding occasionally or predominately on jellyfish. Of these, 11 species appear specialized, and about half belong to the perciform fishes. The size distribution of the fish species feeding on jellyfish is presented in Fig. 2A. As might be seen, the majority of the fish predators fall in the range of 50 to 200 cm maximum length; also, the number of species feeding on jellyfish decreases rapidly as the size increases.

## Jellyfish in SeaLifeBase

SeaLifeBase ([www.sealifebase.org](http://www.sealifebase.org)) represents an attempt to reproduce the success of FishBase for marine organisms other than fish, thus including jellyfish. Its coverage of jellyfish relies on a taxonomy provided by the Catalogue of Life ([www.catalogoflife.org](http://www.catalogoflife.org)), based, in the case of jellyfish, on the work of Van der Land (2006).

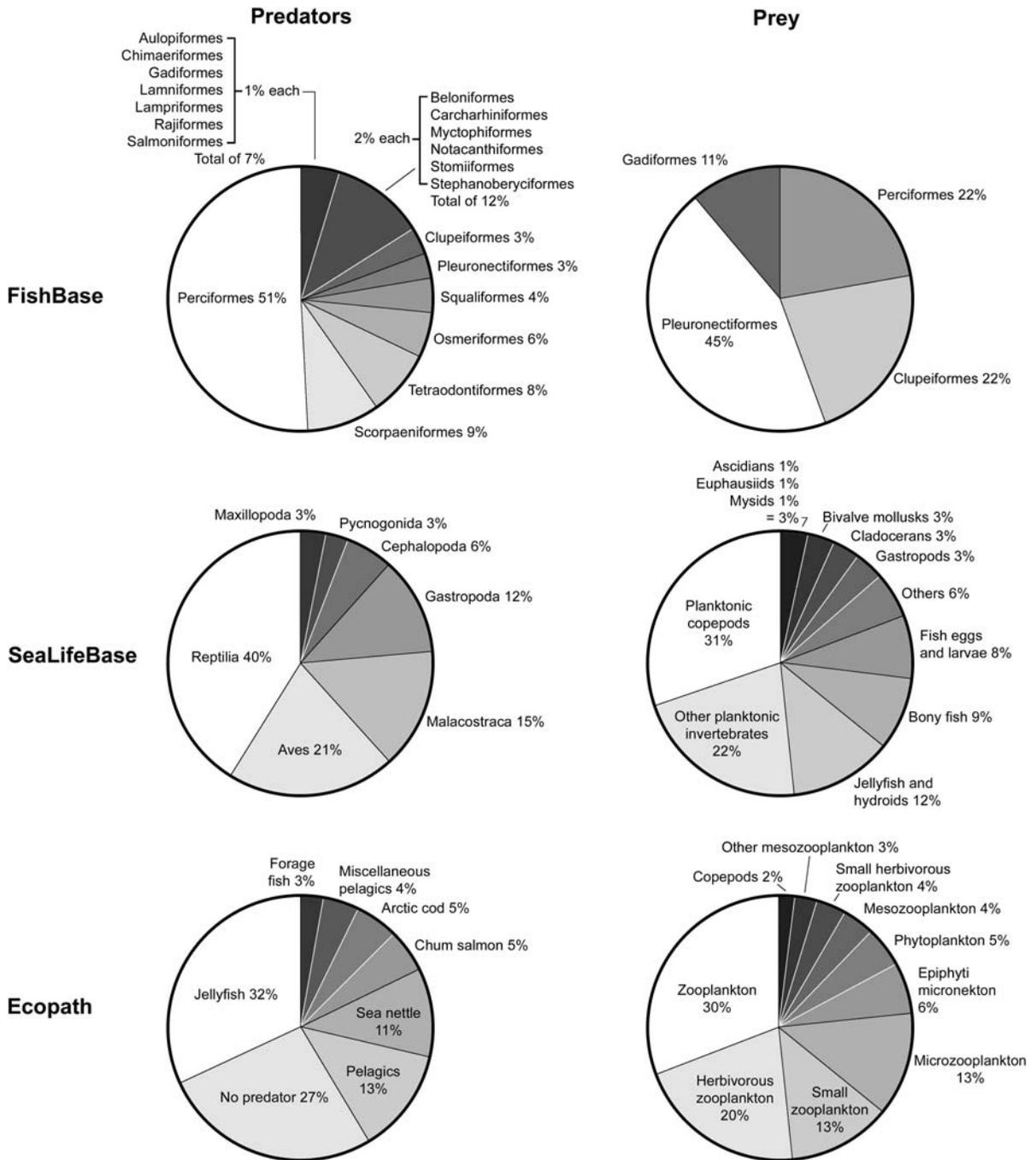
SeaLifeBase has the same basic structure as FishBase, and thus can similarly be used to summarize

jellyfish predator/prey information, but for animals other than fish. This is presented here in Fig. 1 (middle) and Fig. 2B. As might be seen, 34 non-fish marine organisms, mainly reptiles, birds, and crustaceans, are reported as feeding, at least occasionally, on jellyfish. The size distribution of these predators evidences, similarly to that observed for fish predators, a decrease in the number of non-fish predator species as the size increases. We do not believe that this pattern will change as the coverage of SeaLifeBase is extended.

## Jellyfish in (Ecopath) ecosystem models

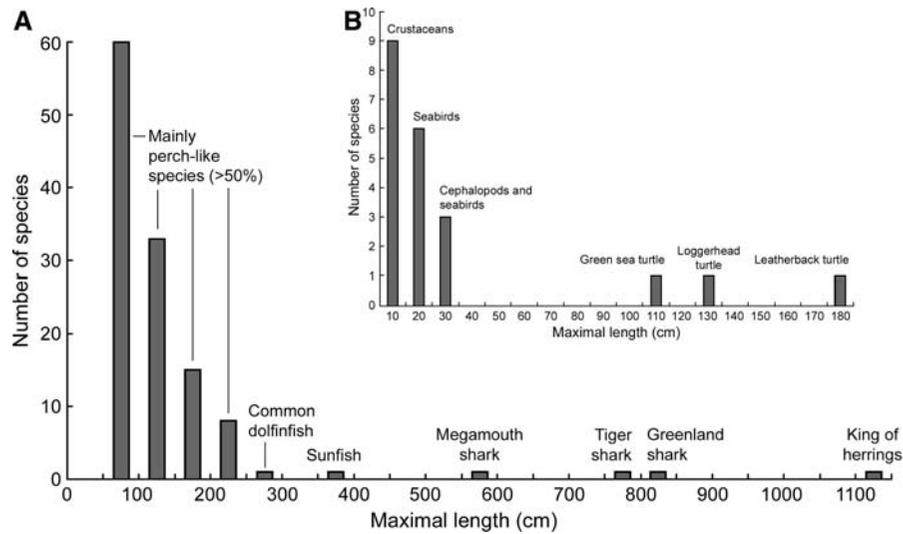
There are various ways to represent ecosystems through formal, quantitative models. The model structure will depend on whether its prime intent is to summarize and validate one’s knowledge of an ecosystem, to draw inference on ecosystem properties, to test hypotheses on various aspects of ecosystem structure and functioning, or to run various management scenarios. One of the most commonly used ecosystem modeling approaches is that incorporated in the Ecopath with Ecosim (EwE) software (see [www.ecopath.org](http://www.ecopath.org)). Central to this method is the representation of mass-balance trophic flows between functional groups for basic parameterization (i.e., ‘Ecopath models’; Christensen & Pauly, 1992). These interactions can then be run in ‘Ecosim’ and ‘Ecospace’ for time-dynamic and spatial simulations, respectively (Walters et al., 1997, 1998; Pauly et al., 2000), but this contribution focuses exclusively on Ecopath and Ecosim.

