Rev Fish Biol Fisheries
DOI 10.1007/s11160-016-9445-y

REVIEWS

Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds

Lucas Brotz · Agustín Schiariti · Juana López-Martínez · Javier Álvarez-Tello · Y.-H. Peggy Hsieh · Robert P. Jones · Javier Quiñones · Zhijun Dong · André C. Morandini · Mercy Preciado · Enrique Laaz · Hermes Mianzan

Received: 17 November 2015 / Accepted: 10 September 2016

Abstract Jellyfish (primarily scyphomedusae) fisheries have a long history in Asia, where jellyfish have been caught and processed as food for centuries. More recently, jellyfish fisheries have expanded to the Western Hemisphere, often driven by demand from Asian buyers and collapses of more traditional local fish stocks. Jellyfish fisheries have been attempted in numerous countries in North, Central, and South America, with varying degrees of success. Here, we chronicle the arrival of jellyfish fisheries in the Americas and summarize relevant information on jellyfish fishing, processing, and management. Processing technology for edible jellyfish has not advanced, and presents major concerns for environmental and human health. The development of alternative processing technologies would help to eliminate these concerns and may open up new opportunities for markets and species. We also examine the biodiversity of jellyfish species that are targeted for fisheries in the Americas. Establishment of new jellyfish fisheries appears possible, but requires a specific combination of factors including high

Hermes Mianzan: Deceased.

L. Brotz (✉)
Sea Around Us, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada
e-mail: lucasbrotz@gmail.com

A. Schiariti · H. Mianzan
Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Buenos Aires, Argentina

A. Schiariti
Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Buenos Aires, Argentina

J. López-Martínez · J. Álvarez-Tello
Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, Mexico

Y.-H. Peggy Hsieh
Department of Nutrition, Food and Exercise Sciences, Florida State University, Tallahassee, Florida, USA

R. P. Jones
Southeastern Fisheries Association, Tallahassee, Florida, USA

J. Quiñones
Laboratorio Costero de Pisco, Instituto del Mar del Perú (IMARPE), Paracas, Ica, Peru

Z. Dong
Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, Shandong, China

A. C. Morandini
Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (USP), São Paulo, São Paulo, Brazil

M. Preciado · E. Laaz
Instituto Nacional de Pesca, Guayaquil, Guayas, Ecuador

Published online: 19 September 2016

abundances of particular species, processing knowledge dictated by the target market, and either inexpensive labor or industrialized processing facilities. More often than not, these factors are not altogether evaluated prior to attempting a new jellyfish fishery. As such, jellyfish fisheries are currently expanding much more rapidly than research on the subject, thereby putting ecosystems and stakeholders' livelihoods at risk.

Keywords Jellies · Jellyfish fishery · Scyphomedusae · Scyphozoa · Zooplankton fisheries · Gelatinous zooplankton

Introduction

Jellyfish (herein referring to members of the Phylum Cnidaria with a pelagic phase, primarily in the Class Scyphozoa) are notorious for interfering with human activities and industries including fisheries, aquaculture, and tourism (Purcell et al. 2007; Lucas et al. 2014). However, jellyfish (or 'medusae') are also acclaimed for their utilization as food in Asia. The Chinese have savored jellyfish for centuries as cuisine to be served regularly, as well as on special occasions such as holidays, weddings, and celebrations (Hsieh and Rudloe 1994). Consumption of jellyfish is also popular in Asian countries other than China, including Japan, Malaysia, Korea, Taiwan, Singapore, and other nations where there is strong market demand (Kingsford et al. 2000; Hsieh et al. 2001; Omori and Nakano 2001). Interestingly, cnidarians were also consumed in ancient Rome, as indicated by the Latin cookbook *Apicius* (Vehling 1977), but whether the "sea nettles" referred to in the text are indeed jellyfish or rather sessile anemones remains unresolved. Regardless, it is amusing to note that the recipe suggests that when the cnidarians are served atop of eggs in a type of omelette, "no one at the table will know what they are eating" (Grocock and Grainger 2006).

Chinese emigrants likely first introduced jellyfish fisheries to Southeast Asia. Countries such as Malaysia and Indonesia appear to have established jellyfish fisheries around the middle of the twentieth century, with Thailand and the Philippines following suit in the 1970s. Additional Asian countries have initiated jellyfish fisheries in recent decades, including Myanmar, Vietnam, India, Sri Lanka, and Russia (Brotz 2016). To keep up with demand, jellyfish fisheries have also spread to the Western Hemisphere, often preceded by local collapses of more traditional fisheries resources. While jellyfish fisheries have been explored in at least eight countries in North, Central, and South America, the degree to which jellyfish fisheries have successfully established in the Americas varies (Table 1; Fig. 1). Most consumption continues to be in Asia, with the majority of the traded product being exported to China, Japan, and South Korea (Huang 1986, 1988; Hsieh and Rudloe 1994; Omori and Nakano 2001; Kitamura and Omori 2010).

Jellyfish fisheries are typically characterized by large interannual fluctuations in abundance and biomass, short fishing seasons of usually less than a few months, as well as limited research and management. These circumstances can cause instability of jellyfish fisheries and may prevent fishers, stakeholders, and policy-makers from supporting development. In addition, the species being targeted have complex life cycles including both pelagic (medusa) and benthic (polyp) stages, making it difficult to model and predict population dynamics and responses to fishing pressure. While jellyfish catches are reported by the Food and Agriculture Organization of the United Nations (FAO), the data are not reliable. Many countries do not report their jellyfish catches explicitly, including them as either miscellaneous invertebrates or not at all. In fact, catches of jellyfish as food for humans are significant, with global landings recently exceeding 1 million tonnes (Brotz 2016; Brotz and Pauly 2016). The catch from jellyfish fisheries in the Americas is still relatively small compared to that from Asia, comprising only about 3 % of the global catch (Brotz 2016). Nonetheless, the geographical expansion of jellyfish fisheries is real, albeit with mixed results regarding successful establishment. The consequences of this expansion remain unclear for fishers and ecosystems, as scientific studies are not keeping pace. As such, we aim to discuss some of the relevant issues regarding jellyfish fisheries in the Americas, including where jellyfish are being caught, how much is landed, and which species are being targeted. We also review knowledge and diversity of rhizostome jellyfish in the Americas, the potential impacts of jellyfish fisheries on ecosystems, and some of the more relevant aspects for management of these understudied fisheries.

Table 1 Jellyfish fisheries in the Americas

Country	Region	Status	Year(s)	Species	Gears	Estimated current annual catch (tonnes)
Argentina	Buenos Aires Province	Under investigation	2007–present	*Lychnorhiza lucerna*	Dip-net; gillnet; demersal trawl	–
Canada	British Columbia	Discontinued	1984	*Aurelia labiata*	Dip-net; seine net	–
Canada	Newfoundland	Discontinued	2002	*Aurelia* sp.	Beam trawl	–
Ecuador	Guayaquil Gulf Estuary	Under investigation	2013–present	*Stomolophus meleagris*	Modified gillnet; tidal set-net	48,600[a]
Honduras	Near Caratasca Lagoon	Under investigation	2007	*Stomolophus meleagris*	Dip-net	–
Honduras	Gulf of Fonseca	Under investigation	2016	*Stomolophus meleagris*	Dip-net	
Mexico	Gulf of Mexico	Discontinued	2000	*Stomolophus meleagris*	Dip-net	–
Mexico	Gulf of California	Expanding	2001–present	*Stomolophus meleagris*	Dip-net	15,000
Nicaragua	Tuapi	Expanding	2008, 2013–present	*Stomolophus meleagris*	Dip-net	1300
Peru	Pisco	Under investigation	2013-present	*Chrysaora plocamia*	Dip-net	–
USA	Puget Sound	Discontinued	1960s–1990s	*Aequorea victoria*	Dip-net	–
USA	Atlantic coast	Expanding	1990s–present	*Stomolophus meleagris*	Shrimp trawl; seine	4000
USA	Gulf of Mexico	Continuing	1990s–present	*Stomolophus meleagris*	Shrimp trawl; skimmer trawl; seine	1100

[a] Estimate based on only 2 years of landings with exceptionally high landings in 2015

Fishing for jellyfish

When located in surface waters, jellyfish can be very abundant and caught with relatively little effort. In fact, one of the traditional concerns for jellyfish was not how to catch them, but rather how to exclude them from the catch (e.g., Broadhurst and Kennelly 1996). The design of turtle excluder devices (TEDs), which are now required in many American trawl fisheries, was adapted from devices originally devised by fishers to exclude cannonball jellyfish (*Stomolophus meleagris*) from shrimp trawls (Jenkins 2012). Ironically, this species of jellyfish is now the target of a growing fishery in the USA and elsewhere (see below).

A wide variety of gears are used around the globe to catch jellyfish, including dip-nets, set nets, drift nets, hand-nets, gill nets, hooks, beach seines, purse seines, weirs, and trawl nets. In some cases, combinations of gears may be used to increase the quality and size of the catch. For example, in the Ariake Sea (Kyushu, Japan) and Sarawak (Malaysia, Borneo), jellyfish may be concentrated using set nets and then collected using dip-nets (AS personal observations; Rumpet 1991). Mesh size is also an important consideration for fishers and managers, as it affects not only the abundance and quality of the catch, but also the bycatch. Minimum size limits (MSLs) are in place in some countries in order to avoid catching juvenile medusae. However, the effectiveness of MSLs in jellyfish fisheries has not been evaluated. While larger mesh sizes are likely to help minimize bycatch and avoid juvenile medusae, they can also damage larger and more valuable medusae, depending on the methods and gear being used. As such, mesh sizes should be carefully considered based on specific circumstances (also see *Management* below).

