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DEDICATION. *This paper is dedicated to our beloved friend and colleague, Hermes Mianzan, for his innumerable contributions to fisheries, zooplankton, and gelatinous zooplankton ecology.*

Jellyfish, Forage Fish, and the World's Major Fisheries

By Kelly L. Robinson, James J. Ruzicka, Mary Beth Decker, Richard D. Brodeur, Frank J. Hernandez, Javier Quiñones, E. Marcelo Acha, Shin-ichi Uye, Hermes Mianzan, and William M. Graham

ABSTRACT. A majority of the world's largest net-based fisheries target planktivorous forage fish that serve as a critical trophic link between the plankton and upper-level consumers such as large predatory fishes, seabirds, and marine mammals. Because the plankton production that drives forage fish also drives jellyfish production, these taxa often overlap in space, time, and diet in coastal ecosystems. This overlap likely leads to predatory and competitive interactions, as jellyfish are effective predators of fish early life stages and zooplankton. The trophic interplay between these groups is made more complex by the harvest of forage fish, which presumably releases jellyfish from competition and is hypothesized to lead to an increase in their production. To understand the role forage fish and jellyfish play as alternate energy transfer pathways in coastal ecosystems, we explore how functional group productivity is altered in three oceanographically distinct ecosystems when jellyfish are abundant and when fish harvest rates are reduced using ecosystem modeling. We propose that ecosystem-based fishery management approaches to forage fish stocks include the use of jellyfish as an independent, empirical "ecosystem health" indicator.

CONCERN ABOUT SHIFTING MARINE ECOSYSTEMS FROM FISH TO JELLYFISH

Fisheries management in many nations has transitioned to ecosystem-based approaches, with the United States following suit (NMFS, 1999; Pikitch et al., 2004; Marasco et al., 2007). Because ecosystems are inherently complex, with numerous fished and unfished components, ecosystem-based fishery management (EBFM) efforts tend to emphasize only the elements directly linked to fished species (i.e., fish, fish food, and fish predators). Large coastal jellyfish are undeniably major consumers of plankton, including fish eggs and larvae (Purcell, 1985). Yet, because jellyfish are not in the direct ascension from fish food to fish predators (with the exception of their predation on fish eggs and larvae), they are routinely overlooked as important components in survey programs and production models used for EBFM (Pauly et al., 2009).

The lack of scientific appreciation for jellyfish when implementing EBFM is particularly troublesome because evidence suggests that jellyfish populations undergo prolonged periods of high abundance (Condon et al., 2013; Figure 1). Jellyfish blooms can be enhanced as a consequence of human influence, including fishing, climate change and variability, habitat modification, and cultural eutrophication (e.g., Duarte et al., 2012; Purcell, 2012). Protracted phases of high abundance in ecosystems supporting major forage fish fisheries (e.g., herrings, anchovies, capelin; Brotz et al., 2012; Graham et al., 2014), with evidence of jellyfish-forage fish replacement cycles in recent decades (Figure 1), have intensified concerns that some ecosystems are shifting from fish to jellyfish (Richardson et al., 2009; Utne-Palm et al., 2010; Uye, 2011; Riisgård et al., 2012; Roux et al., 2013; Mianzan et al., 2014).

One reason for the heightened concern about the increased size or frequency of jellyfish blooms in coastal ecosystems is the perception that they represent a "trophic dead-end." Jellyfish are nutritionally poor prey given their high water (> 97%) and low carbon (0.9–2.5%) content (Lucas et al., 2011) relative to nongelatinous zooplankton groups and fish (12% carbon per unit wet mass; Postel et al., 2000). *Pelagia noctiluca*, a common scyphomedusae in the Atlantic, has a mean energy density of 0.41 kJ g^{-1} ± 0.01 SD wet mass, a value 20 times smaller than co-occurring fish (Cardona et al., 2012). Yet, despite their low energy content, multiple fishes (e.g., tuna, spearfish, swordfish, salmon, and gadids), invertebrates, and seabirds regularly feed on jellyfish, in addition to obligate consumers like ocean sunfish, butterfishes, and leatherback sea turtles (Purcell and Arai, 2001; Sweetman and Chapman, 2011; Cardona et al., 2012; Fossette et al., 2012).

Forage fish are relatively small planktivorous fishes that are often found in large pelagic schools in productive coastal environments. They are an important prey source for upper-level consumers like piscivorous fishes, seabirds, and marine mammals and often support large commercial fisheries (Engelhard et al., 2013; Pikitch et al., 2014). They serve as a major conduit between primary and secondary production and higher trophic levels (Bakun et al., 2010) and likely compete with other zooplanktivores (including jellyfish) for prey resources (Engelhard et al., 2013). As such, forage fish species include many clupeids (menhadens, herrings, sardines, sprat), engraulids (anchovies), osmerids (capelin, smelt), and ammodytids (sand eels), as well as some scombrids (e.g., chub mackerel), carangids (e.g., Atlantic bumper, round scad, jack mackerels), and gadids (blue whiting, pollock juveniles).

Forage fish and jellyfish often overlap considerably in diet, space, and time in marine coastal ecosystems (Brodeur et al., 2008, 2014; D'Ambra, 2012), but commercial and recreational fishers target only forage fish in most regions. Because of these overlaps, it has been hypothesized that harvest removal of forage fish can lead

