

JELLYFISH FISHERIES OF THE WORLD

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Abstract

Fisheries for jellyfish (primarily scyphomedusae) have a long history in Asia, where people have been catching and processing jellyfish as food for centuries. More recently, jellyfish fisheries have expanded to the Western Hemisphere, often driven by demand from buyers in Asia as well as collapses of more traditional local finfish and shellfish stocks. Despite this history and continued expansion, jellyfish fisheries are understudied, and relevant information is sparse and disaggregated. Catches of jellyfish are often not reported explicitly, with countries including them in fisheries statistics as “miscellaneous invertebrates” or not at all. Research and management of jellyfish fisheries is scant to nonexistent. Processing technologies for edible jellyfish have not advanced, and present major concerns for environmental and human health. Presented here is the first global assessment of jellyfish fisheries, including identification of countries that catch jellyfish, as well as which species are targeted. A global catch reconstruction is performed for jellyfish landings from 1950 to 2013, as well as an estimate of mean contemporary catches. Results reveal that all investigated aspects of jellyfish fisheries have been underestimated, including the number of fishing countries, the number of targeted species, and the magnitudes of catches. Contemporary global landings of jellyfish are at least 750,000 tonnes annually, more than double previous estimates. Jellyfish have historically been understudied, resulting in the current dearth of knowledge on population dynamics and jellyfish fishery management. However, many of the tools used in traditional fisheries science, such as length-frequency analysis, can be applied to jellyfish, as demonstrated herein. Research priorities are identified, along with a prospective outlook on the future of jellyfish fisheries.

Preface

This dissertation represents a synthesis of existing information and original work that was led by the author, and includes information contributed from numerous collaborators. The work is presented here in its entirety in order to provide the entire global overview. However, selected material has been extracted as contributions to 6 publications, including 2 peer-reviewed journal articles, 2 book chapters, and 2 report sections.

Specifically, selected information formed the basis of a peer-reviewed journal article [Brotz, L., A. Schiariti, J. López-Martínez, J. Álvarez-Tello, Y.-H.P. Hsieh, R.P. Jones, J. Quiñones, Z. Dong, A.C. Morandini, M. Preciado, E. Laaz, & H. Mianzan *in press*. Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Reviews in Fish Biology and Fisheries* doi:10.1007/s11160-016-9445-y].

Information from Chapters 1-3 was used as the basis for a book chapter [Brotz, L. 2016. Jellyfish fisheries – a global assessment, pp. 110-124 *in* D. Pauly & D. Zeller (eds.) *Global Atlas of Marine Fisheries: A Critical Appraisal of Catches and Ecosystem Impacts*. Island Press, Washington, D.C., U.S.A.]; which also had an abbreviated version that was published in a report [Brotz, L. 2014. Jellyfish fisheries – a global assessment, pp. 77-81 *in* D. Pauly & D. Zeller (eds.) *So long, and thanks for all the fish: The Sea Around Us, 1999-2014 – A Fifteen-Year Retrospective*, a report to the Pew Charitable Trusts, University of British Columbia].

Material gleaned from this dissertation was also combined with additional contributions and was published as a peer-reviewed book chapter [Brotz, L. & D. Pauly *in press*. Studying jellyfish fisheries: toward accurate national catch reports and appropriate methods for stock assessments *in* G.L. Mariottini (ed.) *Jellyfish: Ecology, Distribution Patterns and Human Interactions*. Nova Publishers, Hauppauge, New York, U.S.A.].

A summary of relevant information, especially using selections from Chapter 3, will also be published as a report section [Brotz, L. *in press*. Jellyfish Fisheries *in* R. Brodeur & S. Uye (eds.) *Jellyfish blooms around the North Pacific Rim: Causes and consequences*, PICES Scientific Report No. 51].

Finally, some conclusions and opinions related to this dissertation, especially from Chapters 2 and 5, were also expressed in another peer-reviewed journal article [Gibbons, M.J., F. Boero, & L. Brotz 2016. We should not assume that fishing jellyfish will solve our jellyfish problem. *ICES Journal of Marine Science* 73(4): 1012-1018].

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1. Introduction

Jellyfish (herein referring to members of the Phylum Cnidaria, Subphylum Medusozoa with a pelagic phase, primarily in the Class Scyphozoa) are notorious for interfering with human activities and industries including fisheries, aquaculture, and tourism, as well as power generation and desalination (Purcell *et al.* 2007; Lucas *et al.* 2014). However, jellyfish (or ‘medusae’) are also considered traditional cuisine in China, where they have been eaten for more than 1,700 years (Omori & Nakano 2001; Li & Hsieh 2004). Eating jellyfish continues to be very popular in China, evidenced by the wide availability of not only edible jellyfish, but also the many available imitation or artificial jellyfish products that are primarily made from brown seaweeds (You *et al.* 2007). Consumption of jellyfish is also popular in Asian countries other than China, such as Japan, Malaysia, Korea, Taiwan, and Singapore (Kingsford *et al.* 2000; Hsieh *et al.* 2001; Omori & 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 & Grainger 2006).

Jellyfish fisheries are typically characterized by large interannual fluctuations in abundance and biomass, as well as short fishing seasons of usually less than a few months (Omori 1978; Omori & Nakano 2001). It has been suggested that rapid changes in exploitable biomass of jellyfish are more of a concern than for any other fishery (Kingsford *et al.* 2000), not least because the ecology is poorly understood. These circumstances can cause instability of jellyfish fisheries and may prevent fishers, stakeholders, and policy-makers from supporting development. A contributing factor is that the species being targeted have complex life cycles and are historically understudied organisms, making it difficult to model and predict population dynamics and responses to fishing pressure. As a result, information and research is lagging far behind the expansion of jellyfish fisheries, with potentially negative consequences for both stakeholders and ecosystems. In the Western Hemisphere, jellyfish have undergone a dramatic transition in some locations, shifting from being a nuisance to a valuable fishery resource. In most cases, this transition appears to have been preceded by declines of more traditional fisheries resources such as finfish and shrimp. It remains uncertain if this transition should be celebrated as an example of adaptability, or if it is yet another warning sign that we are rapidly fishing down the food web (Pauly *et al.* 1998). The examination of

jellyfish fisheries around the globe presented herein will help to elucidate some of the questions raised by the rapid development of jellyfish fisheries.

Despite the long history of jellyfish consumption, information on jellyfish fisheries is sparse and disaggregated. In the scant available literature on the subject, there is often conflicting information about the number of targeted species, as well as which countries fish for jellyfish. Even basic data, such as the magnitudes of catches, differs between sources. It is widely recognized that catch statistics are crucial for fisheries management (Pauly 1998; Jennings *et al.* 2001; Pauly 2016). Clearly then, it follows that such statistics should be as accurate as possible. The primary organization compiling national and global fishery catch statistics is the Food and Agriculture Organization of the United Nations (FAO). However, FAO is entirely dependent on what individual countries report, with relatively little in the way of incentives or enforcement to ensure accurate reporting. As such, catch statistics are often underreported (Pauly & Zeller 2016a), or may even be over-reported in rare cases (*e.g.*, Watson & Pauly 2001). For jellyfish, the situation is even more confounded, as many countries do not report their catches of jellyfish explicitly, including them either as “miscellaneous marine invertebrates” or not at all. Fisheries for jellyfish have heretofore not been reviewed on a global scale. It may be argued that the review by Kingsford *et al.* (2000) is an exception; however, that review, while

excellent, focused primarily on the management of jellyfish fisheries and the emergent fishery in Australia. While catch values from other countries were included, they were simply quoted from FAO statistics. The present study is the first global examination of jellyfish fisheries and their associated catches.

As jellyfish populations tend to exhibit dramatic interannual variation in abundance and biomass even when they are not subject to exploitation (Brotz 2011), developing management programs with a goal of sustainable jellyfish catches is sure to remain a challenge. Nonetheless, many of the tools available to traditional fisheries science, such as length-frequency analysis, can be adapted and applied to jellyfish. As jellyfish fisheries continue to expand around the globe, the development of such techniques will be important for informing management decisions.

2. From ocean to plate – aspects of jellyfish fisheries

Jellyfish may be targeted for a number of reasons, including for use in agriculture, materials science, and pharmaceuticals; but by far the largest use of jellyfish is as food for humans. A number of species are consumed, mostly from the scyphozoan Order Rhizostomeae. Jellyfish have unique life cycles, adding to the complexity of managing jellyfish fisheries. Consumption is primarily in Asia, whereas discussion of eating jellyfish in the Western Hemisphere is typically met with reactions ranging from surprise to disgust. While jellyfish fisheries have expanded throughout the world in recent decades, the nascent fisheries are primarily serving growing Asian markets. Consistent with Traditional Chinese Medicine, some research has demonstrated the positive health effects associated with consuming edible jellyfish. However, the chemicals used in jellyfish processing have also been shown to be detrimental to human health.

2.1. Ecology

2.1.1. Target species

With the exception of Mexico, currently all catches of jellyfish reported by FAO are classified as "*Rhopilema* spp.", which is incorrect in many cases. The number of identified species of edible jellyfish worldwide is unclear, and is typically

underestimated (e.g., Omori 1981; Sloan 1986; Hsieh & Rudloe 1994; Omori & Nakano 2001; Armani *et al.* 2013), due in part to the taxonomy of edible jellyfish being confused (Omori & Kitamura 2004; Kitamura & Omori 2010). A synthesis of available information reveals approximately 35 species of jellyfish that have been documented as being consumed by humans. The majority of these, including all jellyfish fisheries operating at commercial scales, are from the scyphozoan Order Rhizostomeae (Table 1). These jellyfish are typically large, with relatively tough and rigid tissues. All members lack marginal tentacles, and instead have prominent oral arms (sometimes called 'legs' or incorrectly referred to as 'tentacles'). *Rhopilema esculentum* is the most valuable species and is currently the choice for hatchery and aquaculture operations in China (see 3.3.4 *China*). The giant jellyfish, *Nemopilema nomurai*, is also widely exploited in East Asia, in much larger quantities than have been reported until recently. Other rhizostomes may also be edible, as the diverse order contains 92 extant species (Daly *et al.* 2007).