Owing in part to the ease with which such models can be constructed based on previously published data, over 400 EwE models of (mostly marine) ecosystems have been built and documented in media ranging from Masters and PhD theses to reports and articles in the peer-reviewed literature (see [www.ecopath.org](http://www.ecopath.org)). Over 100 of these models (all representing marine ecosystems, and most developed by fisheries scientists) were examined in the context of a wider study examining the relationship between the ‘quality’ of Ecopath models (as defined by the level of detail included and the types of data for model construction) and the resilience exhibited in their time-dynamic behavior (Morissette, 2007). Of these, only 23 explicitly included gelatinous zooplankton (medusae,



**Fig. 1** Summary of data on the predators and prey of jellyfish available in three online sources. Top left: Orders to which the 124 fish species belong that are reported to prey on gelatinous organisms (from 181 food items records in FishBase); Top right: Orders to which the 11 fish species belong that are preyed on by gelatinous organisms (data from FishBase); Middle left: Non-fish marine organisms (34

species) preying on gelatinous organisms (data from SeaLifeBase); Middle right: Non-fish marine organisms (89 species) consumed by gelatinous organisms (data from SeaLifeBase); Bottom left: Main predators of gelatinous organisms assembled from 21 (Ecopath) ecosystem models; Bottom right: Main prey of gelatinous organisms assembled from the same 21 ecosystem models



**Fig. 2** Size distribution of (groups of) predators of jellyfish. Size distribution of fish feeding on jellyfish, with the smallest fish feeding mainly on hydroids, and the largest, the King of herrings (*Regalecus glesne* Ascanius, 1772), being documented by only 4 specimens (data from FishBase) (A); Size distribution

of non-fish organisms feeding on jellyfish, with the smallest consisting mainly of planktonic crustaceans feeding on ephyrae, and the largest consisting of marine turtles (data from SeaLifeBase) (B)

ctenophores, or pelagic tunicates) as a distinct functional group in their food webs.

Consistency among models in how detailed they are with respect to ‘jellyfish’ is an important consideration when attempting to evaluate and compare them. We are mindful that the overwhelming majority of models do not include a jellyfish compartment, and those that do tend to collapse all things considered gelatinous into a single functional ‘jellyfish’ group. With few exceptions, such as the Chesapeake Bay (Baird & Ulanowicz, 1989; Walters et al., 2005) and the eastern Bering Sea (Trites et al., 1999; NRC, 2003) models, a single jellyfish group poorly represents the true diversity of taxa and trophic interactions involving jellyfish. Hopefully, this can be overcome in the future, in part, by online databases such as SeaLifeBase.

We suspect the low number of models incorporating jellyfish, far from reflecting the true importance of jellyfish in marine ecosystems, in fact highlights the limited knowledge many fisheries scientists or marine biologists have of jellyfish. However, we also believe that the crude representation of ‘jellyfish’ as a single, undifferentiated functional group in most models that did include gelatinous zooplankton (see Table 1) may also indicate lack of access to or appreciation for the key literature on these taxonomic

groups. With this caveat in mind, the main prey and predators of jellyfish included in these 23 models are summarized in Fig. 1 (bottom).

The outcome of a modeling effort is only as good as its initializing parameters. For EwE, there are a suite of common parameters utilized, sometimes available from the above databases, most of the time not. Following is a brief summary of key EwE parameters and how they, typically, have been handled for jellyfish in most existing models. Additionally, we provide brief insight on how these parameters can be individually measured or estimated so that future modeling efforts can handle jellyfish more realistically.

**Diet and Trophic Level.** Within the EwE construct, the diet composition of functional groups (typically species, or groups thereof) defines the position in the food web, and ultimately Trophic Level (TL). To assume that all jellyfish have the same diet and exist at the same trophic level would be very wrong. Indeed, their different morphologies, swimming modes, prey capture, and nematocyst composition yield widely different diets (Purcell & Mills, 1988; Costello & Colin, 1995; Peach & Pitt, 2005). Even within a species, diet may change simply due to an increase in size (Graham & Kroutil, 2001). Finally, it is particularly important to consider multiple jellyfish

**Table 1** Summary of major features of the (Ecopath) ecosystem models used in the analyses of trophic interaction presented here (i.e., Fig. 4); models with an asterisk (\*) were also used for Ecosim runs