A wide range of vessels is used for fishing jellyfish. While diesel-powered trawlers are used in select locations (e.g., USA), most fishing is done from small (5–10 m), powered boats operating relatively close to shore, which often carry somewhere between 1 and 5 t of catch when fully loaded. Large catches of jellyfish on the decks or in holds of boats can result in concerns regarding vessel stability. In rough conditions, it may be especially important for vessels to have baffles in their holds in order to contain the catch and prevent it from shifting (Kingsford et al. 2000). Fishing is usually carried out during the daytime when fishers can locate medusae in surface waters. However, in some cases jellyfish may be targeted outside of daylight hours in order to avoid warm temperatures that can speed spoilage of the catch. As oceanographic

Fig. 1 Map of jellyfish fisheries in the Americas. For additional information, see Table 1

conditions such as currents, rainfall, wind, and thermal stratification influence vertical and horizontal distribution of jellyfish (Graham et al. 2001), these conditions will impact fishing activity. If jellyfish are not aggregated near the surface or visibility is not sufficient to locate them, fishers need to employ different methods and gears, which may include trawls, seines, or set nets. Each jellyfish fishery will employ gears based on a variety of factors, including access, cost, efficiency, and catchability. Kingsford et al. (2000) concluded that dip-netting is the most favorable method for catching jellyfish as it minimizes bycatch, habitat damage, catch quality, and conflict with other commercial fisheries.

Target species and rhizostome diversity in the Americas

While the FAO usually reports edible jellyfish as "*Rhopilema* spp.", this is incorrect in many cases. As many as 35 species of jellyfish have reportedly been consumed by humans (Table 2), with the majority of commercial jellyfish fisheries focusing on species from the scyphozoan Order Rhizostomeae. Although this (and many other) groups of jellyfish are polyphyletic, the taxonomy of jellyfish still requires significant revision and an updated system remains to be proposed, so the traditional nomenclature will be used here. Rhizostome jellyfish typically have tougher and more rigid tissues than other jellyfish, thereby producing the desired crunchiness that is characteristic of processed edible jellyfish. In the Americas, most established jellyfish fisheries are targeting cannonball jellyfish, usually assumed to be *Stomolophus meleagris*, as they are abundant in many regions and have proven to sell successfully in Asian markets. There are however, attempts to exploit other species of jellyfish in the Americas, with limited success (Table 1).

Most rhizostome jellyfish that have been studied have a polymorphic life cycle including both pelagic medusoid and sessile polypoid phases (Fig. 2). The medusoid phase typically persists for 4–8 months, but this varies depending on the species and environment in question. Indeed, the life span of some individual medusae may extend beyond a year in some cases (Arai 1997). Rhizostome medusae are dioecious and eggs may be fertilized in the water column, in the oral arms or gastrovascular cavity of the female, or even in the ovary as is the case with *Cotylorhiza tuberculata* (Widersten 1965; Kikinger 1992; Arai 1997; Schiariti et al. 2012a). Planulae typically form within hours of fertilization and settle upon hard substrate before metamorphosing into polyps (scyphistomae). Finding suitable habitat is likely critical for polyp recruitment. Natural habitats, such as the roots of mangrove forests, are declining in tropical regions due to coastal development (Valiela et al. 2001). Conversely, coastal development is also creating additional habitat for polyps due to a dramatic increase in artificial structures (Duarte et al. 2013). Exactly how such changes will affect edible jellyfish species remains to be seen, but developing a better understanding of polyp populations should be a priority for jellyfish fisheries researchers and managers. Polyps may asexually produce more polyps through several different modes, or may form dormant cysts under a variety of conditions (Adler and Jarms 2009; Arai 2009; Lucas et al. 2012; Schiariti et al. 2014). Ephyrae are released asexually through strobilation and subsequently join the pelagic realm, growing rapidly into medusae (Arai 1997; Palomares and Pauly 2009), after which they may be targeted by the fishery. As polyps do not necessarily perish after strobilation, and usually recover to reproduce repeatedly, this life cycle may provide a buffer against overfishing. However, jellyfish population dynamics are not well understood, and overfishing of jellyfish stocks appears possible. In fact, overfishing is likely one of the main reasons for the decline of *Rhopilema esculentum* catches in Chinese waters (Dong et al. 2014).

According to the literature, there are at least 13 species of rhizostome jellyfish along the American continental coastlines (Table 3) (not considering islands in the Pacific Ocean that belong to different countries). An additional 2 records are identified only to genus level (Table 3). Some species are relatively common (e.g., *Cassiopea frondosa, Cassiopea xamachana, Lychnorhiza lucerna, Phyllorhiza punctata*, and *Stomolophus meleagris*), and there is a considerable amount of literature concerning their biology and ecology (e.g., Mayer 1910; Hummelinck 1968; Calder 1973, 1982; Bolton and Graham 2004; Morandini et al. 2005; Haddad and Nogueira 2006; Schiariti et al. 2008; Rodriguez-Saenz and Segura-Puertas 2009; Carvalho-Saucedo et al. 2012; Sal Moyano et al. 2012; Schiariti et al. 2012a). Several other species have also been reported, but only once or slightly more (e.g., *Cassiopea vanderhorsti, Catostylus cruciatus, Catostylus ornatellus, Catostylus tagi, Lychnorhiza arubae*, and *Mastigias roseus*; see references in Table 3). The validity of such records and species remains uncertain given that only a few specimens are available for comparison, some misidentifications are likely, and some specimens were only seen by the author who described them. However, Appeltans et al. (2012) suggest that the number of scyphozoan species may increase after further research and more comprehensive studies. Regarding the genus *Stomolophus*, there may be more than the two species considered here (*S. meleagris* and *S. fritillaria*); some authors indicate morphological variation as a different variety (e.g., Morandini et al. 2005; Soares et al. 2009). Larson (1990) mentioned the dramatic color difference between the Pacific and Atlantic forms of what he considered to be *S. meleagris* ("prussian blue" and "milky or milky with dark chocolate pigmentation on the exumbrella" respectively). Indeed, there appears to be at least five varieties of *Stomolophus* cf. *meleagris* in the Gulf of California and Pacific Mexico

Table 2 Edible species of jellyfish around the world

Class	Order	Family	Species	Country	References
Cubozoa	Carybdeida	Carybdeidae	*Carybdea rastoni*	Taiwan	Purcell et al. (2007)
			Chiropsalmus sp.	Philippines	Heeger (1998)
			Tamoya sp.	Tarawa	Shih (1977)
Scyphozoa	Coronatae	Periphyllidae	*Periphylla periphylla*	Norway	Wang (2007)
	Rhizostomeae	Cassiopeidae	*Cassiopea ndrosia*	Philippines	Omori and Nakano (2001)
		Catostylidae	*Acromitus hardenbergi*	Malaysia; Indonesia; Thailand	Kitamura and Omori (2010)
			Catostylus mosaicus	Australia	Fisheries Victoria (2006)
			Catostylus perezi	Pakistan	Muhammed and Sultana (2008), Gul and Morandini (2013)
			Crambione mastigophora	Indonesia	Omori and Nakano (2001), Kitamura and Omori (2010)
			Crambionella annandalei	Myanmar	Kitamura and Omori (2010)
			Crambionella orsini[a]	India; Sri Lanka	Kuthalingam et al. (1989), NARA (2010)
			Crambionella helmbiru	Indonesia	Nishikawa et al. (2015)
			Crambionella stuhlmanni	India	Kuthalingam et al. (1989), Mohan et al. (2011)
		Cepheidae	*Cephea cephea*	Thailand	Omori and Nakano (2001)
			Cotylorhiza tuberculata	Italy	This study
		Lobonematidae	*Lobonema smithi*	China; India; Philippines	Kingsford et al. (2000), Hong (2002), Murugan and Durgekar (2008)
			Lobonemoides gracilis[b]	China; Philippines	Omori (1981), Hong (2002), Kitamura and Omori (2010)
			Lobonemoides robustus	Indonesia; Myanmar; Vietnam; Thailand; Philippines	Kitamura and Omori (2010)
		Lychnorhizidae	*Lychnorhiza lucerna*	Argentina	This study
		Mastigiidae	*Mastigias* sp.	Thailand	Sloan and Gunn (1985)
			Phyllorhiza punctata	Australia	Coleman et al. (1990), Kailola et al. (1993)
		Rhizostomatidae	*Rhizostoma octopus*	United Kingdom	T. Doyle (personal communication)
			Rhizostoma pulmo	Turkey	Ozer and Celikkale (2001)
			Rhizostoma sp.	India	Chidambaram (1984)
			Rhopilema esculentum	China; India; Indonesia; Japan; Korea; Malaysia; Thailand; Russia; Vietnam	Omori (1978), Morikawa (1984), Sloan (1986), Kingsford et al. (2000), Omori and Kitamura (2004), Yakovlev et al. (2005), Nishikawa et al. (2008), Panda and Madhu (2009)
			Rhopilema hispidum	China; Indonesia; Japan; Malaysia; Pakistan; Thailand; Vietnam	Kingsford et al. (2000), Omori and Kitamura (2004), Muhammed and Sultana (2008), Kitamura and Omori (2010), Gul and Morandini (2015)
			Rhopilema nomadica	Turkey	Kingsford et al. (2000)
			Rhopilema verrilli	USA	Rudloe (1992), Kingsford et al. (2000)
		Rhizostomatidae?	(suspected unique sp.)	Indonesia	Omori and Nakano (2001), Kitamura and Omori (2010)
		Stomolophidae	*Nemopilema nomurai*	China; Japan; Korea	Omori (1978), Morikawa (1984), Li et al. (2014)
			Stomolophus meleagris	USA; Mexico; Nicaragua; Ecuador; Honduras	Hsieh et al. (2001); López-Martinez and Álvarez-Tello (2013), this study

Table 2 continued

Class	Order	Family	Species	Country	References
	Semaeostomeae	Cyaneidae	*Cyanea nozakii*	China	Lu et al. (2003), Zhong et al. (2004), Dong et al. (2010)
		Pelagiidae	*Chrysaora pacifica*	Japan	Morikawa (1984), Huang et al. (1987)
			Chrysaora plocamia	Peru; Chile	This study
			Pelagia noctiluca	?	Armani et al. (2013)
		Ulmaridae	*Aurelia aurita*	Canada	DFA (2002a, b)
			Aurelia labiata	Canada	Sloan and Gunn (1985)
			Aurelia sp.	India	Govindan (1984)

[a] May be = *C. annandalei* (see Kitamura and Omori 2010)

[b] May be = *L. robustus* (see Kitamura and Omori 2010)

alone (JAT personal observations); however, little formal research has been conducted on the subject (but see Nevárez López 2010).