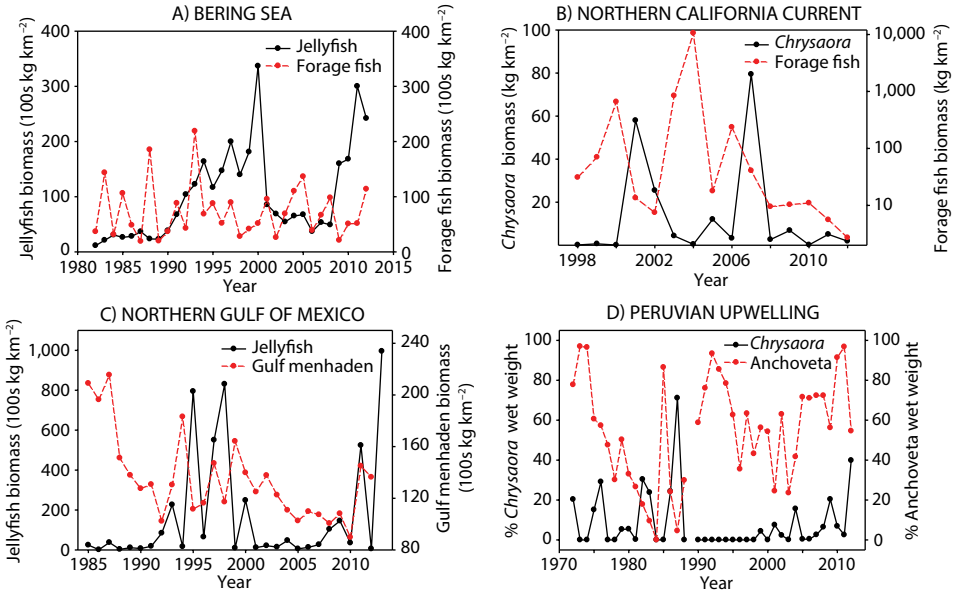


FIGURE 1. Time-series plots of jellyfish and forage fish species in (A) the eastern Bering Sea (Decker et al., 2014), (B) the northern California Current, (C) the northern Gulf of Mexico, and (D) the northern Humboldt Current (Mianzan et al., 2014) suggest that jellyfish-forage fish replacement cycles occur on intradecadal time scales. Forage fish (age-1 walleye pollock and Pacific cod, subadult Pacific Herring, capelin) were summed to generate the eastern Bering Sea forage fish time series. The Gulf of Mexico jellyfish times series was created as described in Robinson and Graham (2013) with one exception. Station-specific *Chrysaora* sp. and *Aurelia* spp. densities (number m^{-2}) were converted to biomass (kg m^{-2}) using individual wet weights of 0.0829 kg and 0.342 kg, respectively.

to a competitive release for jellyfish, indirectly enhancing their production (Utne-Palm et al., 2010; Purcell, 2012; Roux et al., 2013; Angel et al., 2014). However, interactions among jellyfish, forage fish, and fisheries are not well understood. This lack of understanding ultimately contributes to little or no appreciation for jellyfish populations in either traditional or EBFM for important coastal fisheries.

Here, we review interactions among jellyfish, forage fish, and fisheries, and we examine the global extent of these interactions as well as the socioeconomic risks jellyfish blooms present for the management of forage fisheries. We then discuss why forage fish are particularly vulnerable to jellyfish blooms. Lastly, we explore the role of jellyfish in pelagic food webs relative to forage fish and the consequences for energy transfer when blooms occur or fishing pressure is reduced in the eastern Bering Sea (EBS), the northern California Current (NCC), and the northern Gulf of Mexico (GOM) using food web model analysis (Aydin and Mueter, 2007; Steele and Ruzicka, 2011; Ruzicka et al., 2012; and recent work of author Robinson and colleagues). These three ecosystems are oceanographically distinct from one another (Table 1), but each supports large forage fish stocks, fisheries, and seasonal jellyfish blooms.

SCOPING THE PROBLEM: THE GLOBAL DISTRIBUTION OF JELLYFISH AND THEIR SOCIOECONOMIC IMPACTS ON FISHERIES

Populations of bloom-forming jellyfish are globally distributed and overlap spatially with 20 of 27 of the world's largest net-based fisheries, including those that harvest forage fish (Graham et al., 2014; Figure 2). These fisheries are centered primarily in coastal regions with high biological productivity (e.g., upwelling areas, large river plumes, and shallow seas). The great plankton productivity that drives these fisheries also supports large jellyfish biomass. A suite of socioeconomic consequences can occur when large coastal jellyfish bloom (Dong et al., 2010; Graham et al., 2014); for example, problems of gear fouling have been reported in all major fishing areas of the world (Table 2), resulting in injuries to fishers, destruction of nets, loss and lower quality of harvest, and increased effort without increased yield (Purcell et al., 2007).

Jellyfish outbreaks have caused economic losses ranging from hundreds of thousands of dollars to a one billion dollars. Blooms of *Nemopilema nomurai* (Nomura's giant jellyfish) around China, Japan, and Korea during the past decade have been especially damaging (Graham et al., 2014). Estimated losses range from ca. $20 million in northern Honshu Island, Japan, alone (Kawahara et al., 2006) to ca. $300 million for Japan and Korea combined (Graham et al., 2014). Jellyfish blooms cost Adriatic Sea fishers $327,773 and nearly 90,000 human hours in 2011 (Palmieri et al., 2014), and the Peruvian anchoveta fishery more than $200,000 (Quiñones et al., 2013). Costs associated with the invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and subsequent collapse of fisheries in the late 1980s in Turkey are among the greatest at more than a billion dollars (Kideys et al., 2005).

Adverse economic effects associated with jellyfish blooms have caused fishers to implement a variety of coping, adapting, or transforming responses as expected costs rise nonlinearly with impacts (Graham et al., 2014). Fishers tend to cope at low densities (e.g., repair nets), adapt at moderate densities (e.g., jellyfish exclusion devices), and transform at highest densities (e.g., retreat from fishing grounds). For example, fishers in the eastern Bering Sea in the late 1800s adopted a transformative response during years of high jellyfish abundance by displacing their effort, opting not to fish the "Slime Bank" waters north of the Aleutian Islands, where large *Chrysaora melananster* aggregations persisted (Rathbun, 1892).

PRODUCTION CYCLES THAT FORCE FORAGE FISH ALSO FORCE JELLYFISH

Both forage fish and jellyfish exhibit rapid fluctuations in population size in response to environmental variability at multiple scales (seasonal to decadal) due to their heavy dependence on primary and secondary production cycles (Purcell, 2005; Pikitch et al., 2012). In addition, many jellyfish life histories involve alternating periods of sexual reproduction and asexual propagation that enable them to expand their population size rapidly (i.e., "bloom"; Hamner and Dawson, 2009; Box 1). Large-scale oceanic-climatic forcing such as the El Niño–Southern Oscillation (ENSO) often drive biological production cycles. Climate forcing can indirectly affect the reproduction, growth and feeding rates, and distribution of many forage fish (Alheit and Niquen, 2004; Twatwa et al., 2005; Ward et al., 2006; Vaughan et al., 2011; Takahashi et al., 2012) and jellyfish (Purcell et al., 1999; Liu et al.,

TABLE 1. Characteristics of the three modeled ecosystems: eastern Bering Sea (EBS), northern California Current (NCC), and the Gulf of Mexico (GOM).