There are reports that humans also consume other types of jellyfish (Table 2). This includes scyphozoans from the Order Semaestomeae, such as *Aurelia*, *Chrysaora*, and *Cyanea*; however, in most cases it appears that these species are less desirable and are not currently targeted at commercial scales. There is also limited information to suggest that cubozoans are consumed in some regions. Shih (1977)

reported that the people of the “Tawara” consume freshly caught or sun-dried *Tamoya* sp. after boiling them. As the author refers to “Natives of Tawara in the Pacific Ocean”, it is assumed the author was referring to Pacific atoll of *Tarawa*, Kiribati. Purcell *et al.* (2007) noted that aboriginal peoples in Taitung, Taiwan also eat cubomedusae.

Rhizostome jellyfish appear to be preferred for consumption as they produce the desired crunchy and crispy texture that is characteristic of edible jellyfish products. However, the documentation of other species, such as sennaeostomes and cubomedusae are testament to the fact that other types of jellyfish are indeed “edible,” if not preferred. As such, the development of fisheries for the dozens of non-rhizostome scyphozoans may be possible in the future, albeit with economic challenges. Of course, jellyfish may also be targeted for a number of reasons other than as for food for humans, thus increasing the total number of fished jellyfish species (see 2.3 *Use*).

Table 1. Edible species of jellyfish in the Order Rhizostomeae

Family	Species	Country	Reference
Cassiopeidae	<i>Cassiopea ndrosia</i>	Philippines	Omori & Nakano (2001)
Catostylidae	<i>Acromitus hardenbergi</i>	Malaysia; Indonesia; Thailand	Nishikawa <i>et al.</i> (2009); Kitamura & Omori (2010)
	<i>Catostylus mosaicus</i>	Australia	Fisheries Victoria (2006)
	<i>Catostylus perezii</i>	Pakistan	Muhammed & Sultana (2008); Gul & Morandini (2013)
	<i>Catostylus tagi</i>	Portugal	Amaral <i>et al.</i> (2016)
	<i>Crabionella mastigophora</i>	Indonesia	Omori & Nakano (2001); Kitamura & Omori (2010)
	<i>Crabionella annandalei</i>	Myanmar	Kitamura & Omori (2010)
	<i>Crabionella orsini</i> ¹	India; Sri Lanka	Kuthalingam <i>et al.</i> (1989); NARA (2010)
	<i>Crabionella helmbirui</i>	Indonesia	Nishikawa <i>et al.</i> (2015)
Cepheidae	<i>Crabionella stuhlmanni</i>	India	Kuthalingam <i>et al.</i> (1989); Mohan <i>et al.</i> (2011)
	<i>Cephea cephea</i>	Thailand	Omori & Nakano (2001)
Lobonematidae	<i>Cotylorhiza tuberculata</i>	Italy	pers. obs.
	<i>Lobonema smithi</i>	China; India; Malaysia; Philippines	Kingsford <i>et al.</i> (2000); Hong (2002); Murugan & Durgekar (2008); Nishikawa <i>et al.</i> (2009)
	<i>Lobonemoides gracilis</i> ²	China; Philippines	Omori (1981); Hong (2002); Kitamura & Omori (2010)
Lobonematidae	<i>Lobonemoides robustus</i>	Indonesia; Myanmar; Vietnam; Thailand; Philippines	Kitamura & Omori (2010)
	<i>Lychnorhiza lucerna</i>	Argentina	Schiariti (2008)
Mastigiidae	<i>Mastigias</i> sp.	Thailand	Sloan & Gunn (1985)
	<i>Phyllorhiza punctata</i>	Australia	Coleman <i>et al.</i> (1990); Kailola <i>et al.</i> (1993)
Rhizostomatidae	<i>Rhizostoma octopus</i> ³	United Kingdom	Elliott <i>et al.</i> (2016)
	<i>Rhizostoma pulmo</i> ⁴	Turkey	Ozer & Celikkale (2001)
	<i>Rhizostoma</i> sp.	India	Chidambaram (1984)
	<i>Rhopilema esculentum</i>	China; India; Indonesia; Japan; Korea; Malaysia; Thailand; Russia; Vietnam	Omori (1978); Morikawa (1984); Sloan (1986); Kingsford <i>et al.</i> (2000); Omori & Kitamura (2004); Yakovlev <i>et al.</i> (2005); Nishikawa <i>et al.</i> (2008); Panda & Madhu (2009); Ullah <i>et al.</i> (2015)
	<i>Rhopilema hispidum</i>	China; Indo.; Japan; Malaysia; Pakistan; Thailand; Vietnam	Kingsford <i>et al.</i> (2000); Omori & Kitamura (2004); Muhammed & Sultana (2008); Kitamura & Omori (2010); Gul & Morandini (2015)
	<i>Rhopilema nomadica</i>	Turkey	Kingsford <i>et al.</i> (2000)
Rhizostomatidae?	<i>Rhopilema verrilli</i>	U.S.A.	Rudloe (1992); Kingsford <i>et al.</i> (2000)
Rhizostomatidae?	(suspected unique sp.)	Indonesia; Malaysia	Omori & Nakano (2001); Kitamura & Omori (2010)
Stomolophidae	<i>Nemopilema nomurai</i>	China; Japan; Korea	Omori (1978); Morikawa (1984); Li <i>et al.</i> (2014)
	<i>Stomolophus meleagris</i>	U.S.A.; Mexico; Nicaragua; Ecuador; Honduras	Hsieh <i>et al.</i> (2001); López-Martínez & Álvarez-Tello (2013); this study

¹May be a synonym of *C. annandali* (see Kitamura & Omori 2010); ²May be a synonym of *L. robustus* (see Kitamura & Omori 2010); ³edibility unconfirmed, currently targeted for collagen; ⁴also targeted for collagen in France

Table 2. Non-rhizostome edible species of jellyfish (none at commercial scale)

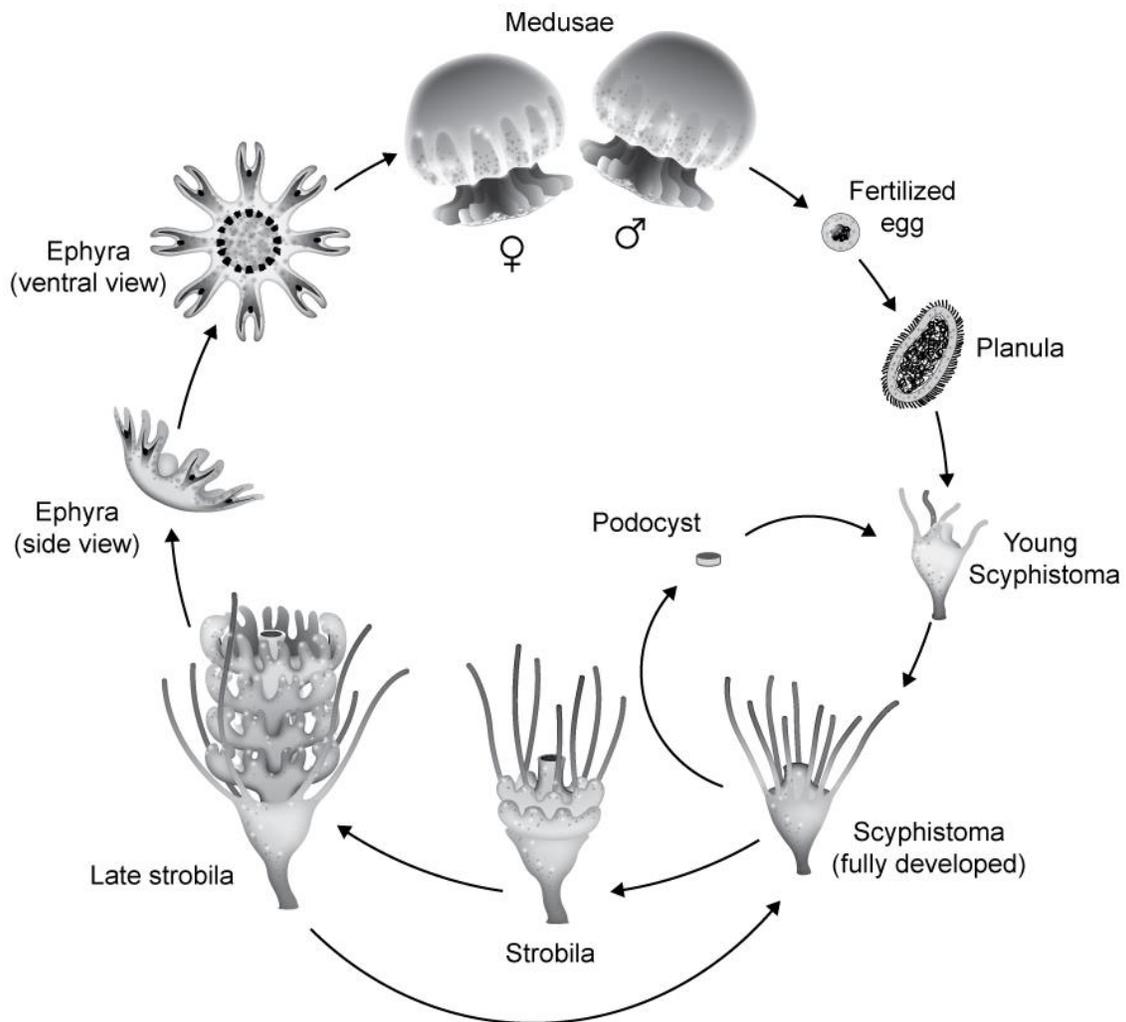
Class	Order	Family	Species	Country	Reference
Cubozoa	Carybdeida	Carybdeidae	<i>Carybdea rastoni</i>	Taiwan	Purcell <i>et al.</i> (2007)
			<i>Chiropsalmus</i> sp.	Philippines	Heeger (1998)
			<i>Tamoya</i> sp.	Tarawa, Kiribati	Shih (1977)
Scyphozoa	Coronatae	Periphyllidae	<i>Periphylla periphylla</i>	Norway	Wang (2007)
	Semaestomeae	Cyaneidae	<i>Cyanea nozakii</i>	China	Lu <i>et al.</i> (2003); Zhong <i>et al.</i> (2004); Dong <i>et al.</i> (2010)
		Pelagiidae	<i>Chrysaora pacifica</i>	Japan	Morikawa (1984); Huang <i>et al.</i> (1987)
			<i>Chrysaora plocamia</i>	Peru; Chile	this study
			<i>Pelagia noctiluca</i>	?	Armani <i>et al.</i> (2013)
		Ulmaridae	<i>Aurelia aurita</i>	Canada	DFA (2002a; b)
			<i>Aurelia labiata</i>	Canada	Sloan & Gunn (1985)
<i>Aurelia</i> sp.	India; U.S.A.		Govindan (1984); Cox (2014)		