There is considerable knowledge of jellyfish diversity in certain regions of the Americas, such as the Gulf of Mexico, the east and west coasts of the USA, and the coastlines of Brazil and Argentina (Larson 1990; Mianzan and Cornelius 1999; Morandini et al. 2005; Calder 2009; Oliveira et al. in press). However, surveys for jellyfish outside of these areas are rare, and regions including the Caribbean Sea, Pacific Central America, and northern parts of South America remain understudied. Although these areas have some species listed (Mayer 1910), they are predominantly tropical waters with an expected higher diversity of rhizostomes (Kramp 1970). Moreover, simply knowing the biodiversity of rhizostome jellyfishes is not enough. In order to successfully develop jellyfish fisheries in the Americas, it is imperative that basic abundance and distribution data be collected, along with more comprehensive studies of potential areas of exploitation. Gathering and analyzing information will lead to better management practices and conservation policies.

As more coastlines of the Americas are surveyed for jellyfish, the 13–15 species of rhizostomes so far identified (Table 3) may increase. However, only five of these recognized species are known to be abundant: *Cassiopea xamachana, Lychnorhiza lucerna, Phyllorhiza punctata, Rhopilema verrilli,* and *Stomolophus meleagris*. Of these, *S. meleagris* is already being exploited in some regions (Fig. 1) and *L. lucerna* is currently being investigated in Argentina. The two remaining species (*P. punctata* and *C. xamachana*) are not targeted at commercial scales, likely due to the fact that they are not preferred as edible species (see Table 2). As non-rhizostome jellyfish have yet to be successfully exploited at commercial scales, new opportunities for expanding jellyfish fisheries in the Americas may be limited, at least until new processing technologies are developed and market demand for semaeostome jellyfish increases.

Processing jellyfish

Most jellyfish catch is processed into a semi-dried product through a stepwise procedure of soaking in various mixtures of salts. Although rare by

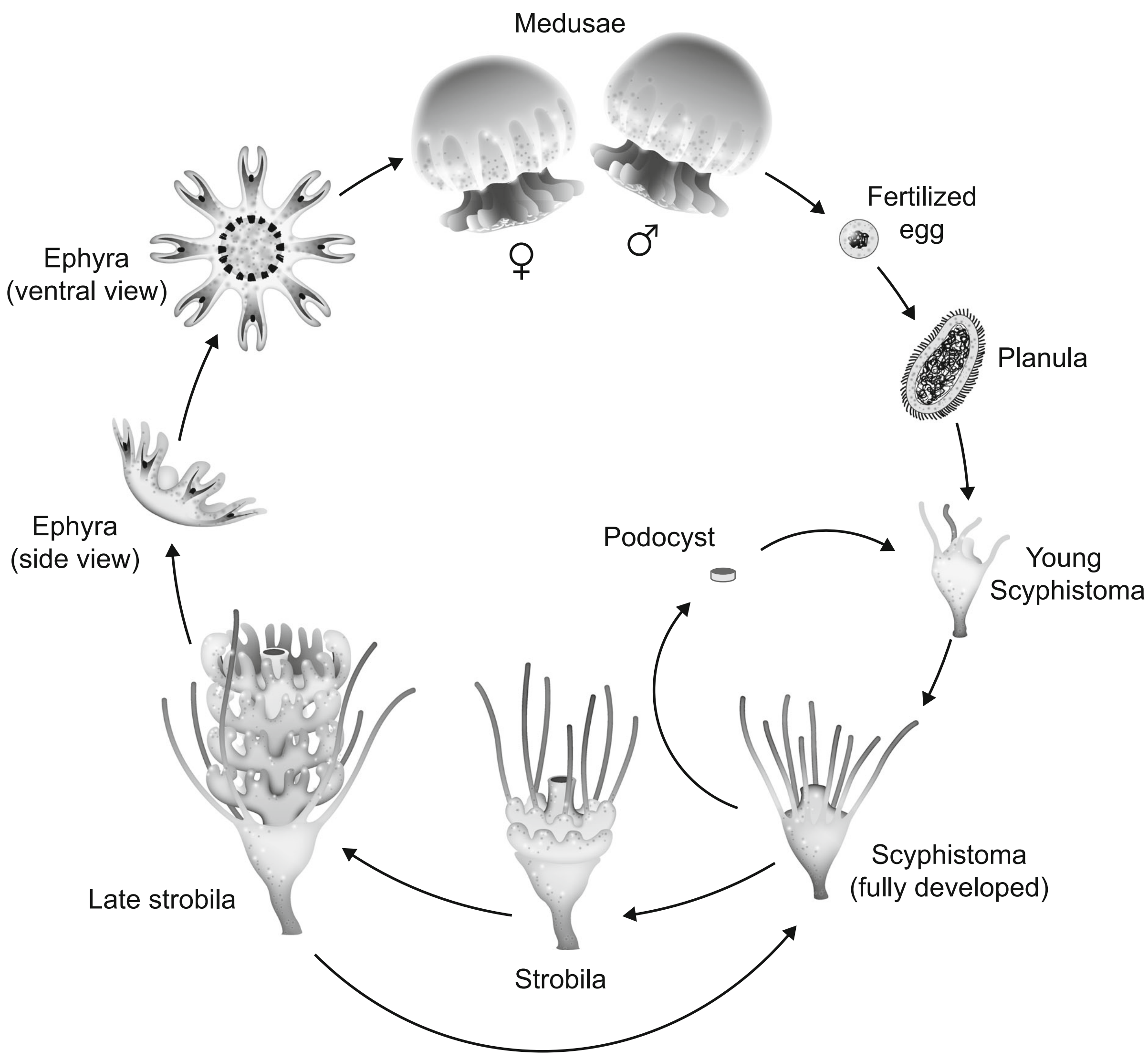

Fig. 2 Life cycle of the cannonball jellyfish *Stomolophus meleagris*. Gametes are released by sexually mature medusae. Fertilized eggs develop into motile, short-lived planulae larvae, which settle onto hard substrates and metamorphose into sessile scyphistomae. Scyphistomae may increase their abundance by the asexual formation of podocysts. Young medusae (ephyrae) are produced and released into the water column by polydisc strobilation

comparison, some jellyfish may be used as a fresh ingredient immediately after it is caught, as is occasionally the case with *Rhopilema esculentum* and *Nemopilema nomurai* in China (Yang and Shuang 2015). There are a number of detailed accounts on processing jellyfish written in English (e.g., Soonthonvipat 1976; Wootton et al. 1982; Chidambaram 1984; Govindan 1984; Santhana-Krishnan 1984; Sloan and Gunn 1985; Huang 1988; Suelo 1988; Rumpet 1991; Rudloe 1992; Jones and Rudloe 1995; Ozer and Celikkale 2001; Nishikawa et al. 2008), Spanish (e.g., Álvarez-Tello 2007; Schiariti 2008; Schiariti and Mianzan 2013; Schiariti et al. 2015), and Chinese (e.g., Wu 1955; Liu 1973; Yin et al. 2000). Processing methods and techniques vary by species, market preferences, facilities, and producers. As such, here we provide only a general overview of processing techniques common to most methods.

Unlike other seafood, jellyfish are almost never frozen at sea, and are typically processed within hours of being caught in order to avoid spoilage. However, one of us (LB) recently ate reconstituted *Cotylorhiza*

Table 3 Rhizostome diversity in the Americas

Classification	Family	Species	Ocean	Distribution	Main records
Suborder Kolpophorae	Cassiopeidae	*Cassiopea frondosa*	W Atlantic	Carribean, S USA	Mayer (1910), Hummelinck (1968)
		Cassiopea vanderhorsti[a,b]	W Atlantic	Curaçao	Stiasny (1922a)
		Cassiopea xamachana[c]	W Atlantic	Carribean, S USA	Mayer (1910), Hummelinck (1968)
	Mastigiidae	*Mastigias* sp.[a,d]	W Atlantic	Puerto Rico, S USA	Bayha and Graham (2011)
		Mastigias roseus[a,b]	Atlantic	Tropical Atlantic	Reynaud (1830)
		Phyllorhiza punctata[d]	W Atlantic; NE Pacific	SW + SE U.S.A; Puerto Rico; Brazil	Moreira (1961), Garcia (1990), Larson and Arneson (1990), Silveira and Cornelius (2000), Bolton and Graham (2004)
Suborder Daktyliophorae	Catostylidae	*Catostylus cruciatus*[a,e]	SW Atlantic	S Brazil	Lesson (1830), Morandini (2009)
		Catostylus ornatellus[a]	SE Pacific	Ecuador	Vanhöffen (1888)
		Catostylus tagi[a,d]	E Pacific	W Panama	Stiasny (1922b)
	Lychnorhizidae	*Lychnorhiza arubae*[a]	W Atlantic	Aruba	Stiasny (1920)
		Lychnorhiza lucerna	SW Atlantic	Colombia to Argentina	Mayer (1910), Silveira and Cornelius (2000)
		Lychnorhiza sp.	NE Pacific; W Atlantic	Mexico; Colombia	Larson (1990), Cedeño-Posso and Lecompte Pérez (2013)
Superfamily Rhizostomatoidea	Rhizostomatidae	*Rhopilema verrilli*	NW Atlantic	S + E USA	Calder (2009)
	Stomolophidae	*Stomolophus fritillaria*[a]	SW Atlantic	Venezuela to French Guyana	Haeckel (1880), Ranson (1949)
		Stomolophus meleagris	W Atlantic; E Pacific	SE USA to Brazil; SW USA to Ecuador	Mayer (1910), Calder (2009)

[a] Found only once or a few times

[b] Species validity in question

[c] ? = *C. andromeda*, non-indigenous (see Holland et al. 2004)

[d] Reported as non-indigenous

[e] ? = *Lychnorhiza lucerna* (see Mianzan and Cornelius 1999)

tuberculata that had been frozen at ultra-low temperature (close to −80 °C), and the quality and taste of the product was excellent, suggesting that freezing of some jellyfish species may be possible as an alternative to traditional chemical processing. Storage onboard fishing vessels sometimes includes chilled seawater slurries to delay degradation. Processing facilities range from small beachside tents to industrial factories. Processing sometimes begins onboard the fishing vessel, and is often carried out thereafter by the fishers, their families, or fishing cooperatives near the fishing grounds.