Ecosystem	Climate	Type	Forage Fish	Jellyfish
EBS	Arctic/Sub-Arctic	Shelf	Juvenile walleye pollock, juvenile Pacific cod, capelin, herring, sandlance, and eulachon	*Chrysaora melanaster*
NCC	Temperate	Upwelling	Northern anchovy, Pacific sardine, and Pacific herring	*Chrysaora fuscescens, Aequorea* sp.
GOM	Subtropical-tropical	Shelf	Gulf menhaden, sardines, herrings, Atlantic bumper, scads, and anchovies	*Aurelia* spp., *Chrysaora* sp.

2009; Robinson and Graham, 2014) through the alteration of regional hydroclimatological factors such as upwelling intensity, water temperature, freshwater discharge, and wind (Mantua and Hare, 2002; Di Lorenzo et al., 2008; Sanchez-Rubio et al., 2011).

On an annual scale, for example, variability in the growth and production potential of young-of-the-year Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay is predictably coupled with regional temperature and chlorophyll-*a* concentrations (Annis et al., 2011). Temperature is also a key predictor of the timing and distribution of scyphomedusae (*Chrysaora quinquecirrha*) and the production of the comb jelly (*Mnemiopsis leidyi*) in Chesapeake Bay (Costello et al., 2006; Decker et al., 2007). In the Gulf of Mexico, there may be a domed relationship between Mississippi River discharge and Gulf menhaden (*Brevoortia patronus*) production on a decadal scale. Recruitment is negatively affected during years with exceptionally high flows (Govoni, 1997; Vaughan et al., 2007, 2011), but adult growth potential is likely enhanced (as observed elsewhere), with greater primary and secondary production driven by riverine nutrient inputs (Lohrenz et al., 1997; Annis et al., 2011). Abundances of the scyphomedusae *Aurelia* spp. and *Chrysaora* sp. in the northern Gulf of Mexico also appear to vary annually with plankton production cycles, favoring large blooms during years with wet springs and summers in the Mississippi River watershed (Robinson and Graham, 2013).

The effects of climate-driven variability (intra- to interdecadal) on forage fish and jellyfish population dynamics is evident worldwide. Major shifts in forage fish and jellyfish abundances in the Pacific have been related to fluctuations in ENSO, the Pacific Decadal Oscillation, and the North Pacific Ocean Gyre Oscillation (Dawson et al., 2001; Mantua and Hare, 2002; Chavez et al., 2003; Tian et al., 2004; Suchman et al., 2012; Chiaverano et al., 2013; Litz et al., 2014; Mianzan et al., 2014). In the Atlantic Ocean, the North Atlantic Oscillation can indirectly alter the timing, magnitude, and distribution of planktonic production (Fromentin and Planque, 1996) that supports larval

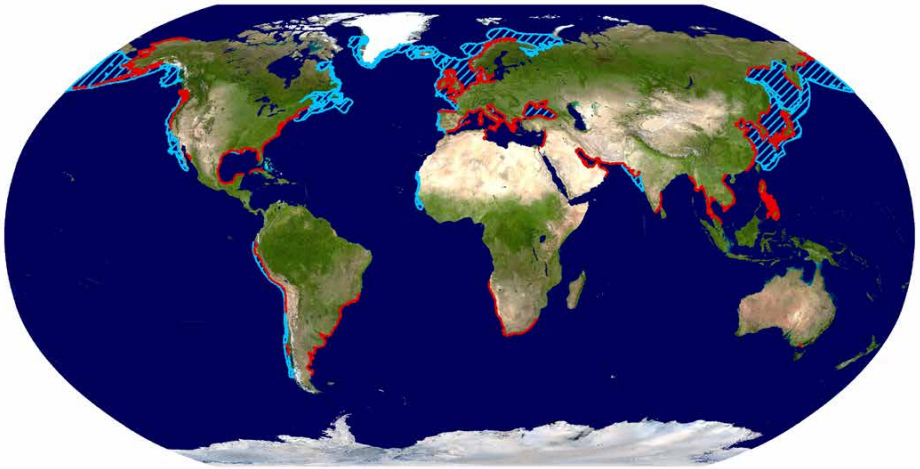


FIGURE 2. Map of the extent of coastal jellyfish occurrences (red lines) along coastlines of the world. Light blue areas are the 20 largest landings of net-based fisheries excluding tuna. Data that supported this analysis can be found in Graham et al. (2014).

TABLE 2. Ecosystems where blooms of large jellyfish have adversely impacted fishing operations.

Region	Ecosystem	Impact	Jellyfish Species (Phylum)	Reference(s)
Asia	Japan/East Sea, Inland Japan/East Sea, East China Sea	Damage to gear, reduced catch and reduced catch quality, increased labor, net clogging	*Nemopilema nomurai*; *Aurelia* spp., *Cyanea* sp. (Cnidaria)	Uye and Ueta, 2004; Uye and Shimauchi, 2005; Kawahara et al., 2006; Uye, 2008, 2011; Dong et al., 2010; Kim et al., 2012
North America	East Bering Sea, Northern California Current, Northern Gulf of Mexico	Net clogging, gear fouling, reduced revenue, displaced fishing effort	*Chrysaora melanaster, Chrysaora fuscescens, Phyllorhiza punctata* (Cnidaria)	Rathbun, 1892; Graham et al., 2003; Conley, 2013
South America	North Humboldt Current, South Brazilian Bight, North Argentinian Bight	Reduced catch quality, net clogging, displaced fishing effort, forced change in gear type, prevent fishing	*C. plocamia, Lychnorhiza lucerna* (Cnidaria)	Schiariti et al., 2008; Nagata et al., 2009; Quiñones et al., 2013
Africa	Northern Benguela	Net clogging	*Chrysaora hysoscella* (Cnidaria)	Brierley et al., 2001
Europe	East Mediterranean Sea, North Adriatic Sea, Black Sea	Damage to gear, net clogging, reduced catch and catch quality, displaced fishing effort, extra time and effort	*Rhopilema nomadica, Rhopilema pulmo, Aurelia aurita* (Cnidaria), *Mnemiopsis leidyi* (Ctenophora)	Nakar, 2011; Kideys et al., 2005; Palmieri et al., 2014
Middle East	Gulf of Oman	Damage to gear, reduced catch quality, net clogging	*Crambionella orsini* (Cnidaria)	Daryanbard and Dawson, 2008

and adult forage fish (Alheit and Hagen, 1997; Pitois et al., 2012; Paiva et al., 2013) and jellyfish (Lynam et al., 2004, 2011; Molinero et al., 2005) through its influence on oceanographic conditions (Hurrell et al., 2003).