2.1.2. *Life cycle*

Rhizostomes, which as mentioned, constitute the bulk of the edible species, have several life history characteristics that may help to mitigate overfishing. The canonical life cycle of these jellyfish is bipartite and metagenic, consisting of a sexual pelagic medusoid phase and an asexual sessile polypoid phase (Figure 1). Medusae are dioecious (*i.e.*, gonochoristic) and females are typically highly fecund, producing millions of eggs (*e.g.*, Huang *et al.* 1985; Kikinger 1992). Fertilized eggs grow into planulae, which are free-swimming and attach to hard substrates in a matter of hours to days, subsequently transforming into polyps, or scyphistomae. Hard substrate required for planulae settlement is essential habitat, of which natural sources may be decreasing, as is the case with mangroves (Valiela *et al.* 2001), while artificial habitat is increasing through anthropogenic substrates (Duarte *et al.* 2013). Polyps of many species may asexually bud additional polyps (Lucas *et al.* 2012), or may also produce or transform into cysts capable of resisting harsh environmental conditions (Arai 2009). When conditions become favourable, polyps begin to segment and asexually release ephyrae through a transverse fission process known as strobilation. Each polyp may release numerous ephyrae and will often strobilate more than once within the same season. Ephyrae join the plankton and grow rapidly into medusae (Palomares & Pauly 2009), at which point they may be targeted for

fisheries. Sexually mature medusae are typically assumed to die off following spawning due to senescence, disease, colder temperatures, or food limitation.

Figure 1. Life cycle of the cannonball jellyfish *Stomolophus meleagris*; based on Calder (1982)



As mentioned, this life cycle was historically deemed to be metagenic and bipartite, indicating an alteration between two forms, namely, medusae and polyps. This was thought to be heavily influenced by seasonality in temperate environments. Recently, there has been considerable discussion of the scyphozoan life cycle in the literature, often questioning the paradigm and terminology. Ceh *et al.* (2015) discuss how medusae of *Chrysaora plocamia* may overwinter, potentially spending time in deeper waters near the benthos, thereby going undetected in surface waters during winter months. This has also been observed for other scyphomedusae, such as *Rhopilema verilli* and *Stomolophus meleagris* in Georgia, U.S.A. (Kraeuter & Setzler 1975) as well as *Aurelia labiata* in British Columbia, Canada (pers. obs.). In addition, limited evidence suggests that certain scyphozoans may sometimes “skip” either the sexual or asexual phase of their life cycle. *Aurelia* in the laboratory have recently been documented developing polyps directly from juvenile medusae and from fragments of more mature medusae (He *et al.* 2015). *Aurelia* spp. have also been shown to sometimes develop ephyrae directly from planulae, thereby occasionally skipping the polypoid phase (Arai 1997; He *et al.* 2015). Some scyphozoan species, such as *Pelagia noctiluca* and most members of the Order Coronatae have evolved to the point where the sessile phase is entirely absent and are thus holoplanktonic. Of

course, the converse is also true, with many species having suppressed medusoid stages.

Despite the extensive variety of scyphozoan life cycles and the myriad of “exceptions” (Jarms 2010), *i.e.*, less frequent features, Morandini *et al.* (2016) argue that a “succession of generations” should still be considered the general paradigm for scyphozoans. However, it seems important to underline the fact that for many species, the polyps often survive after strobilation, and may strobilate more than once within a season. Therefore, calling this a “succession of generations” seems misguided, and perhaps it may be best to refer to the scyphozoan life cycle as “polymorphic” (S. Piraino, Università del Salento, pers. comm., June 2016). In many cases, it is also likely that asexual and sexual reproductive modes often overlap both temporally and spatially. As such, management and research on jellyfish fisheries may need to consider more complex models than the traditional one of a singular, springtime cohort of medusae. Indeed, the peculiar life cycles of jellyfish may provide buffers against overfishing, such as subsequent strobilation (and hence recruitment) from surviving polyps, even without spawning adult medusae. Nonetheless, overfishing of jellyfish stocks by catching medusae is plausible, and appears to have occurred in some locations, such as China (Dong *et al.* 2014; also see 3.3.4 *China*) and the Salish Sea (Mills 2001; also see 3.3.22 *U.S.A.*).

2.2. Fisheries

2.2.1. *Fishing for jellyfish*

Fisheries for jellyfish are usually characterized by short fishing seasons of a few months as well as dramatic interannual variations in catches (Omori 1978; Omori & Nakano 2001). As such, jellyfish fisheries are often subject to instability; a concern for fishers, managers, and other stakeholders alike. A wide variety of vessels may be used for fishing jellyfish. While diesel-powered trawlers are used in select locations (e.g., U.S.A.), jellyfish are most often fished from small (5-10 m) boats powered by outboard engines operating relatively close to shore. These boats often have crews of 1 to 5 fishers and typically carry somewhere between 1 to 5 tonnes of catch when fully loaded. Medusae are visually located in surface waters and caught using dip-nets, also known as scoop nets. Large catches of jellyfish on the decks or in holds of boats can result in concerns regarding vessel stability, and therefore it may be important for vessels to have baffles in the hold to prevent the catch from shifting, especially in rough conditions. Another concern for fishers is the possibility of stings (Kawahara *et al.* 2006a), as jellyfish are often transferred out of nets by hand. Stings from rhizostomes are generally irritating and painful, but most are non-lethal. A possible exception is the giant jellyfish *Nemopilema nomurai*; however, more research is needed to assess the threat of this species to humans (Kawahara *et al.* 2006a).

Although fishers can wear gloves to prevent stings, gloves are often not used as they may be cumbersome, too hot, or unavailable.

A variety of other gears are also used to catch jellyfish including hooks, set-nets, gill nets, drift nets, purse seines, beach seines, weirs, and trawl nets. In some cases, combinations of gears are used to increase the quality and size of the catch. For example, in the Ariake Sea (Kyushu, Japan) and Sarawak (Malaysia, Borneo), jellyfish are concentrated using set-nets and then collected using dip-nets (Rumpet 1991).

2.2.2. Ecological implications

The ecological implications of fishing for jellyfish are largely unknown. Jellyfish are historically understudied animals (Pugh 1989; Hay 2006), and published research on jellyfish fisheries is scant. While jellyfish are often perceived as nuisance species, they play a variety of important roles in ecosystems, often with very significant impacts. Dip-nets, as well as nets with larger mesh sizes, may facilitate the avoidance of bycatch and smaller medusae, and several countries have implemented minimum size limits (MSLs). However, the effectiveness of MSLs in jellyfish fisheries has not been evaluated scientifically (also see *2.4 Management*). Larger mesh sizes can also damage bigger and more valuable medusae, depending on the methods and gear being used. Numerous species of fishes are known 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 & Arai 2001; López-Martínez & Rodríguez-Romero 2008; Mianzan *et al.* 2014). In addition, many invertebrates associate with jellyfish, potentially benefitting from habitat, food, refugia, and transportation (e.g., Brandon & Cutress 1985; Arai 2005; Browne & Kingsford 2005; Towanda & Thuesen 2006; Sal Moyano *et al.* 2012; Schiariti *et al.* 2012a; Álvarez-Tello *et al.* 2013; Fleming *et al.* 2014). As such, the many close associations between jellyfish and other species assure that bycatch concerns cannot be eliminated entirely.

The use of other gears, such as set-nets and trawl nets may increase bycatch further, and commercially important species may be unintentionally caught when associating with jellyfish (Rumpet 1991; Panda & Madhu 2009). Bycatch in the trawl fishery for cannonball jellyfish *Stomolophus meleagris* was examined in detail in Georgia, U.S.A. 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%), butterflyfish *Peprilus triacanthus* (11%), and

blue crab *Callinectes sapidus* (7%). The 3 finfish species (harvestfish, Atlantic bumper, 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 & 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 known 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 at times, and may be of commercial and/or ecological concern. As such, management plans for the jellyfish fishery in the U.S.A. should take these species

into consideration if the fishery is to be scaled up in the future beyond the current small fleet.

Other species caught as bycatch may also be of concern, even if they are less abundant, such as sea turtles, many of which consume jellyfish. In the past, jellyfish were so bothersome to shrimp fishers that modifications were made to trawl gear that facilitated the exclusion of jellyfish while still permitting shrimp to travel into the codend (Jones & 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 to the codend. These device modifications proved to also exclude sea turtles, and ultimately became known as turtle excluder devices or 'TEDs' (Jenkins 2012). TEDs have saved countless numbers of sea turtles and have been the basis for numerous awards (Landers 2011). As one would suspect based on their original purpose, the use of TEDs dramatically reduces the catch of jellyfish, often by more than 80% (Huang *et al.* 1987). As such, most jellyfish fishers in Georgia opt to trawl in federal waters immediately adjacent to state 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 hour in duration (average of 0.55 h), suggesting that mortality of air-breathing species could be significant. There are ongoing efforts to modify TEDs with spacing between the bars that is sufficient for jellyfish to pass through, but not turtles (Page 2015).