Separation stage

All rhizostome jellyfish lack tentacles, and instead have prominent oral arms (sometimes called ‘legs’ or incorrectly referred to as ‘tentacles’). While both the oral arms and the bell are edible, they are typically separated during the initial stages and processed separately. Occasionally, especially with very large specimens (e.g., *Rhopilema hispidum, R. esculentum*), the oral arms are separated into the individual arms and the manubrium, often referred to as the ‘stem’.

Cleaning stage

Whole or separated jellyfish are generally washed with high-volume, low-pressure seawater to remove the mucus, membranes, and gonads, as well as sand and possibly bacteria. The bells may also be scraped (sometimes with bamboo tools) to expedite the cleaning process and remove the surface “skin” if there are denticulations, or washed in industrial stirring machines. Initial washing steps are important to facilitate the penetration of the processing salts into the tissues, allowing osmosis and dehydration to proceed at a faster rate and thereby minimizing spoilage.

Salting/curing stages

Jellyfish are soaked in varying amounts of salt (NaCl) and alum (e.g., $KAl[SO_4]_2 \cdot 12H_20$). Soaking in various mixtures reduces the water content of the jellyfish and transforms the gelatinous tissues into the distinctive crispy and firm texture that is the most desirable characteristic of edible jellyfish. Salt is essential to reduce the water content of the tissues through osmosis, and alum is required to reduce the pH and precipitate the proteins to achieve the unique elastic yet crispy texture. The lowered pH greatly reduces the chances of microbial growth, thereby extending the shelf life of the final product. Using only salt or alum alone may not result in a satisfactory product (Wootton et al. 1982). In some regions, such as Malaysia, Thailand, and the Philippines, a small amount of soda (NaOH) may be added to the salt-alum mix to facilitate additional dehydration. Depending on the market preferences and the variety of jellyfish being used, bleaching agents containing hydrogen peroxide may be added to whiten the product, as is the case for *Stomolophus meleagris* from Mexico bound for China. The quality of the salt used can also have a significant impact on processing, with higher-quality fine salt penetrating the tissues faster, while coarser rock salt will dissolve slower but last longer.

Jellyfish are typically soaked in several different salt-alum mixtures for specified times. The duration of the entire process varies greatly depending on the species and processing formulas, and may last anywhere from 4 to 40 days. Shorter processing times have been developed in the USA, facilitated by automation, industrialization, and the fact that medusae of *Stomolophus* spp. are typically smaller than other species of edible jellyfish. Even minor differences in the amounts of salt and alum used, or in the number and duration of salting stages, can represent important differences in the final product quality. Jellyfish processing is by no means an exact science, but instead is considered an art and is often conducted behind closed doors by so-called 'Jellyfish Masters' using closely guarded recipes (Rudloe 1992; Jones and Rudloe 1995). In areas where jellyfish products are to be exported, processors typically receive instructions from their buyers, as different markets prefer different tastes, colors, and textures of products. The weight of semi-dried processed jellyfish is usually 15–20 % of the original wet weight, but may range from 7 % to more than 25 %, depending on the species and processing method used.

There are a number of concerns about the effluent that is created from processing facilities. Primarily, these concerns surround the disposal of huge amounts of slime-salt wastewater created during the initial processing stages. This issue has been the subject of recent debate in South Carolina, USA, as companies are looking to expand production but are being met with resistance and regulation. Currently, Raffield Fisheries in Florida, USA is dealing with the problem by first reducing the amount of organic matter in the wastewater with aeration and agitation, followed by quantity dilution to an acceptable extent before discharging the wastewater into the sea. The disposal of large quantities of processing wastewater from multiple processing sites is a concern, and this issue would need to be resolved in highly regulated areas, such as the coastal USA, before high-volume shoreside processing can proliferate. In most countries, the effluent from processing facilities is not regulated. Research into the development of improved processing techniques that minimize the harmfulness and toxicity of effluent should be a priority, and potential solutions may have the added benefits of reducing costs, minimizing the negative health effects associated with processing chemicals, such as aluminum (see below), as well as the utilization of new species and markets.

The edible product

Jellyfish may be served on their own or as ingredients in salads, soups, and other dishes. In preparation for consumption, semi-dried, salt-preserved jellyfish products are typically desalted and partially rehydrated by soaking in water for several hours or overnight, often with numerous water changes. Fresh and desalted jellyfish products have little flavor, and are usually served with sauces that can include sesame oil, soy sauce, vinegar, and sugar. Jellyfish may also be an ingredient of more elaborate dishes. Preparation varies depending on the product and region, but jellyfish are often shredded and scalded with hot water prior to serving. More recently, ready-to-use (RTU) jellyfish products have become increasingly popular, as they do not require soaking, and are usually served with sauces as a ready-to-eat snack. Prices for jellyfish vary widely depending on the product, but processed jellyfish may typically be found at market fetching 2–10 USD/kg.

Rehydrated (i.e., desalted) edible jellyfish are typically ~92 to 96 % water and ~3 to 7 % protein, depending on the species, the type of product, and the processing methods used. Levels of carbohydrate, fat, and cholesterol are nearly undetectable in a single serving. With approximately 36 food calories per 100 g (USDA 2015), edible jellyfish have been declared as a natural diet food, comparable to vegetables such as broccoli and carrots, and only double the energy density of cucumber and celery. Macro elements including calcium, magnesium, potassium, and sodium are high in fresh jellyfish tissues as their contents are affected by seawater; however, these elements are substantially reduced in edible jellyfish after desalting. While most salts can be removed by soaking in water, processed jellyfish contain elevated levels of aluminum due to the alum curing agent (Ogimoto et al. 2012; Zhang et al. 2016). The aluminum binds to the proteins in the gelatinous tissue, resulting in the desired crunchy and crispy texture. As oral arms are typically higher in protein, they may contain several times the aluminum level of the bell. As solid salt and alum are usually packaged with the processed jellyfish to preserve the product during shipping and storage, longer exposure to the curing agent increases the salt penetration and tissue-binding of the aluminum, resulting in a higher Al-content. Cannonball jellyfish (*S. meleagris*) typically have relatively lower Al-content due to the shorter processing times compared with jellyfish processed in Asia. As there are negative health effects associated with the consumption of aluminum, including neurobehavioral toxicity (Perl and Brody 1980; Nayak 2002), the development of processing techniques that avoid the use of alum is desirable (Hsieh and Rudloe 1994). Unfortunately, current efforts to develop new processing technologies appear to be limited.

In contrast with the negative effects of aluminum consumption, there are numerous purported health benefits to consuming jellyfish. Traditional Chinese Medicine (TCM), as well as advertisements in magazines and non-scientific publications, claim that eating jellyfish is beneficial for treating arthritis, high blood pressure, bronchitis, cancer, ulcers, fatigue, swelling, burns, as well as softening skin and aiding weight loss. Scientific studies evaluating such claims are rare to nonexistent. However, recently cannonball jellyfish collagen was found to exhibit both preventative and therapeutic effects on antigen-induced arthritis in laboratory animals. The results showed that rats fed with low doses of jellyfish collagen had significantly reduced incidence, onset, and severity of antigen-induced arthritis (Hsieh 2005). No human clinical data are available.

Some individuals may also experience negative reactions soon after consuming processed jellyfish, such as anaphylaxis; however, such cases appear to be extremely rare (Imamura et al. 2013; Inomata et al. 2014). Mild allergic reactions to the consumption of jellyfish have been observed, such as swelling of the mouth, but also appear to be rare (JAT personal observations). There is a solitary case of ciguatera poisoning suspected to be caused by consumption of jellyfish from American Samoa, although the details are vague (Zlotnick et al. 1995).

In general, processed edible jellyfish has a surprising crunchy and crispy texture. The value of the product is often determined based on a combination of textural factors including crunchiness, elasticity, and tenderness. The product's color can also be important, with freshly processed jellyfish having a creamy white color, which will gradually turn to yellow and then brown as the product ages. Depending on the species, edible jellyfish may also have hues of blue and red. As mentioned, some products bound for China may be bleached white during processing.

Information about the shelf life of cured jellyfish varies. Huang (1988) noted that product from *S. meleagris* can be stored for at least 6 months at 10 °C. Hsieh et al. (2001) stated that edible jellyfish products last up to a year at room temperature, which can be extended to more than 2 years if kept cool. Freezing of processed jellyfish for storage is possible for short stages (Govindan 1984; Santhana-Krishnan 1984; Kingsford et al. 2000; Ozer and Celikkale 2001); although frozen jellyfish will begin to dry out and form wrinkles, negatively affecting the appearance and texture of the product, and is therefore not recommended for prolonged periods (Huang 1986; Rudloe

1992; Subasinghe 1992; Hsieh et al. 2001). As mentioned, freezing at ultra-low temperatures may provide alternatives to chemical processing and potential longer-term storage.