Model name	Ecosystem type and location	Years	Living + non-living groups	Gelatinous plankton group (GLP)	GLP ( $t \cdot km^{-1}$ )	P/B ( $year^{-1}$ )	Q/B ( $year^{-1}$ )	EE	Human impacts	References
*Chesapeake Bay	Temperate, enclosed coastal area	1983–1986	33 + 1	Sea nettle; TL = 3.31	0.00020	5.00	2.00	<b>0.000</b>	Highly impacted system	Baird & Ulanowicz (1989) and Walters et al. (2005)
*Central North Pacific	Temperate, open ocean	1990–1998	25 living groups; 9 fishing fleets	'Jellyfish'; TL = 3.0	0.00612	0.79	20.00	<b>0.001</b>	Top predators (tuna) fisheries	After Cox et al. (2002)
*Eastern Bering Sea	Temperate shelf and slope down to 500 m	1955–1960	23 + 2; 5 fishing fleets	Mainly <i>Chrysaora melanaster</i> ; TL = 3.16	0.00016	0.88	2.00	<b>0.018</b>	Exploited, marine mammals declined	Trites et al. (1999) and NRC (2003)
*Georgia Strait	Temperate narrow basin, average depth 156 m	1950s	26 + 1; 3 fishing fleets	'Jellyfish'; TL = 3.02	0.01861	3.00	12.00	<b>0.211</b>	Heavily exploited in the last 90 years	Pauly et al. (1998a, b) Martell et al. (2002) and Walters et al. (2005)
Hong Kong waters	Tropical inshore waters	1990s	36 + 1 detritus pool; 7 fleets	'Jellyfish'; TL = 3.0	0.00578	5.01	25.05	<b>0.257</b>	Stocks re-building	Cheung et al. (2002) and Buchary et al. (2002)
Lancaster Sound	Shallow area in the Canadian Arctic	Late 1980s	31 + 1 detritus pool; 1 fishing fleet	<i>Mertensia ovum</i> ; TL = 2.98	0.01190	8.82	29.41	<b>0.806</b>	Moderate fishing	Mohammed (2001)
North Coast of Central Java	Tropical shelf, shallow coastal area	Mid 1970s	27 + 1 detritus pool; 6 fishing fleets	Mainly Scyphozoans; TL = 3.0	0.00045	5.01	25.05	<b>0.528</b>	Low to moderate fishing; near shore	Buchary (1999)
Norwegian-Barents Sea 1950	Temperate ecosystem; from intertidal area to over 3,000 m depth	1950s	30 living groups; 9 fishing fleets	'Jellyfish'; TL = 3.17	0.01762	3.00	10.00	<b>0.343</b>	Moderate fishing activity;	Dommasnes et al. (2001)
Norwegian-Barents Sea 1997	Temperate ecosystem; from intertidal area to over 3,000 m depth	1997–2000	30 living groups; 9 fishing fleets	'Jellyfish'; TL = 3.19	0.02004	3.00	10.00	<b>0.339</b>	High fishing activity	Dommasnes et al. (2001)
Southeastern United States	Tropical, continental shelf area, from intertidal to 500 m depth	1995–1998	41 + 1 detritus group; 9 fleets	'Jellyfish'; TL = 2.8	0.00028	40.00	80.00	0.950	Intense trawling activity; highly fished	Okey & Pugliese (2001)

Table 1 continued

Model name	Ecosystem type and location	Years	Living + non-living groups	Gelatinous plankton group (GLP)	GLP ( $t \cdot km^{-1}$ )	P/B ( $year^{-1}$ )	Q/B ( $year^{-1}$ )	EE	Human impacts	References
*Gulf of Thailand	Tropical shallow coastal area; 10–50 m depth range	1970s	39 + 1 detritus group; 6 fleets	'Jellyfish'; TL = 3.0	0.02198	5.00	<b>20.00</b>	<b>0.000</b>	Moderate fishing	FAO/FISHCODE (2001) and Walters et al. (2005)
US Mid Atlantic Bight	Temperate continental shelf, from upper intertidal to 200 m isobath	1995–1998	55 + 1; 1 fleet	'Jellyfish'; TL = 3.07	0.00018	18.25	80.00	0.900	Highly exploited area	Okey (2001)
Prince William Sound	Cold temperate coastal area in Alaska	1994–1996	46 + 2; 3 fishing fleets	'Jellyfish'; TL = 2.96	0.01409	8.82	29.41	<b>0.006</b>	Fishing and oil spill impacts	Okey & Pauly (1998)
West Florida Shelf	Tropical shelf area from intertidal zone to 200 m depth		55 + 4 non-living groups; 11 fisheries	Carnivorous jellyfish; TL = 3.39	0.00037	40.00	80.00	<b>0.928</b>	Problems of nutrient enrichment	Okey et al. (2004)
North Central Adriatic Sea	Shelf, 3 miles west (or to 10 m) to 12 miles from the east coast	1990s	37 + 3; 5 fisheries	Mainly <i>Pelagia noctiluca</i> ; TL = 2.66	0.01208	14.60	50.48	<b>0.170</b>	Risk of ecosystem overfishing	Coll et al. (2007)
South Catalan Sea	Upper slope from 3 miles of 50 m depth to 400 m depth.	1994–2000	37 + 3; 4 fisheries	'Jellyfish'; TL = 2.3	0.00659	26.51	56.80	<b>0.017</b>	Large impacts of fisheries	Coll et al. (2006)

Values in bold were estimated by Ecopath; GLP, gelatinous plankton group; P/B, production/biomass ratio; Q/B, consumption/biomass ratio; EE, ecotrophic efficiency (see text)

compartments when strong trophic dynamics occur among gelatinous zooplankton in the so-called jelly web (Robison, 2004).

Figure 1 (right pie charts) shows that ‘jellyfish’ as a functional group tend to be carnivorous zooplankton predators, operating at trophic levels between 2.3 and 3.3 (median = 3.0) (Table 1). Most likely, this is an accurate reflection of the TL range based on available diet information in the published literature (reviewed by Arai, 1997). However, diet estimated from jellyfish gut contents biases toward shell or carapace bearing prey and those prey most common in the plankton (e.g., copepods in Fig. 1, lower right pie chart). True energetic ration of jellyfish likely includes substantial fractions of unrecognizable items such as detritus and soft microzooplankton (e.g., naked ciliates) (Colin et al., 2005) or very large and rare prey (Pitt et al., 2008).

**Biomass (*B*).** Jellyfish are usually not included in fisheries stock assessments, and so estimates of biomass are derived either directly from the literature or from estimates based on occasional by-catch information. Either way, estimates of jellyfish biomass are confounded by their tendency to be overdispersed in nature by seasonal blooms or physical aggregation (Graham et al., 2001). New technologies such as acoustics are being successfully applied to jellyfish biomass assessment (Bamstedt et al., 2003; Colombo et al., 2003; Brierley et al., 2005; Lyman et al., 2006), and with routine time-series surveys, these should provide much-needed information to refine EwE simulations.

Even in existing EwE models, biomass estimates and related parameters of jellyfish, such as annual food production relative to biomass ( $Q/B$ ) and production per unit of biomass ( $P/B$ ), vary widely (Table 1). This is due, to a large extent, to the biomass of jellyfish not being reported in a fashion consistent with their high water content. It is conventional to report biomass of jellyfish as dry or elemental (e.g., C or N) mass, yet most EwE models are constructed using wet weight (i.e., tonnes · km<sup>-2</sup>). Thus, even our own evaluations must be taken with caution until jellyfish biomass is appropriately, uniformly, and consistently parameterized in EwE models.