Although jellyfish are sometimes perceived to be “trophic dead-ends,” whereby their energy is not transferred to higher levels of the food web (*e.g.*, Verity & 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 some populations of leatherbacks are critically endangered, fishing for jellyfish in waters deemed critical habitat could be subject to restrictions in some jurisdictions, and there are concerns that fisheries for jellyfish could deplete important food resources for leatherbacks at local scales (Elliott *et al.* 2016). Recent investigations are also revealing the importance of jellyfish as prey for more than 100 species of fish (Pauly *et al.* 2009). 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, *i.e.*, sequestering carbon to the benthos (Lebrato *et al.* 2012; 2013). However, it is becoming apparent that gelatinous zooplankton may

instead/also be an important nutritional input for benthic animals (*e.g.*, Henschke *et al.* 2013; Sweetman *et al.* 2014; Chelsky *et al.* 2016; Henschke *et al.* 2016).

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 & Arai 2001). In addition, jellyfish are often predators of eggs and larvae of fish, as well as in direct competition for food with many fishes (Purcell 1985; 1997; Robinson *et al.* 2014; Tilves *et al.* 2016). Thus, the consequences of removing jellyfish from the environment could have dramatic effects on ecosystems, impacting organisms from phytoplankton through to top predators.

Beyond their extensive roles in food webs, jellyfish also provide a number of ecosystem services such as carbon transport, nutrient liberation, and ocean 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 are typically ignored or simplified in ecosystem models (Pauly *et al.* 2009), and as such, the impacts of fishing them are not well understood.

2.3. Use

While the overwhelming majority of jellyfish caught are used as food for humans, there are numerous other reasons why jellyfish may be targeted. 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 & Hadfield 2002; Kelsey 2009); however, these cases involved *Cassiopea* spp., which are relatively sedentary (Holland *et al.* 2004). Cannonball jellyfish (*S. meleagris*) have also been removed in the past from canals in Florida, where they clogged the intake pipes of a nuclear power plant (Jones & Rudloe 1995). Fishers have also been paid to remove *Cotylorhiza tuberculata* in Mar Menor in the Mediterranean Sea, a species which appears to have increased largely due to anthropogenic impacts (Brotz & 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 more influential of the population dynamics in question (Prieto *et al.* 2010; Ruiz *et al.* 2012). Research on jellyfish has led to a better understanding of ocular vision (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 (see 3.3.22 U.S.A.). Jellyfish have also informed the field of design engineering (Dabiri

2011; Najem *et al.* 2012; Ristroph & Childress 2014; Costello *et al.* 2015), where their biomechanics are often mimicked due to their simple and efficient design (Gemmell *et al.* 2013; 2015). Jellyfish are also being investigated for a wide variety of applications including agriculture, materials science, and pharmaceuticals (Table 3). Most of these technologies are in their infancy, and thus it will likely be sometime before there is significant demand for jellyfish other than for food. The only current instances of companies targeting wild jellyfish at commercial scales for purposes other than for food are for the extraction of collagen and are located in France and the United Kingdom (see 3.3.24 *Other countries*).

Table 3. Uses for jellyfish other than as food for humans

Category	Uses	Sample reference(s)
Agriculture	Livestock feeds	Hsieh & Rudloe (1994); CIESM (2010)
	Fertilizers	Fukushi <i>et al.</i> (2004); Fukushi <i>et al.</i> (2005); Chun <i>et al.</i> (2011); Kim <i>et al.</i> (2012b); Hossain <i>et al.</i> (2013); Hussein & Saleh (2014); Seo <i>et al.</i> (2014); Hussein <i>et al.</i> (2015)
	Insecticides	Yu <i>et al.</i> (2005); Yu <i>et al.</i> (2014)
Aquaculture	Finfish & shellfish feeds	Gopakumar <i>et al.</i> (2008); Miyajima <i>et al.</i> (2011a); Miyajima <i>et al.</i> (2011b); Wakabayashi <i>et al.</i> (2012); Liu <i>et al.</i> (2015); Wakabayashi <i>et al.</i> (2016)
Cosmetics	Gelatin/emulsifier	Cho <i>et al.</i> (2014); Chancharern <i>et al.</i> (2016)
Environmental monitoring	Pollution detection	Fowler <i>et al.</i> (2004); Templeman & Kingsford (2010); Morabito <i>et al.</i> (2014); Epstein <i>et al.</i> (2016); Muñoz-Vera <i>et al.</i> (2016)
Fishing	Bait	Prabhu (1954); Thomas (1969); Omori & Kitamura (2004); Varghese <i>et al.</i> (2008); Mianzan <i>et al.</i> (2014)
Materials science	Absorbent polymers	Shamah (2014); Belgorodsky <i>et al.</i> (2015)
	Cement additive	CIESM (2010)
	Copolymer films	Thumthanaruk <i>et al.</i> (2016)
	Nanoparticle filtering	Patwa <i>et al.</i> (2015)
Pharmaceuticals	Antihypertensive peptides	Zhuang <i>et al.</i> (2012a; b)
	Anticoagulants	Rastogi <i>et al.</i> (2012)
	Antimicrobials	Ovchinnikova <i>et al.</i> (2006); Yin <i>et al.</i> (2016)
	Antioxidants	Yu <i>et al.</i> (2006); Zhuang <i>et al.</i> (2009); Balamurugan <i>et al.</i> (2010); Zhuang <i>et al.</i> (2010); Leone <i>et al.</i> (2015)
	Bioactive compounds	Rottini <i>et al.</i> (1995); Gusmani <i>et al.</i> (1997); Li <i>et al.</i> (2005); Nishimoto <i>et al.</i> (2008); Morishige <i>et al.</i> (2011); Kawabata <i>et al.</i> (2013); Leone <i>et al.</i> (2013); Badre (2014); Mariottini & Pane (2014); Leone <i>et al.</i> (2015); Mariottini & Brotz (in press)
	Collagen	Nagai <i>et al.</i> (2000); Huang <i>et al.</i> (2005); Song <i>et al.</i> (2006); Addad <i>et al.</i> (2011); Krishnan & Perumal (2013); Barzideh <i>et al.</i> (2014a; b); Klaiwong <i>et al.</i> (2014); Zhang <i>et al.</i> (2014); Derkus <i>et al.</i> (2016)
	Mucins	Masuda <i>et al.</i> (2007); Ohta <i>et al.</i> (2009)

2.3.1. Processing of edible jellyfish

In some locations, jellyfish may be consumed fresh, as is occasionally the case with *Rhopilema esculentum* and *Nemopilema nomurai* in coastal China (You *et al.* 2007; Yang & Shuang 2015), or processed using oak leaves (Morikawa 1984); however, these are rarities in comparison with the vast quantities that are processed for mass consumption. Freshly caught jellyfish can spoil quickly, and therefore the catch is

usually brought to a local processing facility within a few hours. Initial signs of spoilage include sliminess, colour change, and unpleasant smell. Sometimes the catch is stored in containers on board the fishing vessels while in transit in order to delay spoilage, with either seawater or a slurry of ice and alum – usually potassium aluminum sulfate $KAl(SO_4)_2$. Most edible jellyfish species have prominent oral arms rather than conspicuous tentacles. Depending on the species and the target market, the oral arms may be disposed of or processed separately. The bell is usually more expensive, and was historically valued at more than twice as much as the oral arms (Hsieh & Rudloe 1994; Omori & Nakano 2001). However, demand for oral arms is increasing in China (Kitamura & Omori 2010), and there are recent reported cases where only the oral arms are sought, with the bell being disposed of at sea (*e.g.*, Mohan *et al.* 2011).

Processing facilities range from seaside tents and shacks to large, industrialized seafood processing factories. Facilities may employ dozens of labourers, including many women and children who are sometimes the family members of the fishers. Jellyfish are often scraped, sometimes with tools made of bamboo, to remove mucus or the surface 'skin' if there are denticulations. The gastrovascular cavity and any developed gonads are typically removed (Chidambaram 1984), which may also be done near the end of processing (Rudloe 1992). The edges of the bell are sometimes

trimmed and removed (Govindan 1984; Santhana-Krishnan 1984; Nishikawa *et al.* 2008). Jellyfish are usually rinsed with seawater, which appears to be especially important for species that produce a lot of mucus, such as cannonball jellyfish *Stomolophus meleagris* (Jones & Rudloe 1995).

Processing typically involves soaking the jellyfish in large vats or tanks containing different mixtures of salt and alum (which is granular, white, and odourless). These mixtures may be dry or in brine solution, and jellyfish are soaked in different mixtures for specified time periods. The salting process is intended to dehydrate and preserve the jellyfish without denaturing the collagen, resulting in the desirable firmness and crunchiness of the final product (Sloan & Gunn 1985). The alum will also reduce the pH and act as a disinfectant (Hsieh *et al.* 2001), and processing typically eliminates any remaining sting from nematocysts (Hsieh & Rudloe 1994). Using only salt or alum alone does not result in a satisfactory product (Wootton *et al.* 1982). Heat is avoided during processing, as it will quickly denature the collagen (Rigby & Hafey 1972). In some areas of Southeast Asia, such as Malaysia, Thailand, and the Philippines, a small amount of soda (potentially NaHCO_3 or NaOH) may be added to facilitate additional dehydration, thereby increasing the crispiness of the final product (Rumpet 1991; Rudloe 1992; Hsieh *et al.* 2001; PCAMRD 2008). In certain locations, especially those exporting product to China, jellyfish may be

treated with mixtures containing hydrogen peroxide in order to bleach the product white.

Jellyfish processing is stepwise and usually takes weeks before it is complete, although acceptable products have been produced in as little as 8 days using cannonball jellyfish (*S. meleagris*) which has a smaller maximum size than most edible species (Huang 1988). Mechanical drying has also been investigated to reduce processing time, but the resulting products were not satisfactory due to uneven dehydration (Wootton *et al.* 1982; Huang 1988; Hudson *et al.* 1997). Research is also expanding into drying techniques that result in a product that can be either partially rehydrated or used as an additive. Yuferova (in press) demonstrated results that were more promising for *Rhopilema esculentum* than *Aurelia aurita*, due to the increased destruction of proteins and sugars in the latter.