Other uses of jellyfish

Jellyfish may be targeted for a number of reasons other than as food for humans. In some cases, jellyfish have been fished simply to remove them from locations where they are a nuisance to tourism or other industries. Such efforts have proven effective in Hawaii (Hofmann and Hadfield 2002; Kelsey 2009); however, these cases involved *Cassiopea* spp., which are relatively sedentary (Holland et al. 2004). Cannonball jellyfish (*Stomolophus meleagris*) have also been removed in the past from canals in Florida, where they clogged the intake pipes of a nuclear power plant (Jones and Rudloe 1995). Fishers have also been paid to remove *Cotylorhiza tuberculata* in Mar Menor in the Mediterranean Sea, a species which ironically appears to have increased largely due to anthropogenic impacts (Brotz and Pauly 2012). While it appears that fishing of medusae may have helped to reduce the jellyfish population there, it was an extremely expensive program, and environmental conditions are likely much more influential of the population dynamics in question (Prieto et al. 2010; Ruiz et al. 2012).

Jellyfish have been used successfully as partial feedstock for a variety of animals, including farmed chickens and pigs (Hsieh and Rudloe 1994; CIESM 2010). There is also increasing interest in using jellyfish as feed in aquaculture (e.g., Gopakumar et al. 2008; Miyajima et al. 2011a, b; Wakabayashi et al. 2012). Jellyfish may be used as bait, such as in Japan where parts of the giant jellyfish *Nemopilema nomurai* are used for sea bream fishing (Omori and Kitamura 2004). The practice of using jellyfish as bait in fish traps in India extends back decades, and probably longer (Prabhu 1954; Thomas 1969; Varghese et al. 2008). Artisanal fishers in Peru have used gonads from *Chrysaora plocamia* as bait for targeting *Seriolella violacea*, commonly known as *cojinova* or palm ruff (Mianzan et al. 2014). Historically, fishers in Peru also used large blooms of *C. plocamia* to locate leatherback sea turtles (*Dermochelys coriacea*), which were hunted for their meat, especially during the 1960s, 1970s, and 1980s.

Jellyfish have also been central to a range of advances in medical research. These have included several investigations of jellyfish constituents and toxins, some of which have important biomedical and pharmacological properties (e.g., Ovchinnikova et al. 2006; Yu et al. 2006; Masuda et al. 2007; Ohta et al. 2009; Balamurugan et al. 2010; Mariottini and Pane 2010; Zhuang et al. 2010; Morishige et al. 2011; Zhuang et al. 2012a, b; Kawabata et al. 2013; Leone et al. 2015). Research on some groups of jellyfish has led to a better understanding of ocular evolution (Nilsson et al. 2005), as well as two Nobel Prizes: one in 1913 for the discovery of anaphylaxis, and another in 2008 for the discovery and development of green fluorescent protein (GFP). Jellyfish have also informed the field of design engineering (e.g., Dabiri 2011; Najem et al. 2012; Ristroph and Childress 2014), where their biomechanics are often mimicked due to their simple and efficient design (Gemmell et al. 2013). Most of the above applications do not require the removal of jellyfish from the wild at commercial scales. One exception is the processing of jellyfish to extract collagen, which may be used in a variety of applications including cosmetics and pharmaceuticals (Addad et al. 2011). One company based in France (www.javenech.com, accessed 26 June 2015) processes several tonnes of *Rhizostoma pulmo* caught in the Atlantic Ocean for collagen each year. Research into extracting collagen from other species is ongoing, including *Lychnorhiza lucerna* in SE Brazil.

Although the processes involved are new and still developing, jellyfish are being used or proposed for use in a number of industrial applications. In Russia, jellyfish have been successfully added to cement, which ultimately increased the mechanical strength of traditional cement by 50 % (CIESM 2010), although unfortunately the details are vague. Experiments have also demonstrated that jellyfish can successfully be used as fertilizer for a variety of plants, trees, and crops (e.g., Fukushi et al. 2004, 2005; Chun et al. 2011; Kim et al. 2012; Hossain et al. 2013; Hussein and Saleh 2014; Seo et al. 2014; Hussein et al. 2015). There are even recent reports that a company in Israel has developed an absorbent and biodegradable material from jellyfish that could be used in products such as diapers and paper towels (Shamah 2014).

Most of the technologies that propose to use jellyfish in medical and industrial applications are in their infancy, and thus it will likely be sometime before there is significant demand for jellyfish other than for food. Additional applications, such as the use of jellyfish as biomonitors of pollution in the marine environment (e.g., Templeman and Kingsford 2010; Morabito et al. 2014) would likely not require significant numbers of medusae. Nonetheless, it is conceivable that jellyfish could be used in a variety of future applications, a strategy that has been proposed to deal with the increasing problems associated with jellyfish blooms (e.g., Purcell et al. 2007; Richardson et al. 2009; Purcell 2012).

Ecological impacts of fishing for jellyfish

All fisheries affect the environment, but understanding the impacts to food webs and habitats is a challenge. Some impacts are measurable, including habitat damage and bycatch. Habitat damage is mostly a concern with gears such as bottom-trawls and traps, neither of which are typically used for jellyfish fisheries. The most common fishing method employed by jellyfish fisheries is dip-netting, which results in relatively low levels of bycatch and virtually no habitat damage. However, numerous species of juvenile fishes have been documented to associate with jellyfish, presumably using the medusae as food and/or refugia from predators (e.g., Jones 1960; Arai 1988; Kingsford 1993; Brodeur 1998; Purcell and Arai 2001; López-Martínez and Rodríguez-Romero 2008; Mianzan et al. 2014). In addition, many invertebrates are known to associate with jellyfish, potentially benefitting from habitat, food, refugia, and transportation (e.g., Brandon and Cutress 1985; Arai 2005; Browne and Kingsford 2005; Towanda and Thuesen 2006; Sal Moyano et al. 2012; Schiariti et al. 2012b; Álvarez-Tello et al. 2013; Fleming et al. 2014). As such, bycatch concerns from jellyfish fisheries cannot be eliminated entirely, and will likely increase with seine or trawl gears (Panda and Madhu 2009).

Bycatch in the trawl fishery for cannonball jellyfish *Stomolophus meleagris* was examined in detail in Georgia, USA. In total, 133 tows were examined between 2005 and 2012. The results, presented by Page (2015), show that 38 species of fish, as well as 3 species of invertebrates (not including spider crabs *Libinia* spp., which are symbiotic with *S. meleagris*) were recorded as bycatch. The most commonly observed bycatch were harvestfish *Peprilus paru* (41 %), cownose ray *Rhinoptera bonasus* (11 %), Atlantic bumper *Chloroscombrus chrysurus* (11 %), butterfish *Peprilus triacanthus* (11 %), and blue crab *Callinectes sapidus* (7 %). The 3 finfish species (harvestfish, Atlantic bumber, and butterfish) are all known to associate with jellyfish, presumably using them as refugia from predators, and potentially becoming ectoparasites that feed directly on the medusae (Purcell and Arai 2001). As such, it is not surprising that these species form a major component of the bycatch (Page 2015). A similar associative relationship also explains the vast quantities of spider crabs that were caught as bycatch. Other species that are know to associate with *S. meleagris* medusae but were absent as bycatch may be due to the seasonality of the fishery and/or the ability of species to escape the nets (e.g., carangids). Given that the top 5 bycatch species (excluding spider crabs) comprised approximately 80 % of all individuals caught, it can be said that "the commercial cannonball jellyfish trawl fishery in Georgia is dominated by a few recurring species and is minimal relative to the bycatch associated with another important trawl fishery in the state—namely the commercial food shrimp trawl fishery" (Page 2015). Indeed, 24 % of the tows analyzed contained zero bycatch (excluding spider crabs). Nonetheless, those species comprising the majority of the bycatch can be caught in significant quantities, and may be of commercial and/or ecological concern.

Other species caught as bycatch may also be of concern, even if they are less abundant, such as sea turtles. As mentioned, jellyfish were so bothersome to shrimp fishers in the past that modifications were made to trawl gear that facilitated the exclusion of jellyfish while still permitting shrimp to travel into the codend (Jones and Rudloe 1995). Essentially, a series of metal bars is used to divert anything larger than the space between the bars to an escape hatch, whereas anything smaller passes through the codend. These device modifications dramatically reduced the catch of jellyfish, often by more than 80 % (Huang et al. 1987), but also proved to successfully exclude sea turtles, and ultimately became known as turtle excluder devices or 'TEDs' (Jenkins 2012). TEDs are now mandatory in the state waters of Georgia, but since they are so effective at excluding jellyfish, most jellyfish fishers there opt to trawl in the adjacent federal waters where TEDs are not required (Page 2015). During the aforementioned bycatch study, a total of 13 protected species (11 sea turtles and 2 common bottlenose dolphins) were caught during the 133 observed tows (which represented <5 % of all tows during the period). While some animals caught as bycatch are released alive, tows routinely exceed 1 h in duration (average of 0.55 h), suggesting that mortality of air-breathing species could be significant. There are ongoing efforts to design TEDs with spacing between the bars that is sufficient for jellyfish to pass through, but not turtles (Page 2015).