**Production (*P*).** Estimates of population production by jellyfish are rare and usually limited to rapid individual growth periods during the early phase of a cohort (e.g., Van der Veer & Oorhuysen, 1985; Olesen

et al., 1994; Uye & Shimauchi, 2005). For most coastal medusae, the adult stock is derived annually from the benthic polyp stage, and for ctenophores, seasonal bloom cycles may rely on successful overwintering of a small, marginal population (Costello et al., 2006a, b). In such cases, parameterization of production for EwE may best be accomplished from population energetics (i.e., production equals metabolism plus other expenses such as reproductive output and mucus production; Arai, 1997). On the other hand, production, in EwE models (Table 1), is usually estimated from biomass and turnover rates ( $P/B$ ), which is equivalent, under equilibrium, to total mortality (Allen, 1971). Palomares & Pauly (2008) suggest that this approach, which requires estimation of individual growth parameters, can be applied to jellyfish, in spite of major differences in life-history characteristics between jellyfish (medusae and ctenophores) and fish.

**Consumption (*Q*).** Prey consumption rates by jellyfish can be estimated directly from gut contents (Purcell, 2003), but this requires knowledge of digestion times that vary widely by prey type and temperature (reviewed by Arai, 1997). Consumption may also be determined in containers or mesocosms by following losses of the ambient prey, though container effects are usually high owing to the very high clearance rates of larger jellyfish (de Lafontaine & Leggett, 1988; Cowan & Houde, 1992, reviewed by Arai, 1997). Ultimately, EwE utilizes biomass-specific consumption ( $Q/B$ ) and this parameter varies widely among models (from 2 to 80 year<sup>-1</sup> in Table 1). We suspect such differences are again due to inconsistencies in reporting jellyfish biomass as dry or wet mass.

**Ecotrophic efficiency (*EE*).** This parameter of EwE expresses the fraction of the production of jellyfish that ultimately passes on to their predators (or a fishery). Obviously, the value of EE one chooses will depend on one’s knowledge of the organisms that prey on jellyfish. As seen in Fig. 1 (pie charts on the left), predation on jellyfish by non-jellyfish consumers occurs (mostly by fish, but also sea turtles, seabird, and a few invertebrates). Indeed, some organisms are obligate jellyfish predators (e.g., ocean sunfish *Mola mola* (Linnaeus, 1758) and leatherback turtles *Dermochelys coriacea* Vandelli, 1761). However, very little is known about predation rates on jellyfish. Thus EE is often set at or near zero (Table 1), assuming jellyfish are largely trophic ‘dead

ends.’ This may be a good approximation in many ecosystems, and seasonal declines in jellyfish are often noted to be coincident with senescence (e.g., Yamamoto et al., 2008; personal observation (WG)). In a few ecosystems (e.g., the Central North Pacific), the top predators rely on throughput of energy from jellyfish to higher trophic level predators in which case EE would have to be set near to 1 (Table 1). Finally, we should mention that the EE is calculated by Ecopath for each functional group for which B, P/B, Q/B, and the diet composition are known.

**Mutual impacts through food webs**

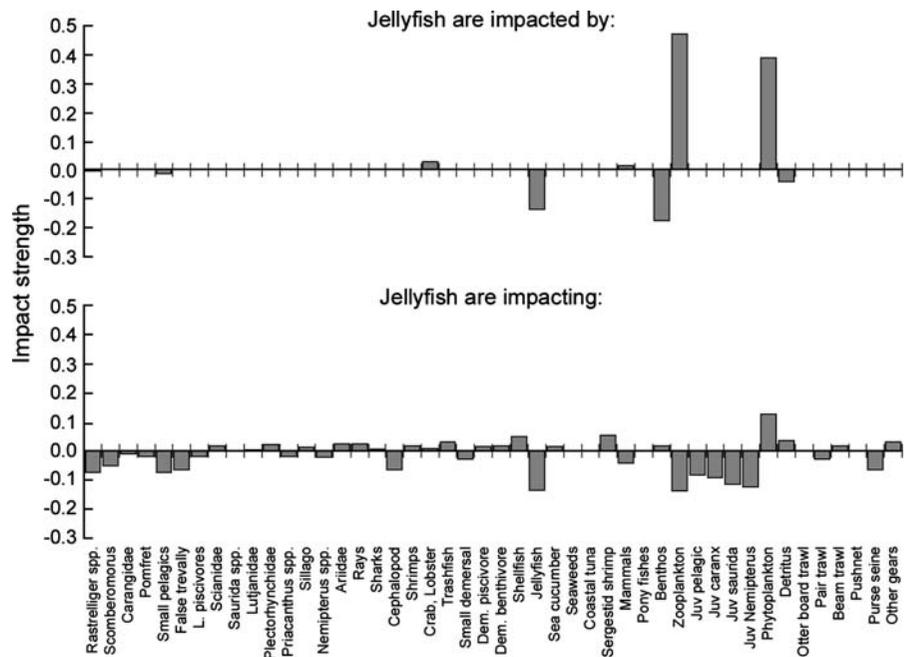
In order to further investigate the role of jellyfish in ecosystem models, we selected 5 high quality EwE models, i.e., with highly disaggregated functional groups (Pinnegar et al., 2005), parameterized mostly on the basis of accurate, locally sampled data (Morissette, 2007). These models, each representative of different regions also included EwE simulations that had been fitted to time-series data of the abundance of several of their functional groups (although none was fitted with jellyfish time-series data), which precludes model parameterizations from

generating pathological behaviors, e.g., system self-simplification (Christensen & Walters, 2004). All five of these models (highlighted in Table 1) were rechecked by the persons who created them, and they all fitted the available time-series reasonably well.

The mutual impact matrix within Ecopath was used to compare the ‘with/without’ impact of predation by jellyfish on the ecosystem as a whole (Fig. 3). This method allows the estimation of the relative direct or indirect impact of a (small) change in the biomass of one group on all other functional groups in the ecosystem, given the assumption that their diet composition remains constant (Ulanowicz & Puccia, 1990; Christensen & Pauly, 1992). As can be seen from Fig. 3 (upper panel), jellyfish are mainly impacted by plankton groups (phytoplankton and zooplankton) which are their direct and indirect prey. Figure 3 represents an example for the Gulf of Thailand, but this was true for all studied ecosystems.