As jellyfish processing is usually time-consuming and labour-intensive, it is a potential limiting economic factor in countries where labour costs are high. Processing techniques and formulas vary by region and species, and potentially even by batch, so many Asian processors will employ “Jellyfish Masters” who make adjustments to obtain an acceptable product, often keeping their formulas as guarded secrets (Rudloe 1992; Jones & Rudloe 1995). Several different processing protocols based on Japanese and Thai preferences are outlined in Sloan & Gunn

(1985), and numerous overviews of jellyfish processing are available in English (*e.g.*, Soonthonvipat 1976; Wootton *et al.* 1982; Chidambaram 1984; Govindan 1984; Santhana-Krishnan 1984; Huang 1988; Suelo 1988; Rumpet 1991; Rudloe 1992; Jones & Rudloe 1995; Ozer & Celikkale 2001; Nishikawa *et al.* 2008), Spanish (*e.g.*, Álvarez-Tello 2007; Schiariti 2008; Schiariti & Mianzan 2013; Schiariti *et al.* 2015), and Chinese (*e.g.*, Wu 1955; Liu 1973; Yin *et al.* 2000). After stepwise processing in salt-alum solutions, bells are often stacked in a pile and allowed to drain for several days (Subasinghe 1992). Salt may be sprinkled on the bells before stacking, and the bells are often rotated during dehydration to ensure evenness and proper drainage.

There are a number of concerns regarding pollution from effluent created by 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, U.S.A., as companies are looking to expand production but are being met with resistance and regulation (see 3.3.22 U.S.A.). 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 benefit of reducing costs as well as minimizing the

negative health effects associated with processing chemicals, such as aluminum (see below).

2.3.2. *The edible product*

As stated by Hsieh *et al.* (2001), in China “jellyfish is more than a gourmet delicacy: it is a tradition.” In many Asian countries, jellyfish is consumed in the home as well as at restaurants, ceremonies, and banquets. While jellyfish are targeted and caught in numerous countries around the world, these countries export nearly all of their catch to Asia, usually after processing. Most consumption occurs in China, Japan, Malaysia, South Korea, Taiwan, Singapore, Thailand, and Hong Kong, with demand in Japan having increased especially in the 1970s (Omori & Nakano 2001). Smaller markets for jellyfish exist in many cities with inhabitants of Asian descent, where consumption typically involves jellyfish imported from China. Depending on the original source, such jellyfish may have been re-exported, but no supply chain tracing mechanisms are in place for jellyfish. While jellyfish as food continues to remain a novelty for most people in the Western Hemisphere, increasingly diversified urban populations have resulted in higher imports of jellyfish in many major cities. Combined with a growing and wealthier population in China, global demand for jellyfish is thus likely to continue to increase. Prices for jellyfish vary

widely depending on the product, but processed jellyfish can typically be found at market fetching 2-10 USD/kg.

Both classically semi-dried and ready-to-eat jellyfish products are sold in a variety of different presentations and packaging. These may include bulk bins, plastic jars, soft plastic sealed bowls, and sealed plastic envelopes. Mislabelling of jellyfish products appears rampant (as it does for fish products - Jacquet & Pauly 2008), and may include a lack of adherence to local labelling regulations, a high rate of misidentifying species, and even labelling of the product as a vegetable, such as bamboo or tuber mustard (Armani *et al.* 2012; 2013). Unfortunately for consumers, new seafood labelling regulations being implemented by the European Union (EU) exclude invertebrates (D'Amico *et al.* 2016).

Processed jellyfish can weigh anywhere from 7 to 30% of the original wet weight, depending on the species in question and the specific processing formula used (Wootton *et al.* 1982; Huang 1986; Hsieh *et al.* 2001). Variation in the final moisture content is typically dictated by different market preferences. For example, product bound for Japanese markets tends to be much crunchier (*i.e.*, lower water content) than for Chinese markets. Products are often graded, and quality is determined based on size, texture, and colour; with larger products that are whiter in colour and of the preferred texture fetching the highest prices (Rudloe 1992). Colour tends to

turn from white to yellow to brown as the product ages, with the latter being unacceptable. Jellyfish may be packed into crates or buckets for export, sent to local auctions, or sold in small packages at retail markets. The shelf life of processed jellyfish varies depending on the product and storage temperature. 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. It is generally reported that the product will spoil if frozen (Huang 1986; Rudloe 1992; Subasinghe 1992; Hsieh *et al.* 2001); however, freezing of processed jellyfish for storage is possible for short periods (Govindan 1984; Santhana-Krishnan 1984; Kingsford *et al.* 2000; Ozer & Celikkale 2001). Eventually, frozen processed 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). A sample of *Cotylorhiza tuberculata* that was frozen fresh near -80°C and then thawed before preparation by a chef is the tastiest edible jellyfish the author has ever tried, demonstrating that traditional salt-alum processing of jellyfish is not the only method available for future consumption of jellyfish (also see 5.1 *Research priorities*). Fresh moon jellyfish (*Aurelia* sp.) has also been declared as “not only edible, but actually quite delicious” and “best described

as a slightly salty oyster, with a clean flavour and more enjoyable texture” (Cox 2014).

Processed jellyfish has almost no intrinsic flavour, and is therefore usually served with sauces that may include sesame oil, soy sauce, vinegar, and/or sugar. Edible jellyfish has a surprising crunch, and the sensation of biting into the crisp ‘meat’ is sometimes referred to as the product’s ‘sound.’ In preparation for consumption, processed jellyfish is usually soaked for several hours or overnight, sometimes with numerous water changes, in order to desalt and partially rehydrate the product. Traditional recipes may even call for jellyfish to be soaked for several days (Wootton et al. 1982). After soaking, the jellyfish may be scalded or blanched briefly in boiling water, which forms ‘curls.’ Jellyfish is most often served at room temperature and sliced into thin strips. It may be served with sliced vegetables and/or sliced meat as an appetizer, salad, or soup. There are also many other Asian dishes that include jellyfish as an ingredient. Ready-to-use or ready-to-eat jellyfish products have been developed more recently, which, as their name suggests, do not require soaking or scalding prior to eating. These products are sometimes packaged with spices and/or sauces as a ready-to-eat snack.

Rehydrated edible jellyfish are primarily composed of water, accounting for 92-97% of the weight, depending on the species, the type of product, and the processing

methods used. The main organic component is collagen (Kimura *et al.* 1983; Khong *et al.* 2016), a connective tissue protein making up about 3-7% of the rehydrated product weight (again, a value that varies according to the species in question and the processing method used). Levels of fat, cholesterol, and carbohydrates are extremely low or undetectable. Lipid content may increase in specimens with well-developed gonads, but these are typically removed during processing. Tryptophan has been identified as the limiting amino acid in some edible species (Kimura *et al.* 1983; Leone *et al.* 2015) but not others (Khong *et al.* 2016). With approximately 36 food calories per 100 g serving (USDA 2015), these characteristics have led to edible jellyfish being declared as a natural diet food, comparable to many vegetables.

2.3.3. Health effects of jellyfish consumption

A number of inorganic constituents are detectable in processed jellyfish, the most concerning of which is aluminum from the alum used in processing. Many salts and minerals may be removed through soaking and scalding; however, aluminum has been detected in the final edible product in significant quantities (Ogimoto *et al.* 2012; Zhang *et al.* 2016). Ready-to-eat jellyfish products are not rinsed by the consumer prior to consumption, and have also been shown to have high aluminum content (Wong *et al.* 2010; Armani *et al.* 2013). Consumption of aluminum has been linked to a number of negative health effects, including neurobehavioural toxicity

and Alzheimer's disease (Perl & Brody 1980; Nayak 2002). The links between aluminum consumption and the associated negative health effects are still not well understood, and further research is needed. Nonetheless, the development of processing methods that avoid the use of aluminum for edible jellyfish is desirable (Hsieh & Rudloe 1994), and should be a priority for the industry (see 5.1 *Research priorities*). The United Nations and the European Union have both recently reduced their limit for tolerable weekly intake of aluminum, and the Food and Drug Administration of Taiwan has indicated that it will be ramping up monitoring and enforcement of aluminum additives in food products such as jellyfish (I-chia 2016). Additional additives may also be included in processed jellyfish, including monosodium glutamate or potassium sorbate (Armani *et al.* 2012).

In contrast to the negative effects associated with aluminum found in edible jellyfish products, there is also a long list of purported health benefits from consuming jellyfish. Traditional Chinese Medicine (TCM) claims that eating jellyfish is beneficial for curing arthritis and gout, decreasing hypertension, treating bronchitis, alleviating back pain, curing ulcers and goiter, easing swelling, simulating blood flow (especially during menstruation), remedying fatigue and exhaustion, softening skin, aiding weight loss, improving digestion, and for treating cancer (Rudloe 1992; Hsieh & Rudloe 1994; Jones & Rudloe 1995; Hsieh *et al.* 2001; You *et al.* 2016).

Australian Aborigines have used dried jellyfish powder to treat burns (Hsieh & Rudloe 1994). Fishers in the Philippines believe that consumption of jellyfish will increase resistance to hypertension, back pain, arthritis, and malaria (PCAMRD 2008). Very few clinical trials have been conducted to test these claims, and while most remain neither proven nor disproven, many seem unlikely while some are plausible. Hsieh *et al.* (2001) report the findings of a small study whereby several rats were fed jellyfish collagen after being injected with an arthritis-inducing reagent. Those rats that were fed jellyfish collagen reportedly showed significantly reduced incidence, onset, and severity of arthritis in comparison to the control group. More details are presented in Hsieh (2005); however, no human clinical data are available. Zhang *et al.* (2008) also found that jellyfish collagen had positive effects on rats with arthritis. In another study presented by Ding *et al.* (2011), mice were administered various doses of jellyfish collagen hydrolysate. All groups that were administered collagen showed a statistically significant increase in exercise tolerance and glycogen levels, along with reductions in lactic acid and blood urea nitrogen. In addition, mice that had been induced to represent aging showed antioxidative effects when administered jellyfish collagen hydrolysate. Collagen peptides derived from jellyfish may also have beneficial effects on immune functions in mice (Deng *et al.* 2009). There are several studies reporting positive results for the treatment of

hypertension in rats using extracts from jellyfish (Su *et al.* 2008; Liu *et al.* 2009; 2013). Despite these experiments, no clinical trials have been performed using humans and edible jellyfish, and the effects of treating arthritis with collagen in humans have generally been mixed (Henderson & Panush 1999). Therefore, it remains plausible but unproven that consumption of jellyfish by humans has at least some of the health benefits purported by TCM.