INTERACTIONS BETWEEN JELLYFISH AND FORAGE FISH: IS THERE COMPETITION FOR RESOURCES?

The effects on many of the fisheries in regions where forage fish and jellyfish co-occur (Figure 2) can extend to indirect effects on fish production through intraguild predation by co-occurring jellyfish (Figure 3). Field and modeling studies indicate that jellyfish can negatively impact fisheries because they compete with planktivorous fish, feed on early life stages of fish, and indirectly compete with the food web as a whole by diverting plankton production away from upper trophic levels (Brodeur et al., 2008, 2011; Ruzicka et al., 2012). Thus, the overlap between jellyfish blooms and forage fish fisheries represents a considerable risk to a major portion (35%) of the protein resources harvested from the world ocean, as jellyfish are important consumers of zooplankton and can significantly restructure food webs when their abundance is high (Deason and Smayda, 1982; Pitt et al., 2007). However, we lack a quantitative understanding of how jellyfish affect energy flow through the ecosystem and how forage fish may be impacted (Figure 3).

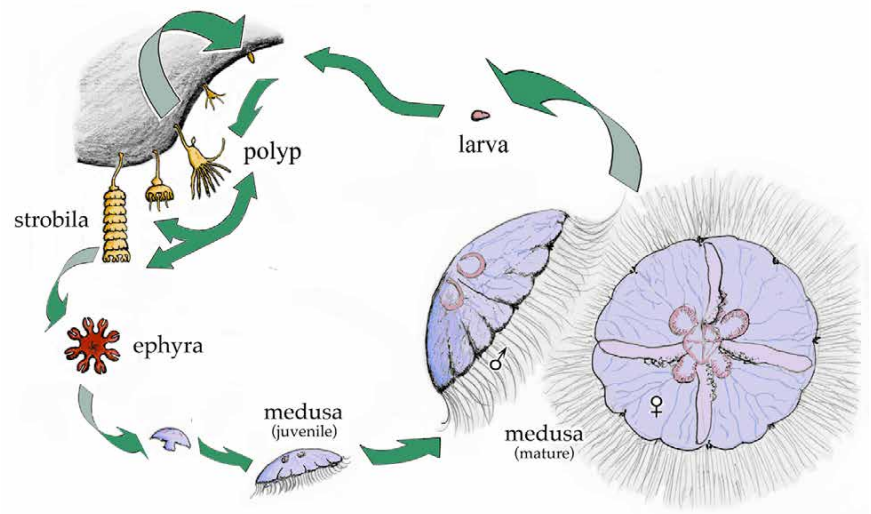
Jellyfish and Forage Fish Overlap

Jellyfish populations share the pelagic environment with many important forage fish (Brodeur et al., 2008; Eriksen et al., 2012), thus increasing the potential for resource competition. In the northern California Current, the spatial overlap of two jellyfish species and nine forage fish species were compared from trawl surveys at small (station) and large (survey area) scales (Brodeur et al., 2008). Several fish species had high overlap, especially with the nearshore jellyfish species (*Chrysaora fuscescens*) and less overlap with the more offshore species (*Aurelia aurita*). Further analyses found that while the degree of spatial overlap between *C. fuscescens* and forage fish was highly variable among seasons and years, average co-occurrence was 32% (Brodeur et al., 2014). There is also evidence that jellyfish (i.e., *Aurelia* spp. and *Chrysaora* sp.) and forage fish, particularly gulf menhaden, overlap in northern Gulf of Mexico. Gulf menhaden are highly concentrated in waters shoreward of the 20 m isobaths during the same time ctenophore and scyphozoan production is typically accelerating (March–May) or peaking (June–October) (Roithmayr and Waller, 1963; Graham, 2001; Smith, 2001; Robinson and Graham, 2014).

Jellyfish are potential competitors with planktivorous fish. The diets of three large scyphomedusae in the northern California Current were examined by Suchman et al. (2008) in relation to available prey resources. The diets of these jellyfish were compared with those of the dominant forage fish collected during the same cruise, and Brodeur et al. (2008) found substantial diet overlap of *C. fuscescens* and *A. labiata* with several pelagic fish species (Pacific herring (*Clupea pallasi*), northern anchovy (*Engraulis mord*ax), and Pacific sardine (*Sardinops sagax*), suggesting possible shared use of zooplankton resources. Possible resource competition between scyphomedusae *A. labiata* and *Cyanea capillata* and four forage fish species (Pacific sandlance (*Ammodytes hexapterus*), Pacific herring, juvenile walleye pollock (*Theragra chalcogramma*), and juvenile pink salmon (*Oncorhynchus gorbuscha*) was also identified in Prince William Sound. Dietary overlaps between jellyfish and fish collected there in the same purse seines averaged 50 ± 21% (Purcell and Sturdevant, 2001). The potential for competitive interactions was also evident in the subtropical northern Gulf of Mexico where

Box 1. Scyphozoan Jellyfish (*Aurelia* spp.) Life Cycle

Many scyphozoan species overlapping with forage fish have bipartite life histories that include a pelagic medusa stage and a benthic polyp stage. Polyps can reproduce through asexual budding, which results in new polyps called scyphistoma; the formation of podocysts, which can remain viable for at least two years (Dawson and Hamner, 2009); or the production of multiple strobilae that become ephyrae upon release. In temperate species, ephyrae are released from strobilating polyps in spring, and medusae become sexually mature in fall, then enter senescence in late fall (Kawahara et al., 2006). For example, developmental time for the giant-bodied jellyfish *Nemopilema nomurai* is thought to be nine months.