The relatively few reported predators (both diversity and number) of jellyfish in ecosystems do not generate an important overall impact on the group. This strongly suggests that jellyfish species are subject to bottom–up control from their forage base rather than top–down controls from predators. One exception supporting strong top–down control

**Fig. 3** Graphic representation of a partial output of the mutual impact matrix of Ecopath, here for the Gulf of Thailand ecosystem model documented in Table 1, and used to evaluate the impacts on jellyfish of a small increase of biomass of the other groups in the system (above), and the impact on the other groups in the system of a small increase of jellyfish in the same system (below)



involves predation by one functional group of jellyfish on another, which of course generates an apparent negative impact of jellyfish on itself. On the other hand, most species of the ecosystem are indirectly impacted by jellyfish (Fig. 3, lower panel). A positive impact of jellyfish predation is seen on phytoplankton (because jellyfish consume herbivorous zooplankton), and on different fish species (for example, Ariidae, rays, shellfish, sergestid shrimp in the Gulf of Thailand) that share the characteristics of being benthivorous species. A negative impact of jellyfish is also seen on different zooplankton groups (their main prey), and indirectly on fish such as Indian mackerels (*Rastrelliger* spp.), Spanish mackerel (*Scomberomorus* spp.), false trevally *Lactarius lactarius* (Bloch & Schneider, 1801), or small pelagics species that are mainly zooplanktivorous.

### Jellyfish keystoneeness

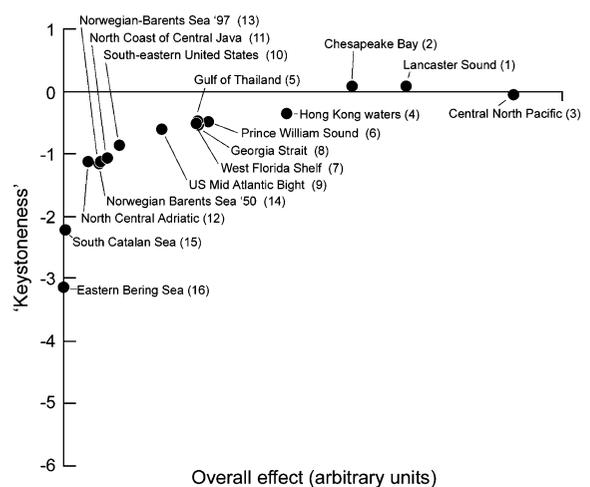
The analysis of the role of jellyfish within ecosystems can be broadened by asking whether they can be labeled as keystone species/group. Keystone species, first identified by Paine (1969), are defined by Power et al. (1996) as species that are important to the structure and productivity of the ecosystem in which they occur, but without being abundant. Using the most famous ‘keystone’ example, in kelp forest ecosystems along the Pacific coast of North America, despite the kelp’s structures and the fact that it fuels the entire system, it is the relatively rare sea otter who plays that role, by keeping sea urchins in check, thus preventing the kelp from being grazed and being turned into an urchin ‘barren’ (Estes & Palmisano, 1974; Power et al., 1996).

One problem with this concept is that assessing whether a given species performs the role of a keystone through field experiments is difficult at best (Paine, 1992), and impossible in the majority of cases. In response to this, Libralato et al. (2006) developed a modeling approach to investigate this concept based on the mutual impact matrix of EwE (see above). Therein the ‘keystoneeness’ of a species in its ecosystem (or more precisely of a functional group representing that species in an ecosystem model) is computed from the ratio of the sum of its direct and indirect impacts on all other groups in the system over its biomass (Libralato et al., 2006).

In this sense, the concept of jellyfish keystoneeness may be an appropriate approach to understand why certain ecosystems appear to be more vulnerable to jellyfish population increases.

Sixteen ecosystem models were used for this analysis, constituting a subset of the original 42 models included in Libralato et al. (2006) that included jellyfish (see Table 1 for a brief description). The habitat types they cover range from semi-enclosed waters in the case of Chesapeake Bay (Baird & Ulanowicz, 1989) and Prince William Sound (Okey & Pauly, 1998) to large areas of the open ocean such as the Central North Pacific (Cox et al., 2002). The ecosystems represented are also subject to different degrees of human impacts, ranging from heavily fished, e.g., the Hong Kong area (Cheung et al., 2002), to exploitation targeting mainly top predators, e.g., the Central North Pacific (Cox et al., 2002). All are well described, and include a minimum of 24 functional groups. Jellyfish represent a highly variable fraction of the total biomass of these ecosystems, ranging from approximately 1/50 in the Norwegian-Barents Sea (Trites et al., 1999) to less than 1/5,000 in the Eastern Bering Sea (Dommasnes et al., 2001).

Overall, the results show that jellyfishes’ keystoneeness ranges widely (Fig. 4), being highest in three ecosystem models, i.e., Lancaster Sound, Chesapeake Bay, and the Central North Pacific. Thus, according to the interpretation proposed in Libralato et al. (2006), jellyfishes may be considered



**Fig. 4** Keystoneeness of jellyfish in 16 ecosystem models documented in Table 1 against their relative overall effect (see text for interpretation)

keystone groups in these ecosystems. The Central North Pacific may be exceptional since the high overall effect of jellyfish is due to its very large positive impact on sea turtles (leatherback and loggerhead). [In this model, sea turtles are the only predator of jellyfish, and jellyfish constitute 100% of leatherbacks' diet (loggerheads also feeds on epipelagic fish; Cox et al., 2002).] This exclusive predator–prey relationship makes the jellyfish–sea turtle coupling extremely strong, thus explaining the high overall effect. Given the very low turnover rates of sea turtles, this degree of coupling is dubious, yet consistent with the very long-term (equilibrium) solution that is at the base of the methodology proposed by Libralato et al. (2006).

Perhaps better examples of realistically high keystone values can be seen in the Lancaster Sound and Chesapeake Bay models. In Lancaster Sound, the large effects are attributable to the very high negative impact that one particular species, the ctenophore *Mertensia ovum* (Fabricius, 1780), has on its main prey, i.e., omnivorous and herbivorous zooplankton, ice amphipods, and chaetognaths (Mohammed, 2001). In Chesapeake Bay, overall keystone values are mainly due to direct positive effects small changes in 'jellyfish' (sea nettle) biomass have on its main predators (fish larvae, blue herring, bay anchovy, menhaden, and shad) and to indirect effects on competitors (zooplankton and ctenophores). In this ecosystem, cascading effects, wherein a predator suppresses a prey, whose own prey then increases, etc., appear to be particularly strong. The positive indirect effects of the sea nettle's predators (bluefish, weak fish, summer flounder, and striped bass) contribute substantially to the sea nettle's overall effect on the food web.