Some individuals may experience negative reactions soon after consuming processed jellyfish, such as anaphylaxis (Imamura *et al.* 2013; Inomata *et al.* 2014; Okubo *et al.* 2015); however, such cases appear to be rare. Mild allergic reactions to the consumption of jellyfish may also occur, such as swelling of the mouth, but also appear to be rare. In fact, preliminary results suggest that consumption of jellyfish may be safe for some individuals with allergies to other seafoods (Amaral *et al.* 2016). 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).

2.4. Management

As mentioned, jellyfish populations typically exhibit dramatic interannual variation in abundance and biomass (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 populations of medusae may exist at relatively small spatial scales (Kingsford *et al.* 2000; Matsumura *et al.* 2005; Mooney & Kingsford 2016a; b; van Walraven *et al.* 2016). This could make some stocks 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). However, other species of edible jellyfish may have low genetic diversity across broad geographic ranges (*e.g.*, Dong *et al.* 2016). As such, management of jellyfish fisheries will need to be informed by both general prescriptions addressing the unique aspects of jellyfish, as well as the local conditions and species in question. 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 & 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 potentially 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 U.S.A. TACs can also be artificially

increased if portions of the jellyfish, such as the oral arms, are discarded at sea. You *et al.* (2016) proposed a system of fishing quotas and a deficit quota buyback system for the jellyfish fishery in Liaodong Bay, China. The fishery for *Rhopilema esculentum* in the region has been subject to a dramatic increase in fleet size from hundreds of boats to approximately 10 thousand, along with a concomitant reduction in the length of the fishing season from months to hours over the course of only a few decades (see 3.3.4 *China*). Combined with collapses of other fisheries in the region, the situation has led to a consistent increase in illegal fishing of jellyfish, with many fishers starting to target jellyfish weeks or even months ahead of the seasonal openings. Despite increased monitoring in recent years, including GPS tracking and video monitoring, illegal fishing of jellyfish in the area continues to be rampant, and often includes far more violators than can be prosecuted. There are even examples of collusion amongst groups of fishermen, whereby a second wave of fishers will agree to pay the fines incurred by the first (You *et al.* 2016). Indeed, it seems that management plans need to include input and support from fishers and other stakeholders if they are to be effective, as monitoring and enforcement is expensive and may even unrealistic in some cases, as illustrated by the situation in Liaodong Bay.

Some countries have also implemented minimum size limits (MSLs) on medusae, such as Australia, Mexico, and the U.S.A. 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.* 2012b). 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 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 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 & Jenssen 1974; Frandsen & 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.

3. Reconstructing the global catch

As it is widely recognized that catch statistics are crucial for fisheries management (Pauly 1998; Jennings *et al.* 2001), it follows that such statistics should be accurate in order to properly inform the decisions dependent upon them. Indeed, “maintaining catches is the *raison d’être* of fisheries science” (Pauly 2016). The primary organization compiling national and global fishery catch statistics is the Food and Agriculture Organization of the United Nations (FAO). This institution began compiling fishery statistics in an annual yearbooks in 1950, soon after its founding, part of the United Nations’ attempt to “quantify the world” (Ward *et al.* 2004). However, FAO is entirely dependent on what individual countries report, and such data are often problematic in a number of ways.

A common response to deficient catch datasets is to develop working groups and intensive projects with the purpose of improving reporting at the regional and national scale. Unfortunately, such projects are usually limited in their scope, especially in time, negating the ability to identify longer-term changes in the data (Pauly 1998). One exception is the *Sea Around Us* (www.seaaroundus.org), a research program supported by The Pew Charitable Trusts and the The Paul G. Allen Family Foundation. The *Sea Around Us* reconstructs, maintains, and updates a global

database of fisheries catches from every maritime country of the world back to 1950 (Pauly & Zeller 2016a). The reconstruction of this dataset has enabled many significant conclusions at the global scale, including the facts that fisheries catches are both of a larger magnitude and declining more rapidly than previously thought (Pauly & Zeller 2016b). Important conclusions can also be drawn at the regional and national scales by evaluation of long-term trends and comparison of neighbouring jurisdictions. Such analyses can inform management decisions about the status of fishery resources and how they might respond to changes in effort.

Catch reconstructions performed by members of the *Sea Around Us* and its collaborators include catches disaggregated into different taxa. However, information on jellyfish catches is often not uncovered during the catch reconstruction process, as many countries do not record jellyfish explicitly. In addition, the taxonomy of jellyfish is still confused (Omori & Kitamura 2004; Kitamura & Omori 2010), confounding the situation further. Nonetheless, just as we must overcome the psychological assumption that there is 'no data' available on fisheries catches (Pauly 1998; 2016), as evidenced by the catch reconstructions performed by the *Sea Around Us*, this is also true for jellyfish catches. As such, a global catch reconstruction focused specifically on jellyfish will be a valuable input for the *Sea Around Us* database, as well as helping to answer important questions

specific to jellyfish fisheries catches, including ‘how much?, ‘where?’, ‘what species?’, and ‘what are the trends?’

3.1. Methods

3.1.1. Catch reconstruction

Jellyfish catches were estimated using an approach known as ‘catch reconstruction,’ which has been applied to all maritime countries of the world (Pauly & Zeller 2016a; b). Regarding the jellyfish catches herein, the results are in fact *landings*, a subset of catches, as no estimates of discarded bycatch of jellyfish from other fisheries were made in this analysis. This was primarily due to the lack of availability of detailed bycatch data for fisheries in most developing countries, as well as the fact that the goal of this project was to estimate the quantity of jellyfish that are caught for human consumption. As such, the true global ‘catch’ (including discards) of jellyfish is likely much higher than what is estimated here.

The catch reconstruction methodology used was based on established procedures (Zeller *et al.* 2007; 2015; Pauly & Zeller 2016a; b), and employed the following steps:

1. Identification and validation of existing reported catch time series (*e.g.*, FAO statistics);
2. Identification of countries and time periods not covered by (1), *i.e.*, missing catch data, via literature searches and consultations;

3. Search for available alternative information sources to supply the missing catch data in (2), through extensive literature searches and consultations with local experts;
4. Development of data anchor points in time for missing data items;
5. Interpolation for time periods between data anchor points for total catch;
6. Estimation of final total catch time series estimates for total catch, combining verified reported catches (1) and interpolated missing data series (5).

Regarding the foundational information that was used as the primary basis for the reconstruction indicated above in point (3), all sources are identified in the individual country sections that follow (see 3.3 *Countries fishing jellyfish*). A wide variety of sources were utilized, and most often include regional and national fisheries catch datasets, import/export statistics, peer-reviewed publications, grey literature, popular media articles, as well as direct communication with industry stakeholders such as processors, brokers, and fisheries scientists.

3.1.2. Scaling factor

Given the stepwise methodology involving salt and alum that is typically employed to process jellyfish, the result is a semi-dried product that is lighter in weight than the original wet weight of the jellyfish catch. In some cases, the only information available for a country's jellyfish fishery is for processed product weight. In such instances, estimates of the original wet weight of jellyfish caught can be calculated using a scaling factor. Scaling factors can vary depending on the species in question

and the processing method used, which is often dictated by varying market preferences (Mohammed 2008). The fraction of semi-dried product to wet weight may range from 7% (Omori 1981; Morikawa 1984; Georges 1991) to more than 25% (Wootton *et al.* 1982; M. Valle, Pesquera Mexico, pers. comm., Feb. 2014). Intermediate values have also been reported, usually ranging from 14-20% (Huang 1986; Jones & Rudloe 1995; Fisheries Victoria & MAFRI 2002; DEH 2006). Therefore, scaling factors may range anywhere from 4 to 15. In addition, jellyfish begin to lose weight after being caught, as water continuously drains from their tissues. If jellyfish are compressed, such as being piled on top of each other in a ship's hold, this process will be accelerated (Jones & Rudloe 1995). As such, simply defining the 'true' weight of jellyfish is difficult, thereby complicating the use of the traditional fisheries catch metric of "wet weight."

If parts of the jellyfish have been discarded, such as the oral arms, the wet weight of the catch will be underestimated in these cases, with perhaps 35-40% of the weight of the whole jellyfish 'missing' (Subasinghe 1992). While this is a common practice in some regions (*e.g.*, Pakistan, Malaysia), other regions process the entire jellyfish (*e.g.*, Mexico). Without knowledge of specific instances of partial discarding, this was not taken into account and therefore the estimated wet weights remain conservative.

In instances where specific scaling factors were reported (*e.g.*, Bahrain), the stated values were used to calculate the wet weight. However, if no specific value was reported, the most conservative scaling factor of 4 was used (*e.g.*, India).

3.2. Results

At least 23 countries have been involved in fishing jellyfish for human consumption (Table 4). Some countries, (*e.g.*, Turkey) appear to have abandoned their jellyfish fisheries, while others (*e.g.*, Canada) had test fisheries that were unsuccessful. Many countries do not explicitly report their catches to FAO, including them as either “miscellaneous marine invertebrates” or not at all. As such, the global catch of jellyfish reported by FAO is a dramatic underestimate of the true landings. In contrast, FAO also reports catches for several countries and territories where there do not appear to be jellyfish fisheries present. These include the Falkland Islands (Malvinas), Namibia, and the United Kingdom (also see 3.3.24 *Other countries*). It is likely that the reported catches from these countries are in fact jellyfish caught and discarded as bycatch from other fisheries. As such, they were not included in this catch reconstruction, although the total for all such reports was only 3,205 tonnes combined, and so would not have dramatically affected the results. While it is positive that FAO reports these catches – as discards should still be considered part

of the total catch – it would be beneficial if they were identified as bycatch and/or discards to differentiate them from targeted landings.