Modified from a Mike Dawson image

D'Ambra (2012) revealed that mesozooplankton contributed similar fractions to the diets of *Aurelia* spp. (55–100%) and gulf menhaden (55–83%).

Jellyfish as Predators

Jellyfish, even though they use direct contact to capture prey, have the potential to functionally replace visual predators, such as planktivorous fish, in food webs. Compared to fish, jellyfish have slower respiration and instantaneous clearance rates when scaled to wet mass; however, when scaled to carbon mass, these rates are similar among jellyfish and fish (Pitt et al., 2013). Acuña et al. (2011) demonstrated that despite their different predation styles, jellyfish and their fish competitors display similar instantaneous prey clearance and respiration rates and have similar potential for growth and reproduction. Thus, Acuña et al. (2011) concluded that in order to achieve this level of production, jellyfish have evolved large, water-laden bodies that act to increase their contact with prey. Furthermore, jellyfish swim in a way that reduces the metabolic demand of their swimming muscles (Gemmell et al., 2013). Some taxa, such as *Rhizostoma octopus*, also exhibit movement patterns that approach the theoretical optimum for locating sparsely distributed prey (Hays et al., 2012). These traits contribute to the ecological success of medusae and their potential to outcompete visual fish predators, particularly in eutrophic coastal environments (Haraldsson et al., 2012).

Jellyfish diets often include forage fish eggs and larvae, when available (Purcell, 1997). Although consumption of fish eggs and larvae by jellyfish is highly variable (Purcell and Arai, 2001), predation impacts can be substantial. In Chesapeake Bay, jellyfish are responsible for 21% of daily egg and 29% of larval mortality of bay anchovy (*Anchoa mitchilli*) (Purcell et al., 1994). Predation on herring larvae by the hydromedusa *Aequorea victoria* in British Columbia averaged 57% per day (Purcell and Grover, 1990). These examples illustrate that jellyfish predation on forage fish early life stages can be quite severe, particularly when spawning occurs in semi-enclosed bays. Increased mortality rate of fish eggs and larvae would be expected to ultimately negatively affect recruitment to adult populations (Houde, 1987) and, thus, the number of adult fish competing with jellyfish for shared zooplankton prey. Conversely, there is little or no evidence of forage fish feeding on the early life stages of jellyfish, though diet data are sparse when early life stages occur in the pelagic zone in the winter and spring months.

These examples illustrate the potential for jellyfish to adversely affect commercially important fish species through direct predation or competition for resources. Lynam et al. (2005) found inverse relationships between jellyfish abundance and herring recruitment in the North Sea. Negative relationships between jellyfish and forage fish biomass

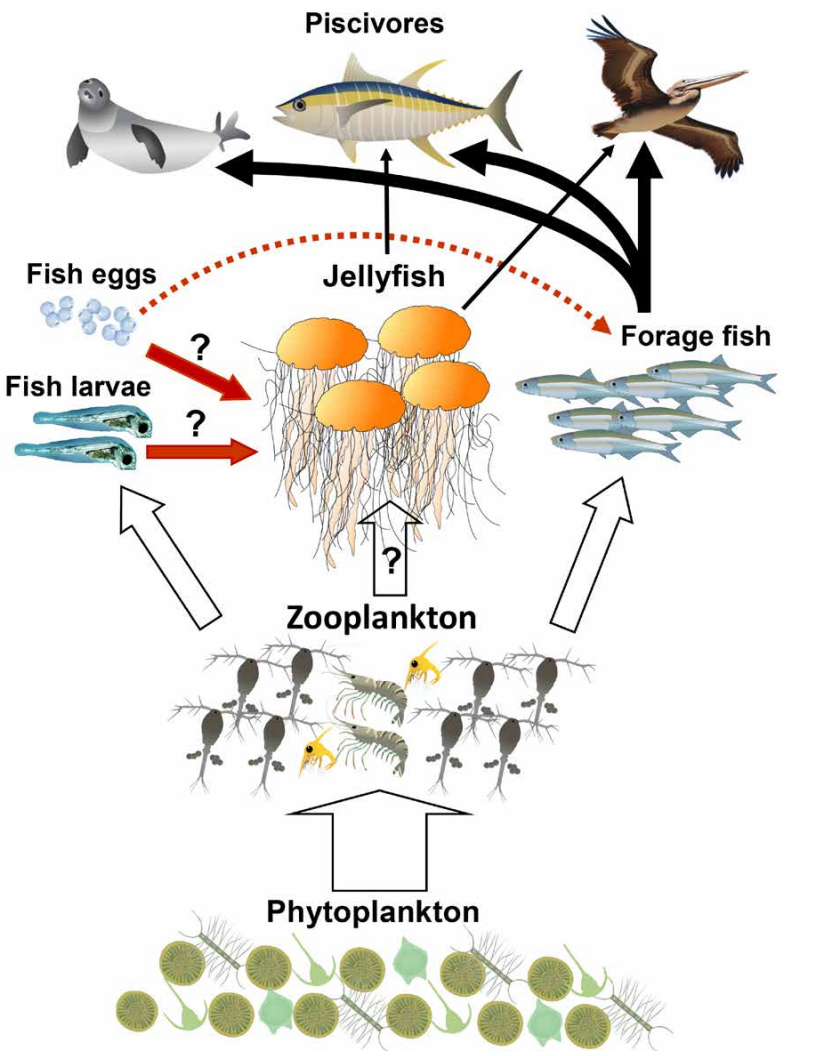


FIGURE 3. Simple conceptual diagram illustrating energy transfer pathways in coastal pelagic food webs. The relative width of the arrows denotes the amount of energy flowing between functional groups. Red arrows are energy flows between members of the same trophic guild (i.e., intraguild predation) following Iriogien and Roos (2011). Dashed lines denote the probable consumption of fish eggs by planktivorous forage fish. Energy transfer and factors affecting its magnitude between many functional groups (i.e., zooplankton and forage fish) are well understood. Much less is known about the predation impact of jellyfish on fish early life stages as well as their contributions to the diets of other consumers. *Fish larvae images provided by Glynn Goricke. Other image credits: Dieter Tracey, Tracey Saxby, Jane Thomas, Kim Kraeer, Lucy Van Essen-Fishman, and Joanna Woerner; Integration and Application Network, University of Maryland Center for Environmental Science (http://ian.umces.edu/imagelibrary/ian.umces.edu/imagelibrary)*