In contrast, jellyfish have low keystone values in the Eastern Bering and South Catalan Seas, and have negligible values of keystone values in the remaining ecosystems (Fig. 4). Between the Eastern Bering Sea and the South Catalan Sea models, the relative abundances of jellyfish differ by two orders of magnitude. However, it is still their low overall effect on other groups, not their abundance, which explains the very low keystone values of jellyfish in these models. In both examples, jellyfish are minor consumers of zooplankton, while cannibalism is the only (Eastern Bering Sea) or the main (South Catalan Sea) form of predation on jellyfish. Such feeding

interactions do not count when keystone values are calculated (see Libralato et al., 2006).

There are also cases where jellyfish have intermediate keystone values. Thus, for example, in Hong Kong, jellyfish prey on the zooplankton, but are themselves preyed upon by many pelagic and demersal fishes (Cheung et al., 2002). Although this creates many direct and indirect impacts, they are relatively small, thus yielding a small overall effect.

In summary, we can conclude that very different structural features might lead to jellyfish assuming a keystone role. One of the obvious patterns emerging from Fig. 4 is the physical size of the ecosystem with smaller semi-enclosed systems (Chesapeake Bay and Lancaster Sound) being most sensitive to 'keystone' jellyfish and larger, more open ones being less sensitive (with the exceptional relationship between turtles and jellyfish in the Central North Pacific excluded). Perhaps this is validation of the expected complexity of multichannel food webs in (larger) open systems being less structured and thus less sensitive to trophic cascades (Polis & Strong, 1996). In addition, we suggest three typical ecological configurations where jellyfish keystone values increase:

- jellyfish are a high-impact predator with a relatively low biomass (Lancaster Sound);
- are a prey of significant importance to some predators in an ecosystem characterized by large indirect effects (Chesapeake Bay); and
- are a part of a mutually exclusive prey–predator pair (Central North Pacific).

### Time-dynamic simulations

Time-dynamic simulations (using the Ecosim component of EwE) were run to complete our preliminary coverage of the behavior of jellyfish in trophic ecosystem models. Specifically, we attempted to identify fishing patterns (on finfishes and invertebrates other than jellyfish) that would generate marked increases in jellyfish biomass within the ecosystem. The simulations were performed on the five representative models identified under the analysis of 'Mutual impacts through food webs' section, and details of how the models were parameterized are provided in Table 1. Only results from four of these models (Gulf of Thailand, Central North Pacific,

Chesapeake Bay, and Eastern Bering Sea) are presented as they best illustrate the range of the 'keystoneness' aspect discussed earlier as well as the ecological differences (notably the presence or absence of predators on jellyfish).

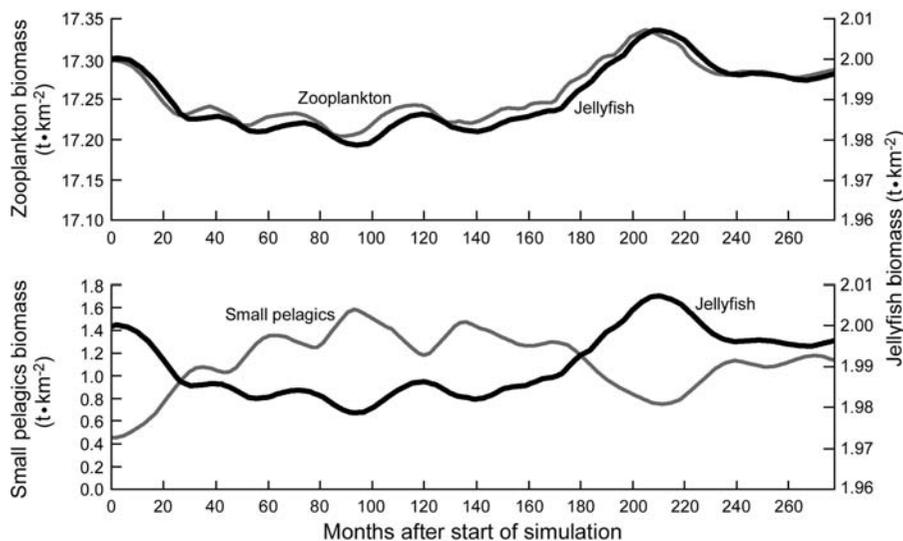
All of the models were forced, in a similar manner, by a linear increase in zooplankton production over time (i.e., bottom-up control). In the case of the Gulf of Thailand and Central North Pacific models, the models were also forced by an artificially enhanced mortality on the predators of jellyfish (i.e., top-down controls). The Chesapeake Bay and Eastern Bering Sea models have no explicit jellyfish predators identified for those models.

In general, the simulations indicate that strong bottom-up control by increased prey resources may be more important than the top-down controls placed on jellyfish by their predators (Figs. 5–7). In all cases, jellyfish biomass increased over time with increased zooplankton production. Predator mortality simulated by increased fishing mortality on small pelagic fishes in the Gulf of Thailand and by increased sea turtle mortality in the Central North Pacific did not yield marked increases in jellyfish biomass. However, this is all very preliminary because, as mentioned earlier, predation on jellyfish by vertebrates and other invertebrates is poorly understood (Arai, 2005; Purcell & Arai,

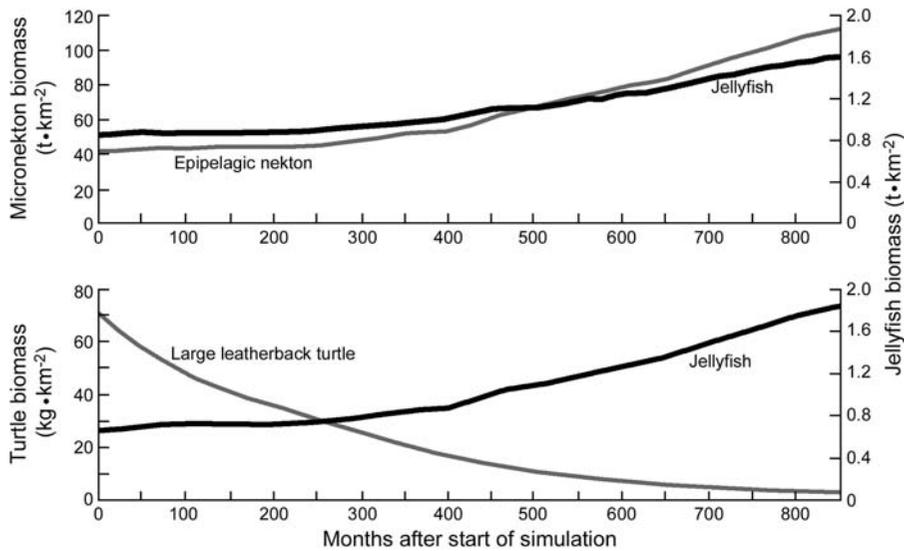
2001) and is likely far underestimated in these modeled systems.