Table 4. Countries known to fish jellyfish for human consumption

Country	Dates
China	<1950 - present
Japan	<1950 - present
Indonesia	<1950 - present
Malaysia	<1950? - present
Thailand	1970 - present
Philippines	1976 - present
Korea (South)	1980s? - present
Canada	1984; 2002
Turkey	1984 - 2006
India	1984 - present
Sri Lanka	1986 - present
Vietnam	1990s - present
U.S.A.	1993 - present
Australia	1995 - present
Myanmar	1995? - present
Mexico	2000 - present
Russian Federation	2000 - present
Bahrain	2004 - present
Pakistan	2007? - present
Nicaragua	2008; 2013 - present
Iran	2010? - present
Ecuador	2013 - present
Honduras	2013 - present

Reconstructed landings for the world are presented in Figure 2 (see *Appendix A* for all catches). Landings are dominated by China, with high variability, typically fluctuating between 100 and 400 thousand tonnes through the second half of the 20th century. Catches from Thailand began to make a significant contribution to the total catch starting in the 1970s, and other countries such as Indonesia, India, and Vietnam increased their production through the 1990s. Many of the fishing locations are in Southeast Asia (Figure 3). Landings of China’s primary target species,

Rhopilema esculentum, began to taper off in the late 1990s, but soon after, fishing for the giant jellyfish *Nemopilema nomurai* quickly escalated, offsetting the declining catches. Indeed, increasing landings of *N. nomurai* have resulted in the estimated global catch exceeding 1 million tonnes for the first time in 2013. Such values demonstrate that jellyfish fisheries are clearly significant, exceeding the catches of jellyfish of other fisheries at a global scale, such as lobsters (Pauly & Zeller 2016a; miscellaneous marine crustaceans excluded). For additional details and discussion on the catch reconstructions in each country, refer to 3.3 *Countries fishing jellyfish*.

3.2.1. Estimating the contemporary global catch

There are at least 21 countries currently fishing for jellyfish (Table 4); however, the fisheries in Ecuador, Honduras, and Nicaragua are new and still developing, and the magnitudes of catches in those countries in the near future remains unclear. For other countries, contemporary catches were calculated by averaging the reconstructed catches over the last 10 years of data (2004-2013). Combining these estimates yields a mean contemporary global catch of more than 750,000 tonnes annually (Table 5), which is more than double the amount based on FAO statistics for the same period. This figure is likely an underestimate of the global jellyfish catch, as it does not include jellyfish that is landed as part of the vast quantities of trash fish from nontargeted fisheries in China that are delivered to factories to be

Figure 2. Estimated global landings for two primary species in China and all species for other countries

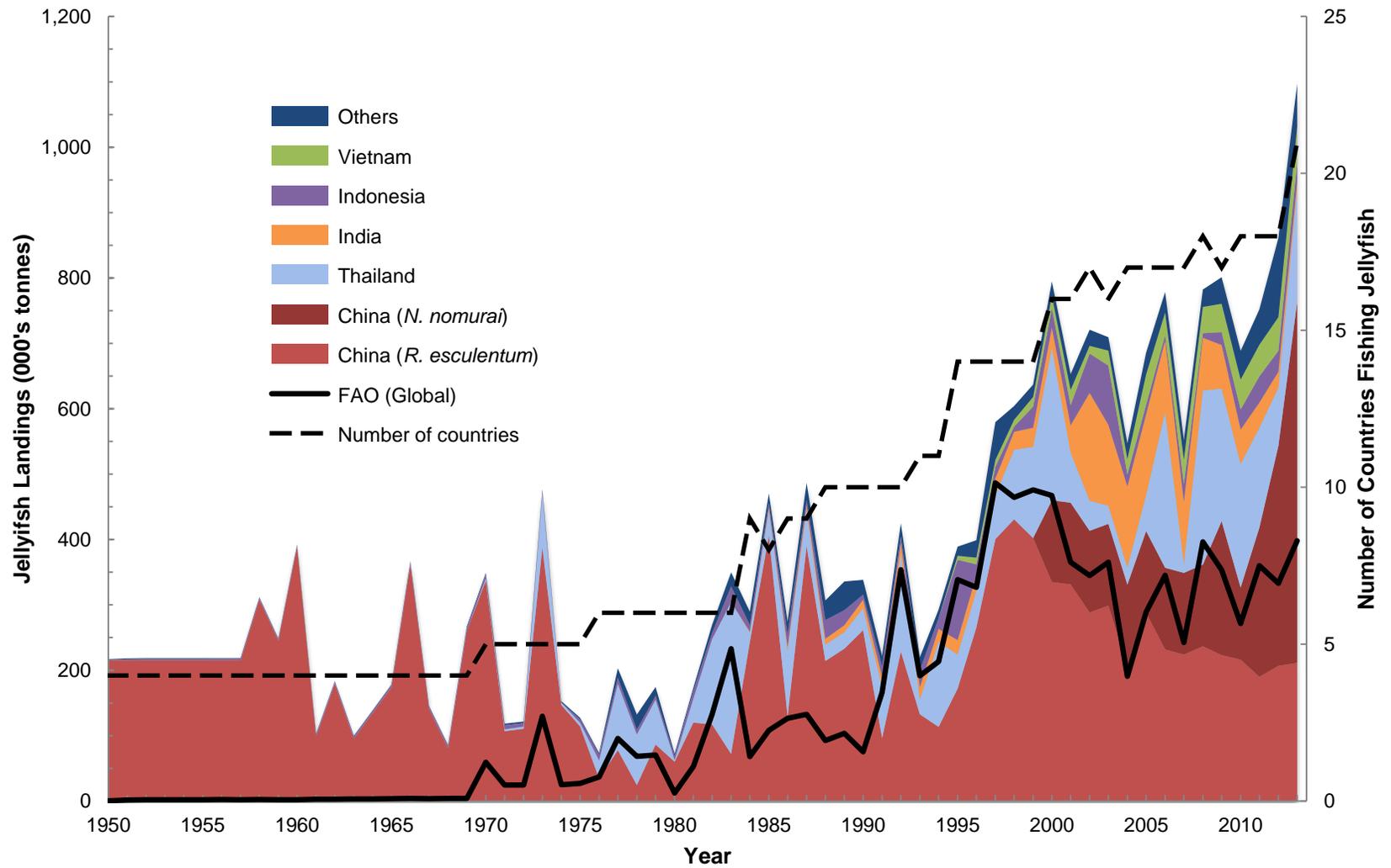


Figure 3. Locations of jellyfish fisheries in Southeast Asia; dark blue indicates shelf (< 200 m); note that there are likely many additional locations that have yet to be documented



turned into ‘fishmeal’ (Cao *et al.* 2015). In addition, the global catch reconstruction presented here does not include any bycatch or discards of jellyfish, which can be huge, often resulting in losses to fishers of ten or hundreds of millions of dollars annually (Purcell *et al.* 2007; Uye 2008; Kim *et al.* 2012a).

China continues to be the dominant player in the jellyfish market, responsible for more than half of the global contemporary catch. Thailand and India follow, with

Vietnam and Indonesia rounding out the top 5 nations targeting jellyfish, which collectively make up more than 90% of the global contemporary catch (Figure 4). While fishing for jellyfish has clearly expanded around the globe (Figure 5), the overwhelming majority of the catch continues to take place in the waters of only a few countries (Figure 4).

Table 5. Estimated contemporary annual jellyfish landings (2004-2013 mean)

Country	FAO landings (tonnes)	Reconstructed landings (tonnes)
China	212,343	428,973
Thailand	75,663	140,786
India	-	72,405
Vietnam	-	42,530
Indonesia	10,852	22,820
Mexico	18,725	13,124
Bahrain	2,278	10,022
Malaysia	6,017	6,087
U.S.A.	740	5,100
Japan	-	4,266
Myanmar	2,722	2,722
Iran	2,588	2,588
Sri Lanka	-	2,511
Pakistan	-	1,663
Russian Federation	293	293
Philippines	19	179
Korea (South)	-	114
Australia	4	5
Total	332,243	756,189

Figure 4. Estimated global contemporary annual jellyfish landings (2004-2013) and reported FAO catches (1950-2013)