Although jellyfish were often perceived to be trophic dead-ends (e.g., Verity and Smetacek 1996; Sommer et al. 2002), this perception is changing. Many sea turtles will prey on jellyfish during some stage of their lives, and the leatherback sea turtle *Dermochelys coriacea* is an obligate jellyfish predator, with individuals potentially eating hundreds of kilograms of jellyfish in a single day (Duron-Dufrenne 1987; Heaslip et al. 2012). As the leatherback turtle is critically endangered, fishing for jellyfish in waters deemed critical habitat could be subject to restrictions in some jurisdictions. Recent investigations are also revealing the importance of jellyfish as prey for more than one hundred species of fish (Arai 1988; Ates 1988; Mianzan et al. 2001; Purcell and Arai 2001; Arai 2005; Pauly et al. 2009; Cardona et al. 2012). In addition, large blooms of jellyfish that die and sink to the ocean floor (known as 'jelly-falls') have mainly been investigated for their role in the biological pump (Lebrato et al. 2012, 2013); however, it is becoming apparent that they may also be an important nutritional input for benthic animals (e.g., Henschke et al. 2013; Sweetman et al. 2014).

Jellyfish can also be voracious predators and often have very significant impacts on the abundance, biomass, and size composition of zooplankton at lower trophic levels (Möller 1980; Mills 1995; Purcell and Arai 2001). In some cases, there is convincing evidence that overfishing of small pelagic fish has resulted in an alternate ecosystem state whereby jellyfish are released from competition and come to dominate, such as the Benguela Current ecosystem (Bakun and Weeks 2006; Lynam et al. 2006; Utne-Palm et al. 2010; Flynn et al. 2012; Roux et al. 2013). Thus, one could posit that the reverse would be true, i.e., that overfishing of jellyfish in such an ecosystem may facilitate the recovery of fish at similar trophic levels. However, in reality, such situations may not be straight-forward or predictable (Gibbons et al. 2016). Nonetheless, the extensive removal of medusae may help to mitigate some of the detrimental impacts of jellyfish on human industry (Purcell et al. 2007; Lucas et al. 2014). Therefore, the removal of jellyfish may be perceived as beneficial or detrimental depending on the food web dynamics, management goals, and species in question.

Beyond their extensive roles in food webs, jellyfish also provide a number of ecosystem services such as carbon transport, nutrient liberation, and oceanic mixing (Doyle et al. 2014). Given all of their influential roles in ecosystems, removing jellyfish in large quantities is likely to have significant consequences. Unfortunately, jellyfish have been understudied and are typically ignored or simplified in ecosystem models (Pauly et al. 2009). As such, the impacts of removing large amounts of jellyfish through fishing are not well understood (Gibbons et al. 2016).

Jellyfish fisheries in the Americas

Argentina

For a number of years, jellyfish have been caught around the Río de la Plata along the northern coast of Buenos Aires province (Schiariti 2008). These jellyfish are being processed by scientists and fisheries researchers in order to investigate the quality of the product produced from *Lychnorhiza lucerna*—a rhizostome jellyfish that has previously not been reported as being consumed (Schiariti and Mianzan 2013). *L. lucerna* interferes with tourism as well as fisheries for finfish and shrimp (Schiariti 2008; Nagata et al. 2009), so there is interest in targeting this species. Moreover, developing an alternative resource for fishers in the area would be welcome, as declining catches of more traditional fisheries resources have created economic hardship for many in the region. Given that the peak season for finfish is in the austral winter, and medusae appear during the summer, a targeted jellyfish fishery could help to compensate for the low fishing activity characteristic of the summer season. This species also occurs in the neighboring waters of southern Brazil and Uruguay as evidenced by bycatch records and scientific studies (Schiariti 2008; Nagata et al. 2009; Schroeder et al. 2014), suggesting the area of potential exploitation for this species is considerable.

Several trials have been conducted in order to produce sample products. When fishing occurs, 15–20 small boats up to 15 m in length will use a variety of gears (depending on the size of the vessel) including demersal trawls, gill nets, and dip-nets. The gears and boats fishing for jellyfish also depend on meteorological conditions, as winds and currents can strongly affect the locations of *L. lucerna* blooms between canals and further offshore. Bycatch is also a concern, as the jellyfish season coincides with the reproductive timing of several commercially important finfish species. Further investigation and refinement of gears and techniques is expected to help minimize bycatch. To date, processing of jellyfish has been performed by fisheries researchers under instruction from potential buyers, and initial responses from Chinese and Malaysian importers has been positive. However, a major hurdle to the establishment of a permanent jellyfish fishery in Argentina is uncertainty regarding how much jellyfish can be produced from the region on a consistent basis, as buyers necessitate a minimum to be involved. Significant investment is required to undertake proper biomass assessments, investigate the costs involved, and acquire a better understanding of jellyfish population dynamics in the region. Policy-makers in the area continue to perceive a potential jellyfish fishery with incredulity, and are dismissive about jellyfish providing significant economic value. Fishers in the region are less dismissive, as they are highly economically motivated and have been working directly with fisheries researchers and potential buyers for several years. Until the economic and ecological knowledge gaps can be filled, a fishery for jellyfish in Argentina remains undeveloped.

Canada

Canada has explored fisheries for jellyfish on the Atlantic and Pacific coasts. However, both test fisheries did not continue, predominantly due to the fact that they targeted *Aurelia* spp., for which there is limited demand.

Fisheries and Oceans Canada (also known as the Department of Fisheries and Oceans, or DFO) explored the possibility of a fishery for *Aurelia labiata* in coastal British Columbia in 1984. Sloan and Gunn (1985) present details for 11 dip-net and two seine fishing cruises conducted between August and November in the northern Strait of Georgia. The total catch was 2.82 t, which was then processed using three different protocols from potential Japanese buyers. Samples were provided to Chinese fish wholesalers and to Japanese and Chinese restaurateurs in Vancouver. The product was deemed unsuitable, based mainly on the poor texture that lacked the preferred crunch. Ultimately, the test fishery for jellyfish in British Columbia did not continue.

The test fishery on Canada's east coast was implemented to understand the methods and costs involved in producing jellyfish, and to evaluate the potential market (DFA 2002a). In addition, jellyfish frequently interfere with active and passive fishing gears in the region, making a targeted fishery even more desirable (DFA 2002b). An estimated 49 t of jellyfish were caught over a period of 2 weeks in September 2002 in Newfoundland's Trinity Bay; however, only about 1 t was retained, with the rest being discarded at sea (DFA 2002b). A 50-foot shrimp beam trawl was used, towed at approximately 1 knot. Catches consisted of approximately 90 % *Aurelia* sp. and 10 % *Cyanea capillata*, with the latter reportedly being too delicate to handle. The subsample of *Aurelia* retained for processing was stored onboard the ship in an insulated container containing a slurry of slush ice and 1 % alum. Approximately 1.1 t of jellyfish were processed and samples were sent to China, Taiwan, and Florida, USA for market testing (DFA 2002b). Due to a lack of demand for semaeostome jellyfish, as well as unrefined handling and processing techniques, the test fishery was discontinued.

Ecuador

In 2013, Chinese dealers began promoting the possibility of catching jellyfish (presumably *Stomolophus meleagris*) from Ecuadorian waters. Shellfish fishers, who have been struggling to generate sufficient income, welcomed the proposal. Approximately 100 small (~10 m) fiberglass and wooden boats began fishing for jellyfish using modified gillnets and set-nets within and around the Guayaquil Gulf Estuary (Fig. 3). In 2014, an astounding 78,000 t of jellyfish were landed (most of which was caught in February and March), processed, and exported to China, Japan, and Thailand. While studies are currently underway to evaluate the impacts of the fishery and to establish management regulations, the fishery was completely closed from May to September 2014 as processing facilities were

Fig. 3 Photographs from active jellyfish fisheries in the Americas. **a** fishers deploy set nets in Ecuador, photo by Richard Panchana, **b** fishers prepare to unload their catch in Ecuador, photo by Evelyn Ramos, **c** fishers catch jellyfish in Mexico's Gulf of California, photo by Javier Álvarez-Tello, **d** processing of jellyfish in Mexico, photo by Javier Álvarez-Tello, **e** trawling for jellyfish in Georgia, USA, photo courtesy Canadian Broadcasting Corporation

shuttered due to a lack of environmental oversight. Catching and processing of jellyfish in Ecuador continued in 2015, but to a lesser degree, with landings of 9135 t. Given the environmental concerns and the supply of jellyfish from nearby in Mexico, the ultimate scale of Ecuador's jellyfish fishery remains unclear.

Honduras

In 2007, samples of a species of *Stomolophus* (likely *S. meleagris*) were caught along the Atlantic coast of Honduras (around the Caratasca Lagoon) using small boats with dip-nets to test for exploitation potential. A small processing facility administered by Chinese dealers has apparently existed there for almost 10 years, but recently ceased operation due to a number of logistical issues. Medusae from the Atlantic coast of Honduras also have a ring around their bell margin, which is generally not favored in Asian markets. A newer facility was built in 2013 (Herrera 2015), a year when FAO reported a catch of 50 t of jellyfish for Honduras. In 2015, a cooperation agreement was signed between the government, an organization representing aboriginal fishers, and a seafood processing company to further investigate the possibility of developing the jellyfish fishery in Honduras, this time in the Gulf of Fonseca in Pacific waters.

Mexico

Mexico began fishing for cannonball jellyfish (*Stomolophus meleagris*) in 2000 in the Gulf of Mexico off the state of Tabasco. However, the fishery moved to the Gulf of California in 2001, primarily to the shallow coastal waters along the state of Sonora. A summary of the fishery is provided by López-Martinez and Álvarez-Tello (2013). Average annual catches are 10,000–15,000 t, but may vary from 1000 t to a peak of more than 30,000 t in 2015. The fishery started relatively small, with about 70 small boats ('*pangas*'), each with a crew of two or three fishers dip-netting for jellyfish (Fig. 3). In 2010, management measures were approved that would set a minimum size limit (MSL), restrict gears, and limit fishing effort, among others. However, the scale of the fishery continued to escalate, partially due to a lack of enforcement, and in 2013, over 1000 *pangas* fished for jellyfish, with the season lasting only 5 days. While catches have remained relatively large, variable fishing seasons and access to the fishery continue to be concerns for those involved. It remains to be seen what additional management and enforcement measures become implemented in Mexico; however, continued research and the development of new processing technologies provide some optimism.