Without explicit predators of jellyfish in the Chesapeake Bay and Eastern Bering Sea models, the linearly increasing function of zooplankton representing bottom-up forcing (possibly via eutrophication) causes interesting patterns that seem to reflect the 'keystoneness' of jellyfish. As discussed earlier, the Chesapeake Bay model is highly structured with respect to jellyfish and shows a strong coupling between zooplankton prey and jellyfish as seen in the nearly linear relationship in Fig. 7 (top panel). In contrast, the Eastern Bering Sea model, forced in a similar manner, shows large sinusoidal variations (Fig. 7, bottom panel). The large variations are likely due to the reduced structure in the larger Eastern Bering Sea system (i.e., more explicit redundancies in trophic pathways involving jellyfish). This is an interesting, albeit preliminary, pattern and could be useful to further identify ecosystem attributes (e.g., physical size, food web complexity, etc.) that make them more vulnerable to jellyfish increases.

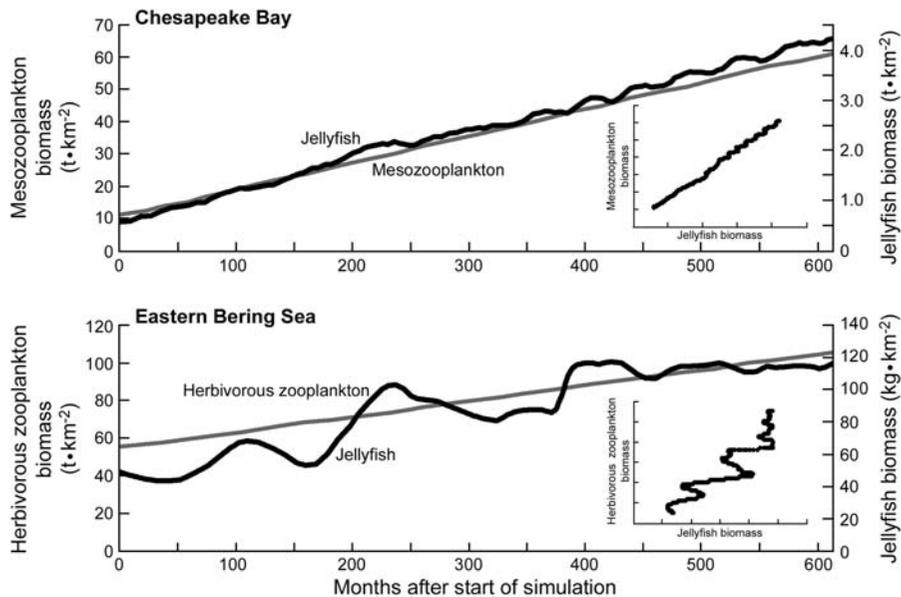
Likewise, the presence of predators on jellyfish may be important in regulating jellyfish biomass increases in some cases. While the Central North Pacific may be unrealistic in its parameterization of trophic flows involving jellyfish, the presence of jellyfish-eating turtles certainly is a highly coupled



**Fig. 5** Example of simulated biomass trends for jellyfish and their main prey (above) and jellyfish and their main predator (below) in the Gulf of Thailand



**Fig. 6** Simulation of a jellyfish bloom with ecosystem models: an example for the Central North Pacific (see text)



**Fig. 7** Simulating the effect of increasing zooplankton in the Chesapeake (top) and Eastern Bering Sea (bottom) ecosystem models. Note the increase of jellyfish, shown in the insets in relation to the biomass of their prey (see text)

relationship which should be explored in more detail. The Gulf of Thailand model may be the most informative for exploring coupled top-down and bottom-up effects, and could explain how multiple pressures such as combined effects of fishing and eutrophication interact to yield large increases in jellyfish biomass. The obvious next step for such models is to further investigate whether a positive feedback loop exists that further depresses jellyfish-

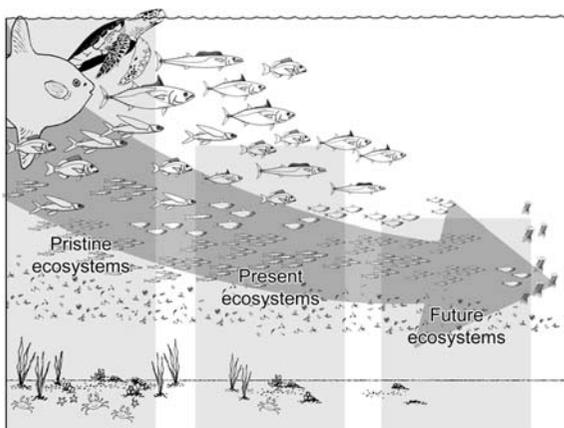
consuming fish through increased ichthyoplankton mortality due to increased jellyfish.

### Fishing down marine food webs and jellyfish outbreaks

The phenomenon wherein fisheries increasingly target smaller fish lower down in the food web, now

commonly referred to as ‘fishing down marine food webs’ (FD; Pauly et al., 1998a, b), is now well documented from a variety of countries and ecosystem types (Pauly & Palomares, 2005). This is one reason why the Convention on Biological Diversity selected the mean trophic level of fisheries catch, renamed ‘Marine Trophic Index,’ as one of eight indicators for ‘immediate testing’ by its >180 member countries (Pauly & Watson, 2005).

It is, however, the ecological changes in food web configuration that accompany FD which are relevant here. These may indeed provide a framework within which changes in marine ecosystems brought about by fishing can be assessed, particularly with respect to their possible impacts on jellyfish populations and their dynamics. Essentially, FD consists of the gradual loss of large organisms, species diversity, and structural diversity, i.e., the replacement of recently evolved, derived groups (marine mammals, bony fishes) by more primitive groups (invertebrates, notably jellyfishes, and bacteria). This is best seen when splitting the FD process into three phases, i.e., 1: ‘pristine’ or ‘past’; 2: ‘present’ or ‘exploited’; and 3: ‘future’ or ‘fully degraded’, corresponding to the three phases of degradation suggested by Jackson et al. (2001) and Pandolfi et al. (2005). We can then characterize each phase by (i) the main features of the fishes and other nektonic organisms and (ii) the pelagic–benthic coupling and its effect on processes in the water column (see also Fig. 8).