have also been observed in the eastern Bering Sea, northern California Current, and Humboldt Current (Brodeur et al., 2002, 2014; Mianzan et al., 2014). Thus, in locations where jellyfish-fish overlap is high and jellyfish are abundant, predation by jellyfish on icthyoplankton and zooplankton would be expected to contribute to larval fish mortality and the reduction of shared prey resources supporting planktivorous fishes.

EFFECTS OF INCREASES IN JELLYFISH AND FORAGE FISH REMOVAL IN THREE OCEANOGRAPHICALLY DISTINCT ECOSYSTEMS

Food Web Energy Transfer

Using food web models, we explored the trophic roles jellyfish and forage fish play, and the consequences for energy transfer, when jellyfish blooms occur or fishing pressure is reduced in three ecosystems (Aydin and Mueter, 2007; Steele and Ruzicka, 2011; Ruzicka et al., 2012; recent work of author Robinson and colleagues [contact author Robinson for a copy of the GOM model]). The relative importance of these groups as energy transfer pathways in the food web can be measured by their "reach" and "footprint" metrics (Steele and Ruzicka, 2011). "Reach" is defined as the fraction of a consumer's production (or energy) that originated with the group of interest (here, jellyfish and forage fish) via all direct and indirect pathways. The "footprint" is the fraction of each prey group's total production that supports the group of interest via all direct and indirect pathways (Ruzicka et al., 2012).

Simulated food webs for the EBS, NCC, and GOM illustrating these metrics for forage fish and jellyfish support the assertion that jellyfish can be a production-loss pathway (Figure 4). These food web plots, which show the relative flow of energy to and from each functional group, demonstrate that in all three ecosystems, forage fish have a greater reach and smaller footprint than jellyfish (Figure 5). They are also a much more important energy transfer pathway than jellyfish, measured by the ratio of reach to footprint, where larger ratios indicate a greater fraction of energy is passing upward to higher-order consumers (Figure 6).

The reach-to-footprint ratio also allows comparisons among ecosystems regarding the importance of forage fish (or jellyfish) as food web energy conduits. Forage fish in the NCC, GOM, and EBS have similar levels of import in terms of moving energy upward to higher order consumers (Figure 6). However, jellyfish in the GOM play a substantially larger role in food web energy transfer compared to populations in the NCC and the EBS (Figure 6) because they are one of the primary pelagic, mid-trophic groups through which lower trophic level production can pass.

Conversely, in the NCC, euphausiids and forage fish are the mid-trophic groups that dominate upward energy transfer (Ruzicka et al. 2012). In addition,