Nicaragua

In 2008, 205 t of jellyfish (a species of *Stomolophus*, most likely *S. meleagris*) were caught and processed in Tuapi, near the city of Puerto Cabezas on Nicaragua's Atlantic coast. There were approximately 34 small wooden and fiberglass boats involved in the fishery, with a typical capacity of about 1.5 t each. Fishermen used dip-nets with a 2-inch mesh size. Bells and oral arms were processed separately, yielding 57 t of processed jellyfish that was exported to Asia. The fishery did not continue in subsequent years, potentially due to a combination of inferior product quality and regulatory obstacles imposed by local authorities. However, interest in catching jellyfish in Nicaraguan waters was recently renewed, and an estimated 659 and 1953 t of jellyfish were caught in 2013 and 2014 respectively.

Peru

There have been recent attempts to exploit *Chrysaora plocamia* along the coasts of Peru, particularly near Pisco, for export to China. While there have been stakeholder meetings and commissioned reports, the fishery has not developed, mainly due to the fact that the target species is a semaeostome, and is therefore less desirable. However, there is potential for development of this fishery given the dramatic abundances of this species, which can sometimes approach the biomass of small pelagic fishes in the region (Mianzan et al. 2014; Quiñones et al. 2015). Large blooms of *C. plocamia* are often a costly nuisance to fishers, aquaculture, desalination plants, tourism, and other industries (Quiñones et al. 2013; Mianzan et al. 2014), suggesting that many would welcome a targeted fishery in the area. Indeed, the nuisance of *C. plocamia* bycatch to fishers was one of the primary motivations to explore the development of a jellyfish fishery in the region. Similarly large abundances of *C. plocamia* also occur in northern Chile, suggesting that if a jellyfish fishery were to be established in Peru, expansion to Chile would be a possibility (Palma 2011). While there are preliminary indications that some buyers in China have found product samples from Peru to be satisfactory, a jellyfish fishery has yet to develop in the region.

USA

The United States of America has both active and discontinued jellyfish fisheries. Active fisheries involve cannonball jellyfish (*Stomolophus meleagris*) in the southeastern part of the country (see below). There was also a historical fishery for jellyfish in Washington State's Puget Sound, but instead of targeting jellyfish for food, that fishery sought the hydromedusan *Aequorea victoria* for research on bioluminescence. The tale is chronicled by Shimomura (1995), and includes the isolation of luminescent proteins 'aequorin' and 'green fluorescent protein' (GFP) in 1962 and 1979 respectively. GFP, which absorbs ultraviolet light and emits a green glow without the addition of any chemical additives, has proven to be an invaluable genetic marker, resulting in a veritable revolution in biotechnology (Zimmer 2005). This immense contribution to science was recognized in 2008, when the Nobel Prize in Chemistry was awarded for the discovery and development of GFP (Coleman 2010; Roda 2010). *A. victoria* has not been targeted from Puget Sound since the 1990s, as synthetic aequorin and GFP are now available. However, during the course of researching the luminescent proteins of *A. victoria*, it has been estimated that a total of one million medusae were collected over the ~25 year period in Friday Harbor (Zimmer 2005). Taking the estimate of Shimomura (1995) of 50 g for a typical specimen, this equates to a total catch of approximately 50 t, or 2 t per year. This is miniscule in the context of most jellyfish fisheries, which may catch tens of thousands or even hundreds of thousands of tonnes of jellyfish in a single season. However, it is worth noting that even these small annual catches may have affected the population of *A. victoria* around Friday Harbor. Upon Osamu Shimomura's arrival on San Juan Island in 1961, the medusae were reportedly "abundant" and provided a "constant stream" flowing passed the docks. However, it was observed that the abundance of this species began to decline in the 1990s (Mills 2001) and has since "almost completely disappeared from the area" (Shimomura 2005). The effects of this apparent overfishing do not appear to be widespread, as *Aequorea* populations in the nearby waters of British Columbia can form extensive blooms with occasional densities of 1–2 medusae/m^3 (LB personal observations).

In the southeastern USA, cannonball jellyfish or 'jellyballs' (*S. meleagris*) have been the source of numerous problems to industries such as power generation and fisheries. Due in part to the nuisance that jellyfish have caused to industry, there have been several attempts to establish fisheries for *S. meleagris* in the USA, with varying degrees of success. The first attempt was reportedly in Medart, Florida in the 1970s for export to Taiwan; however, the venture was unsuccessful, partially due to the reluctance of fishers to target jellyfish (Rudloe 1992). Interest was renewed in the late 1980s, both in Florida and Georgia. At the time, processing techniques were being investigated by Huang (1986, 1988) at the University of Georgia. In 1991, development of a jellyfish fishery was officially launched through a grant from the US Department of Commerce (USDC). Under the grant, marine scientist Jack Rudloe traveled to Malaysia and Thailand to investigate jellyfish fishing and processing methods. Outlined in Rudloe (1992), a jellyfish fishery was proposed for the Florida Panhandle in the northern Gulf of Mexico, where commercial fisheries had suffered dramatic declines due to overfishing and rapid coastal development. The initial report concluded that a fishery for jellyfish could be developed in Florida; however, several challenges would have to be overcome, including economic viability, a lack of processing knowledge, labor costs, and pollution from processing facilities. An additional challenge proved to be the size of the product. Cannonball jellyfish from the region rarely exceed 19 cm in bell diameter, but jellyfish products fetching the highest prices at market at the time were 30 cm or more. Nevertheless, it was thought that a superior product could be produced from cannonball jellyfish and the exploration of the fishery in Florida continued.

Throughout the 1990s, a variety of attempts were made to develop the jellyfish fishery in Florida, whereby small quantities of jellyfish were landed, processed, and sent to potential buyers in Asia (Jones and Rudloe 1995). The darker color of Atlantic cannonball jellyfish was not preferred, and attention shifted to catching jellyfish in the Gulf of Mexico, which are white in color. Challenges for the emerging fishery continued, including high labor costs and an unfamiliarity with the species in Asia (Bynum 2003). Currently, 26 American fishing vessels target cannonball jellyfish in the Gulf of Mexico, with 11 operating out of Apalachicola and 15 out of Port Saint Joe.

The State of Georgia also has an established jellyfish fishery, which began in the 1990s with a solitary processing plant located in Darien (Graitcer 2012). Since 1998, licenses for catching jellyfish have been limited to 6–12 fishers (Page 2015), mainly due to limited processing capacity. The fishers involved in the jellyfish fishery are shrimpers that temporarily convert their boats to fish for jellyfish (Fig. 3), and are reportedly thankful for their newfound opportunity (Bynum 2003; Landers 2011). The jellyfish fishery in Georgia transitioned from experimental to a recognized fishery in 2013, and continues to operate at capacity with an estimated average annual catch around 4000 t and the possibility of future expansion. Current catch levels make jellyfish the third largest fishery in Georgia by weight, behind shrimp and blue crab (Page 2015).

Entrepreneurs in the state of South Carolina are eager to start catching, processing, and exporting cannonball jellyfish. However, development plans have been hampered by concerns over pollution from processing facilities. Proposals have been put forth in Beaufort and Colleton Counties, with capacity in excess of 2000 t per week (Bland 2014). While approximately 6 t of jellyfish were landed and processed at a temporary facility in 2014, these operations have ceased pending further review (Moody 2014; Murdock 2014).

Management

Jellyfish populations typically exhibit dramatic inter-annual variation (Brotz 2011). In fact, changes in biomass of edible jellyfish are probably larger than for any other fishery (Kingsford et al. 2000). This presents extremely large uncertainties for fisheries managers, makes predictions of future catches difficult, and may prevent investment in infrastructure. There is also evidence to suggest that discrete stocks of medusae may exist at relatively small spatial scales (Kingsford et al. 2000; Matsumura et al. 2005). This could make some populations vulnerable to overfishing, especially as fishers are likely to concentrate their effort in areas that are closer to ports or processing facilities (Kingsford et al. 2000). As such, management of jellyfish fisheries is extremely challenging, with research and recommendations still in their infancy. Nonetheless, many of the options for traditional fisheries management are available to jellyfish fisheries, only a few of which have been employed.

In Australia, precautionary total allowable catches (TACs) have been implemented (Fisheries Victoria and MAFRI 2002; Fisheries Victoria 2006), but only a small fraction of the TACs have been utilized, presumably due to a lack of economic viability and onerous regulations. TACs for jellyfish fisheries appear to be rare in most other countries; however, total catch may be limited by processing capacity where it is regulated or industrialized, as is the case in the USA. TACs can also be artificially increased if portions of the jellyfish, such as the oral arms, are discarded at sea. Some countries have also implemented minimum size limits (MSLs) on medusae, such as Australia, Mexico, and the USA. The intent of MSLs is to prevent the capture of medusae before they reach sexual maturity, as well as encouraging higher fecundity, which typically increases with size (e.g., Coleman 2004; Schiariti et al. 2012a). However, there is no guarantee that medusae will spawn successfully at a certain size, or that they will be in a location where planulae can find suitable substrate for settlement. Conversely, medusae may reach sexual maturity over a wide range of sizes, and maturation may be more related to environmental conditions than size (Carvalho-Saucedo et al. 2010, 2011). Of course, a medusa's size is also related to environmental conditions, so the interplay amongst the environment, a medusa's size, and its state of sexual maturity are not well understood. As such, MSLs are likely not enough to guarantee a sustainable jellyfish fishery (admittedly, nor are they sufficient for finfish fisheries). In addition, larger mesh sizes have the potential to damage the medusae, depending on the species in question and the gear used. Nevertheless, implementation of MSLs may be a useful precautionary management technique, especially when knowledge of the target organism's life history and environment is poor. MSLs can also have the added benefit of allowing jellyfish to grow before being caught, which may result in more profit as larger medusae typically fetch higher prices, unless of course natural mortality increases or the jellyfish exhibit degrowth due to poor food availability or other environmental conditions (e.g., Hamner and Jenssen 1974; Frandsen and Riisgard 1997; You et al. 2007; Lilley et al. 2014). Additional research on such topics is essential, especially the exploration of which management techniques are most appropriate for jellyfish fisheries. Due to the poor understanding of jellyfish population dynamics, management decisions for jellyfish fisheries should be adaptive and will likely vary from year to year, or even within a single season.