**Fig. 8** Fishing down marine food webs: the three stages (Pristine, Present, Future) offer increasingly better conditions for jellyfish (see text)

The first ‘pristine’ phase prevailed before humans had a chance to strongly impact ocean ecosystems (Jackson et al., 2001). Few parts of the oceans, notably outlying areas of the North and South Pacific, may still be labeled as pristine. For most of the world’s oceans, estimates of pristine abundances must be recovered based on historical accounts and anecdotes (Sáenz-Arroyo et al., 2005; Palomares et al., 2006), or inferred from archeological data (Jackson et al., 2001, Roberts, 2007).

Invariably, a pristine state is characterized by numerous marine mammals and large fish as top predators, the latter group with biomasses often exceeding their present abundance by one or two orders of magnitude. Elevated biomass of top predators also implies an abundance of small prey fishes and invertebrates, though not necessarily of those opportunistic groups (shrimps, squids) that now support increasingly valuable fisheries.

In the pristine environment, benthic life is dominated by an abundant structure-forming and sessile fauna. It is composed of filter feeders and deposit feeders, which suppress phytoplankton and detritus biomass and prevent re-suspension of sediments. As a result, the water column tends to be free of suspended particles and of nutrients leaching from them, i.e., oligotrophic. It is thus hypothesized that jellyfish were less abundant, and perhaps severe bloom cycles less frequent than now, because:

- The pelagic stage of jellyfish (the medusoids) had less food, and far more predators (e.g., leatherback sea turtles) than now; and
- Their sessile polyp stages were exposed to far more benthic predators, and had to contend with far more benthic zooplankton-feeding competitors than now, because of the intact benthic communities then prevailing.

The second ‘exploited’ phase is where we currently are. It is best characterized by declines, notably in the biomasses of large fishes, sizes and diversity of fishes in fisheries catches, trophic levels of the same (and hence the FD phenomenon), and benthos. Initially, these declines are compensated for by cascade effects (e.g., Myers et al., 2007), manifest in the emergence of new fisheries for squids and other invertebrates, but which eventually decline as well. Benthic life is also modified: biogenic structures, built over centuries by filter and detritus feeders, are

increasingly destroyed by bottom trawling, and replaced by small errant benthic animals (Hall, 1999), a situation advantageous for the benthic (polyp) stages of jellyfishes. The water column becomes progressively eutrophied, owing to the increasing scarcity of animals and structures that were cropping phytoplankton and consuming marine snow (detritus), which is now being re-suspended by storms and by trawling itself. For jellyfish, this generally implies improved conditions (Arai 2001). However, jellyfish outbreaks may still require to be triggered by exceptional abiotic conditions (Purcell, 2005).

The third ‘fully degraded’ phase follows on the continuation of present trends—although in some places, e.g., estuaries such as the Chesapeake Bay, many of the features associated with this third stage have already developed. In the Chesapeake Bay, fishing not only has eliminated virtually all animals above the size of striped bass, the current top predator, but also more importantly has eliminated the key filter feeders, both benthic (oyster; Jackson et al., 2001) and pelagic (menhaden; Franklin, 2007). Oysters, which, until 150 years ago, formed giant reefs, are reported as having been capable of filtering the water of Chesapeake Bay in 3 days (Jackson et al., 2001). Their absence (again, a result of fishing), compounded by the scarcity of menhaden, is the ultimate reason why pollution from effluents can now have such strong effects, and why harmful algae bloom occur. This also applies to other water bodies, estuarine or not, which are rendered less resilient by fishing, and easier for invasive species to overwhelm.

The biological endpoint of ecosystem degradation is the ‘dead zone.’ It is a zone free of oxygen and multicellular life as a result of excess nutrients, with bacteria instead of benthic animals, processing the resulting abundance of marine snow and other detritus. Such dead zones occur throughout the world, from the northern Gulf of Mexico (Rabalais et al., 2002) to the Benguela system off southwest Africa (Bakun & Weeks, 2004), and their number is growing rapidly (Dybas, 2005).

Jellyfish appear to have a competitive advantage over fish in hypoxic conditions (Sagasti et al., 2001). Such adaptation can lead to the dominance of jellyfish in a highly stressed ecosystem, as reported for example by Lyman et al. (2006) for the Benguela upwelling ecosystem.

## Conclusions

Jellyfish clearly play an extremely important role in the processing of energy in fisheries-based ecosystems. Short of conducting large-scale manipulations of marine ecosystems, the best alternative is ecosystem modeling. In this paper, we have documented that representation of jellyfish in existing EwE models is generally poor in terms of both their simple inclusion in models and their parameterization when they are included. Appropriate parameterization is critical, and we have shown in Table 1 that the parameters of jellyfish in EwE (i.e., their Q/B, P/B, TL and) are unacceptably variable. Some of this may be due to inappropriate use of wet biomass-specific measures, which are highly biased for gelatinous animals. We encourage future modeling studies to not only include jellyfish, but also to carefully consider how the models handle their unique biological nature.

Despite these difficulties, we see interesting and potentially important patterns among various EwE models that have included jellyfish. Specifically, we note the ‘keystoneness’ values of jellyfish appear to increase as the size of the ecosystem decreases. This is but one example of how ecosystem models can be used to develop and test hypotheses on the functional role of jellyfish in marine ecosystems.

We are now also able to test specific hypotheses derived from ‘Fishing Down Marine Food Webs,’ an explanation growing in popularity for explaining jellyfish biomass increase in fisheries-based ecosystems. The three phases of fishing down, pristine, exploited, and fully degraded, offering increasingly favorable conditions for jellyfish, are schematic, and they could be further subdivided, and/or defined more rigorously. Still, even in their present, preliminary form, they provide a coherent framework for many of the changes observed in ocean ecosystems, including those that favor jellyfish blooms or outbreaks.

One way to test this framework, and the hypotheses it includes, would be to re-express all models in Table 1 in dry weight or energy units (they currently use wet weight as currency), and rerun all analyses. This would help overcome the likelihood that the high water content of jellyfish has been ignored in some ecosystem models, i.e., that ‘biomass’ consists overwhelmingly of water. Also, the often assumed diets of jellyfish would have to be verified, as they play, in trophic models, as crucial a role as they play

in real ecosystems. Better information on the diet of jellyfish will likely bring to evidence the need for enhancing the resolution currently used for describing these organisms in food web models. Description of jellyfish with a set of appropriate functional groups will certainly help in better understanding their role in food webs and their effects on ecosystems. Once these precautions are taken, however, it should be possible to integrate jellyfish, in spite of their strange biology, into the mainstream of marine biology and fisheries research.

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