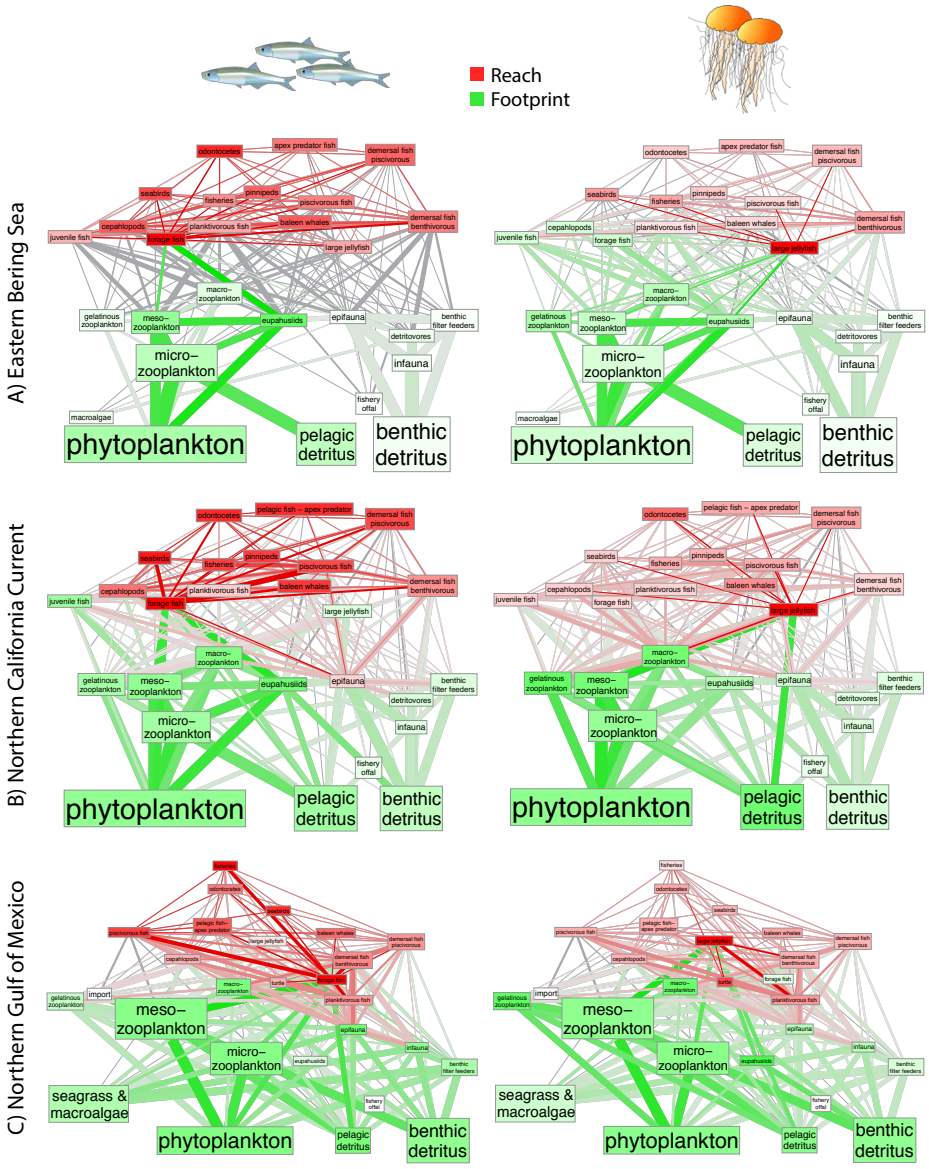


FIGURE 4. Food webs for the eastern Bering Sea, the northern California Current, and the northern Gulf of Mexico. Box size is proportional to biomass density (t km^{-2}), and line width is proportional to flow volume (t km^{-2} yr^{-1}). Color shows the reach (red) and footprint (green) of planktivorous forage fish (left panels) and large jellyfish (right panels). Reach is the fraction of a consumer's production that originated with (or passed through) either forage fish or jellyfish via all direct and indirect pathways. Footprint is the fraction of each prey group's total production that supports either forage fish or jellyfish via all direct and indirect pathways. Color intensity indicates the relative amount of production (i.e., energy) in the flows.

in the EBS, a considerable amount of lower trophic level production is routed through demersal and benthic consumers (Aydin and Mueter, 2007).

These comparisons indicate that when jellyfish dominate the pelagic biomass, the fraction of total system production and the efficiency at which it is transferred upward in the food web is reduced. However, characterizing them as a "trophic dead end" is a misnomer (Purcell and Arai, 2001; Pauly et al., 2009). Jellyfish support a multitude of lower-, mid-, and higher-order consumers (e.g., microbes, parasitic amphipods, juvenile fish, sunfish, sea turtles, seabirds, and predatory fish). These trophic relationships suggest that a better descriptor for jellyfish would be "energy roundabout," because they divert plankton production to numerous groups at varying trophic levels (Figure 4). Forage fish would then be an "energy expressway," serving as an efficient conduit through which a larger fraction of system production can move from plankton producers to fish, mammal, seabird, and human consumers.

No Fishing Scenario

We modeled "no fishing" scenarios in the three ecosystems to examine how production of each functional group changed between "fished" and "not fished" states. Excessive fishing pressure can markedly alter ecosystem structure and function by inducing shifts in taxa abundance across multiple trophic levels (Reid et al., 2000; Frank et al., 2005; Casini et al., 2008) and, when acting in concert with other perturbations such as climate forcing, push an ecosystem into an alternate stable state (Scheffer et al., 2001; Chavez et al., 2003; Kirby et al., 2009; Litzow et al., 2014). For example, overharvesting of pelagic fishes in the northern Benguela Current off Namibia is thought to have led to a rapid increase in large jellyfish, which now dominate the system (Lynam et al., 2006; Roux et al., 2013).

The "no fishing" scenario was constructed by scaling the biomass (t km^{-2}) of each functional group (g) that was fished by the proportion removed by fishery landings and discards (Equation 1):

$$\text{Scaling factor} = (\text{Biomass}_g + \text{Landings}_g + \text{Discards}_g) / \text{Biomass}_g). \quad (1)$$

Static scenario analysis was then performed following methods developed by Steele (2009) to evaluate the effects of individual changes in energy flow through jellyfish, forage fish, and other functional groups. Surplus prey production was distributed proportionally among all other consumers so that total predation on each group remained unchanged. Scenarios were run on the 1,000 random food web models, allowing for ±50% uncertainty around each trophic connection.

The closure of all fisheries in all three ecosystems resulted in increased production in pelagic, demersal, and apex predatory fishes, but did not greatly affect large jellyfish (Figure 7). Changes in jellyfish production were less than 0.1% in the EBS and NCC, and it declined by 4.9% in the GOM. Forage fish in the GOM exhibited the largest gain in production (24%) among the fish functional groups. However, this was not the case for forage fish in the NCC (+0.2%) or the EBS (–1.3%). The decline in jellyfish and increase in forage fish production as result of no fishing in the GOM supports the hypothesis that interplay among forage fish, jellyfish, and forage fish fisheries is a driver of the apparent replacement cycles between jellyfish and forage fish in the GOM during the 1990s (Figure 1). The lack of substantial change in forage fish production in the EBS and the NCC is presumably due to the compensatory increase in consumption by their predators, such as pelagic piscivorous and apex predatory fishes. These groups were among those benefiting the most by the fishery closure in each ecosystem (Figure 7). The increased availability of forage fish in the GOM would also explain the +21% change in seabird production.

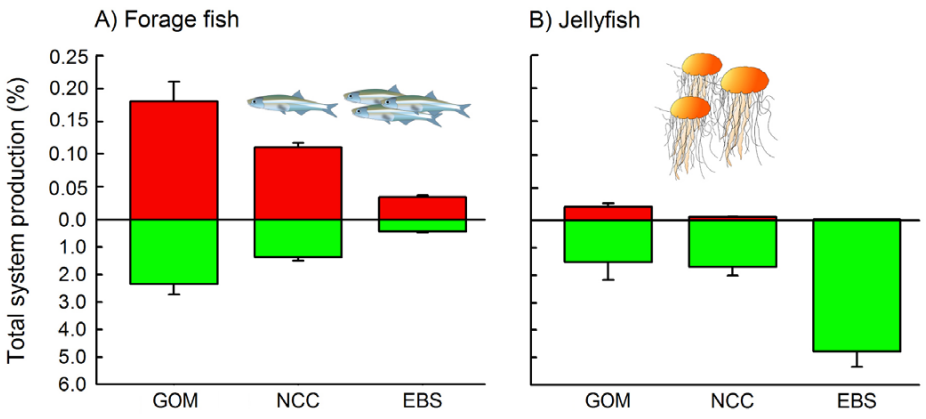


FIGURE 5. System-wide reach and footprint metrics for (A) forage fish and (B) jellyfish in the three ecosystems. Red bars are the reach, the percent of total system production produced by, or passing through, each target group. Green bars are the footprint, the percent of total system production consumed (i.e., footprint) by the target group. NCC = northern California Current. EBS = eastern Bering Sea. GOM = Gulf of Mexico.