While the polymorphic life cycle of edible jellyfish (Fig. 2) likely provides a buffer against overfishing, it should not be viewed as a total safeguard. The impacts of fishing medusae on entire jellyfish populations are not well understood, and overfishing of jellyfish stocks appears possible. For example, overfishing of medusae appears to be the primary cause for the decline of *Rhopilema esculentum* in China (Dong et al. 2014), where there are now extensive aquaculture programs that culture this species in large saltwater ponds (You et al. 2007), as well as hatchery programs that rear hundreds of millions of individual ephyrae in laboratories and subsequently release them into the ocean with the intention of increasing the catch (Dong et al. 2009). Despite limited success from these programs (Dong et al. 2014), catches of *R. esculentum* in Chinese waters remain below the levels of the late 1990s, and effort has shifted to the increasingly abundant giant jellyfish, *Nemopilema nomurai* (Brotz and Pauly 2016).

Jellyfish fisheries are clearly growing and expanding faster than research and regulations on the subject. As such, there are a variety of knowledge gaps that should be a priority for researchers and managers that include, but are not limited to:

- Estimates of medusae abundance in regions where fishing occurs or is proposed to occur;
- Surveys to locate (and potentially protect) important polyp habitat;
- Investigations on the linkages between polyp density and medusae abundance;
- Studies on local populations of jellyfish (every species is different, and there are potential important differences even within species, e.g., dramatic differences in color and morphology between different varieties of *S. meleagris*);
- Investigations on the use of models for jellyfish fisheries (e.g., are traditional models for finfish applicable to jellyfish fisheries?);
- Monitoring and tracking of medusae to identify the factors that control aggregations and mixing of stocks;
- Genetic analyses to determine discrete stocks and mixing of populations;
- Investigations of ephyrae growth and survival.

Conclusions and recommendations

Jellyfish have undergone a dramatic transition in some locations in the Americas, often shifting from being a nuisance to industries such as fisheries, tourism, and power generation to being a valuable fishery resource. In most cases, this transition was preceded by a decline of more traditional fisheries resources such as finfish and shrimp. So, should this transition be celebrated as an example of adaptability, or is it another warning sign of fishing down the food web (Pauly et al. 1998)? And what factors dictate the overall success or failure of such a transition? After all, jellyfish fisheries have clearly arrived in the Americas, but with varying degrees of success. For example, jellyfish fisheries in the USA and especially Mexico have proven to be a boon for local fishers (Álvarez-Tello 2007; López-Martinez and Álvarez-Tello 2013), whereas no market has yet developed for jellyfish from Argentina, Canada, or Peru.

There appear to be a number of factors that are conducive to success for new jellyfish fisheries in the short term, and several additional recommendations that may help to ensure establishment of sustainable jellyfish fisheries in the longer term. Firstly, not just any species of jellyfish will do. There are more than 1400 species of jellyfish worldwide (Purcell 2012), but fewer than 40 of those have been documented as being consumed by humans (Table 2). In fact, the number of jellyfish species that are part of major jellyfish fisheries around the world number fewer than 20, and are all rhizostomes (Brotz 2016). While it is conceivable that consumption of semeaostomes and other types of jellyfish may increase in the future, demand for non-rhizostome jellyfish currently remains very low and is likely a major reason why experimental jellyfish fisheries in Canada and Peru were not successful.

Secondly, attention must be paid to the processing of jellyfish. In order to ensure economic success, specific details regarding the nuances of jellyfish processing should come from potential buyers, likely in Asia. As mentioned, the methods and materials used can vary greatly due to a number of factors, so potential exporters need to work closely with buyers to deliver a suitable product. Jellyfish processing is typically labor intensive, so the time and effort required will have to be factored into the economics of any operation, especially in regions where labor costs are high. Jellyfish fisheries in the USA appear to have overcome this obstacle by a combination of the development of shorter processing times through technical advances and the use of smaller medusae, as well as partial industrialization of processing. Moreover, there are significant environmental and human health concerns regarding the contemporary use of processing chemicals. Large quantities of effluent are generated as a byproduct of jellyfish processing, and need to be dealt with in a responsible way. Edible jellyfish may contain concerning amounts of aluminum (Wong et al. 2010; Ogimoto et al. 2012; Armani et al. 2013; Zhang et al. 2016), the consumption of which is linked to a number of negative health effects, including Alzheimer's disease (Perl and Brody 1980; Nayak 2002). The development of new processing technologies that either reduce the aluminum content in the edible products (e.g., Chen et al. 2016) or eliminate the use of alum altogether is desirable (Hsieh and Rudloe 1994). Such research could easily be undertaken by the vast array of food scientists in industry and academia. As an example, *Cotylorhiza tuberculata* that was frozen fresh at ultra-low temperature (close to −80 °C) and then reconstituted by a professional chef with a small amount of sugar and vinegar was declared to be delectable by one of us (LB). As the seafood industry already has significant infrastructure for freezing, storage, and distribution of food, this may provide an alternative to chemical processing of jellyfish in some places. The development of alternative processing technologies could provide multiple benefits for jellyfish fisheries, including expansion beyond rhizostome species, development of new markets, reduced costs, and the elimination of environmental and human health concerns.

To ensure success of jellyfish fisheries in the longer-term, cooperation between stakeholders appears to be key. In addition to the collaboration between processors and buyers mentioned above, fishers, managers, and researchers all need to work together to help ensure the sustainability of jellyfish fisheries. If it is hoped that jellyfish can fill some of the void left by the collapses of more traditional fisheries, much more research will be required if repeating history is to be avoided. Understanding of jellyfish population dynamics remains extremely poor, and as such, the development of management strategies for jellyfish fisheries continues to be a challenge. Collection of even the most basic fishery data, such as catch amounts, dates, and locations remains poor (Kingsford et al. 2000; Brotz and Pauly 2016), greatly limiting the advancement of research and development of management plans. Given the inverse seasons of the northern and southern hemispheres, the Americas are in a position to provide a reliable source of jellyfish to Asia year-round. However, if a sustainable supply is to be achieved, much remains to be learned. Detailed studies at local scales will help shed light on basic questions, and a shift towards ecosystem-based management would contribute to building knowledge of the interactions between the resource and the environment, as well as helping to quantify the impacts of developing a fishery. Fluctuations in market demand also present additional challenges. Interest in importing jellyfish to Asian countries is highest when the supply of jellyfish is low in Asian waters, which is subject to large variability on seasonal and interannual timescales. Competition for buyers between different jellyfish fisheries in the Americas will also have to be addressed, as was evidenced by the reduced demand for jellyfish from Mexico in 2014, which was due in part to the new supply from Ecuador and Nicaragua. Market demand from particular areas can also be affected by product quality. For example, some jellyfish from Central America may have more denticulations on the bell surface, ultimately leading to undesirable "spots" on the final product. Inexperienced or shoddy processors may also produce a dehydrated jellyfish product that is inferior, potentially causing buyers to turn away from particular regions altogether. Given such challenges of a newfound industry that is constantly in flux, it is clear that market dynamics should be added to the list of knowledge gaps for jellyfish fisheries in the Americas, and future research programs need to consider economic components as well as ecological ones.

Given the extreme variability of jellyfish populations (Brotz 2011), along with additional factors that contribute to high uncertainty in jellyfish fisheries (Kingsford et al. 2000), ensuring long-term sustainability of jellyfish fisheries will likely be difficult. As such, managers should consider employing conservative strategies that may include catch limits, size limits, adaptive management, harvest control rules, the precautionary principle, and the protection of polyp habitat. Combined with economic drivers and concerns related to processing technologies, management of jellyfish fisheries will surely continue to be a challenge.

As jellyfish populations are increasing in many areas of the world (Brotz et al. 2012), it is likely that humans will look for new ways to exploit them. Although increasing abundances of jellyfish will bring some benefits to humans including jellyfish fisheries (Doyle et al. 2014), it has been submitted that the costs associated with the negative impacts of jellyfish blooms will outpace any increased revenues (Graham et al. 2014). Indeed, it is only by increasing our understanding of these understudied creatures through collaboration between fishers, managers, researchers, processors, brokers, and buyers that we will be able to minimize the impacts and maximize the opportunities offered by future jellyfish blooms.

Acknowledgments We dedicate this paper to Dr. Hermes Mianzan, our friend and perpetual inspiration, who always wondered if a jellyfish fishery would be possible in South America. This paper was written because of him and for him. He is missed, but he lives on in our hearts. We thank Dr. Antonella Leone, Dr. Stefano Piraino, and chef Gennaro Esposito for introducing us to alternative preparations of edible jellyfish. This is a contribution from the *Sea Around Us*, a research program supported by The Pew Charitable Trusts and The Paul G. Allen Family Foundation. This paper has been partially funded by CONICET PIP 2013-00615 and PICT 2013-1773. This is CONACYT 249458 Project contribution. This is INIDEP contribution No. 1930. ACM was supported by grants 2010/50174-7, 2011/50242-5, and 2013/50484-4 São Paulo Research Foundation (FAPESP), and by CNPq (301039/2013-5). This is a contribution of NP-BioMar, USP.

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