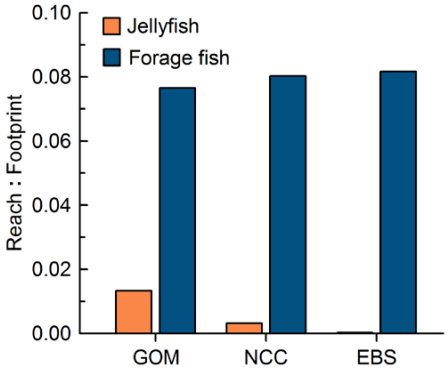


FIGURE 6. The reach-to-footprint ratios for forage fish and jellyfish in the EBS, NCC, and GOM. This ratio measures the relative importance of each group for transferring energy upwards in the food web, with larger ratios indicating greater import (Ruzicka et al., 2012).

AN APPROACH TO ECOSYSTEM MANAGEMENT USING JELLYFISH

Our approach here has been to elucidate some of the ways jellyfish may affect ecosystems and the human endeavors that depend on these ecosystems. The ecosystems we compare here are fairly open systems, with substantial water and biotic exchange with neighboring systems, but we acknowledge that semiclosed systems (e.g., Black Sea, Mediterranean Sea, Chesapeake Bay, Puget Sound, and inland Japan/East Sea) also have similar and often even more acute problems with jellyfish blooms, and there is a need to examine these systems as well in a modeling framework (Pauly et al., 2009). These enclosed systems may be more susceptible to multiple interacting stressors, such as eutrophication and hypoxia, that may negatively affect fish but are neutral or perhaps favorable to jellyfish (Richardson et al., 2009; Purcell, 2012). Clearly, more data are needed for many ecosystems in terms of biomass and production of gelatinous zooplankton and in energy pathways leading to and from them relative to the more typical forage species.

It is unlikely that we may effectively manage these burgeoning jellyfish populations unless we have a clearer understanding of their life histories, trophic ecologies, and ecosystem impacts. This level of research requires a coordinated effort at an international level to bring to bear the extensive expertise available worldwide (Gibbons and Richardson, 2013). One way scientists may contribute to lessening the impact of jellyfish blooms is to develop predictive models for the timing and potential magnitude of impending blooms (Decker et al., 2007; Brown et al., 2012) for use by managers and stakeholders so that appropriate counter or mitigation measures can be anticipated. Monitoring jellyfish populations over time can also provide managers with an important indicator of overall ecosystem health that may be highly sensitive to changes in ecosystem structure or functioning (Samhouri et al., 2009) and may be useful in identifying tradeoffs in ecosystem-based management decisions (Samhouri et al., 2010).

Building on recommendations to take a precautionary approach to the management of forage fish stocks (Pikitch et al., 2012, 2014), we are developing a tool set that uses jellyfish as an indicator for management targets. Moreover, we suggest that the fisheries management paradigm, which currently emphasizes only the elements linked directly to fished species (i.e., fish, fish food, and things that eat fish), should be revised to include jellyfish, a seasonally abundant consumer of shared prey resources and fish early life stages.

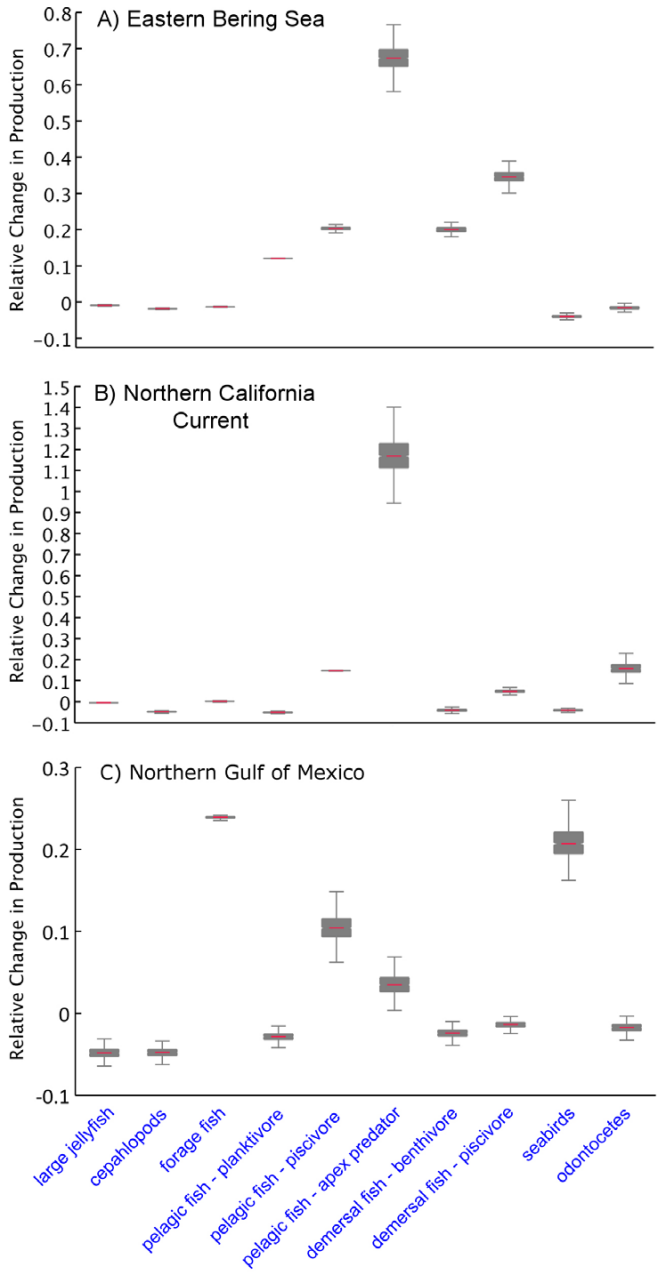


FIGURE 7. Structural scenarios showing the effects of halting all fishing on the productivity of major functional groups in each ecosystem. The effects of the scenarios are expressed as the production of the functional groups in the scenarios-modified model relative to the production in the base model (relative change in P = ($P_{scenario}$ – P_{base}) / P_{base}).

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