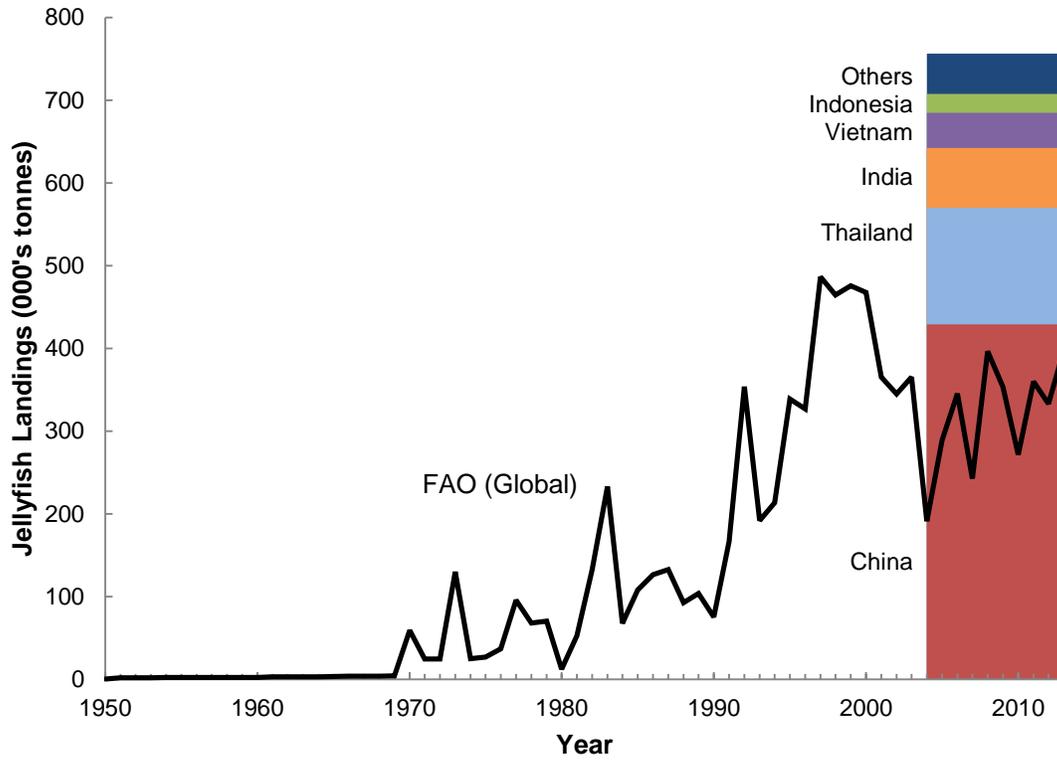
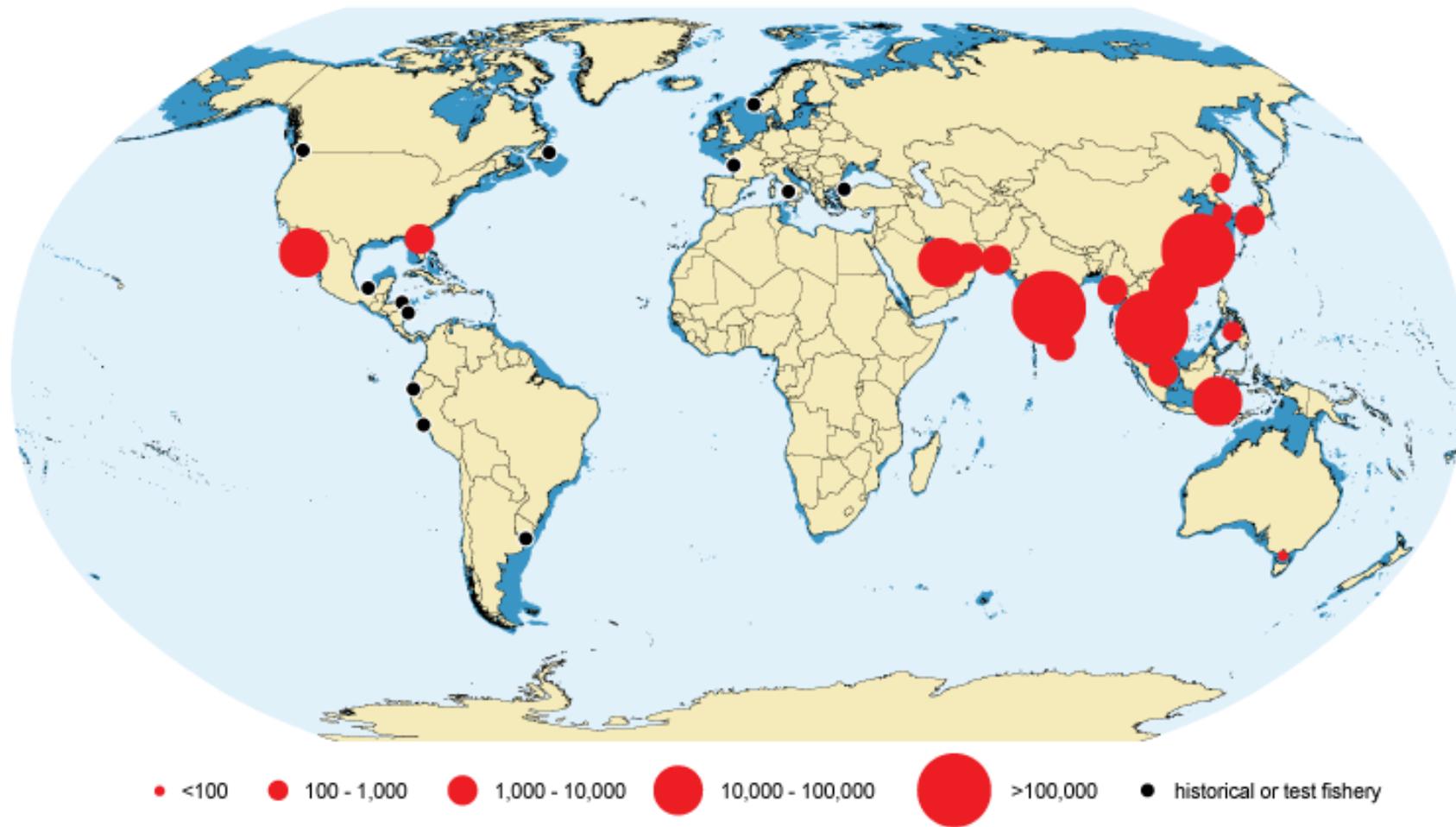


Figure 5. Jellyfish fisheries around the world; red circles indicate magnitude category of catch in tonnes (see legend); circles are only approximately representative of catch locations



3.3. Countries fishing jellyfish

3.3.1. Australia

Several attempts to establish jellyfish fisheries in Australia have been for the most part unsuccessful, and the current scale of the fishery continues to remain small. In 1980-1981, a product and market feasibility study was carried out by the Clarence River Fishermen's Co-operative at Iluka in New South Wales (Davis 1982). Around the same time, processing methods were being investigated in the School of Food Technology at the University of New South Wales. Wootton *et al.* (1982) reported that a satisfactory edible product could be produced from *Catostylus mosaicus* caught in Botany Bay. Nearly 10 years later, a report was prepared by Georges (1991) for the targeting of *C. mosaicus* in New South Wales. It was proposed that medusae with a minimum bell diameter of 20 cm would be caught using surface trawl gear. Fishing would take place between December and June in a region limited by Broken Bay and the border with Queensland. Ironically, it was suggested that the proposal would contribute to the conservation of *C. mosaicus* by facilitating research and management of the species. The author also stated that fishing for jellyfish was unlikely to have a measurable effect on the ecosystem and may help to mitigate nuisance to fishers and swimmers. Despite apparent interest, along with a solitary report of *C. mosaicus* being targeted in Lake Illawarra in 1990 (Kailola *et al.* 1993),

immediate development of the Australian jellyfish fishery did not proceed in New South Wales. This may have been due to criticism of the “management program” developed by Georges (1991). Wells & Wellington (1992) published a scathing commentary of the report, calling it “a pathetic example of how information can be manipulated for a particular purpose without apparent concern for scientific accuracy...” Indeed, the authors highlight numerous inconsistencies and unsubstantiated claims contained in the report, and stated that they “seriously caution allowing such an operation to proceed without a full and complete understanding of both the ecological and economic implications of the industry on the marine environment.”

Subsequent to these attempts, renewed interest in establishing a jellyfish fishery in New South Wales prompted additional research and a new management plan, culminating in a trial fishery of 10 tonnes which was processed and exported to Asia in 1996 (Hudson *et al.* 1997). Catches ranged between 10 and 33 tonnes from 1995 to 1998, apparently limited by processing capacity (Coleman 2004). However, a fishery was not established in New South Wales, and attention shifted to the neighbouring state of Victoria.

Hudson *et al.* (1997) report on surveys made in 1997 that estimated the biomass of *C. mosaicus* in several locations within Port Philip Bay. The authors suggested that

biomass and densities were sufficiently high to support a fishery. Subsequent studies were made in the years following, and in 1998 one company was granted a developmental permit to catch jellyfish for 3 years, which was extended for an additional year (Coleman 2004). Later it was recommended that the permit be renewed for an additional 3 years. The Total Allowable Catch (TAC) is set between 1,000 and 1,200 tonnes annually, a conservative limit representing approximately 10-15% of the estimated biomass (Fisheries Victoria 2006). However, only a tiny fraction of this TAC is caught in Australia, representing 0-1%. Small TACs of 100 tonnes were also set for 3 other locations (Fisheries Victoria & MAFRI 2002); however, it appears that fishing for jellyfish has been limited to Port Philip Bay (Fisheries Victoria 2006).

Fishers targeting jellyfish in Australia are required to use dip-nets, along with limited use of seine nets for corralling purposes only. Specific permits for catching jellyfish are required, and fishers targeting other species are prohibited from retaining jellyfish as bycatch, and are instead required to return them to the water with the least possible damage (Fisheries Victoria 2006). A minimum size limit of 23 cm (bell diameter) is well above the 13 to 16 cm at which maturity is generally achieved for the species (Pitt & Kingsford 2000). While a *minimum* catch of 150

tonnes was proposed for 2006 in order to encourage at least a minor level of activity (Fisheries Victoria 2006), catches have continued to remain low.

With the exception of catches of 14 and 11 tonnes in 2008 and 2013 respectively, catches have been 0, 1, or 2 tonnes since 1998 (FAO 2015a). Despite the potential for a jellyfish fishery with annual catches of several thousands of tonnes (Fisheries Victoria 2006), the jellyfish fishery in Australia does not appear to be expanding. As mentioned, up to at least 2005, only a single development permit for fishing jellyfish was being issued in the State of Victoria (Fisheries Victoria & MAFRI 2002). It is unclear why the jellyfish fishery in Australia remains undeveloped despite investments of approximately \$500,000 (AUD) in equipment and personnel (Fisheries Victoria & MAFRI 2002). Potential factors involved include poor recruitment in some years (Fisheries Victoria & MAFRI 2002), economic viability, and possibly onerous management regulations. The product resulting from processed *C. mosaicus* is reportedly not as large or firm as jellyfish products from other regions (Hudson *et al.* 1997), resulting in a 'B-grade' labelled product.

There have been attempts at exploiting jellyfish in several other locations in Australia. Around 1989-1990, *Phyllorhiza punctata* was apparently being considered for possible capture, processing, and export in the Swan River Estuary in Western Australia near Perth; however, a fishery was not established (Coleman *et al.* 1990;

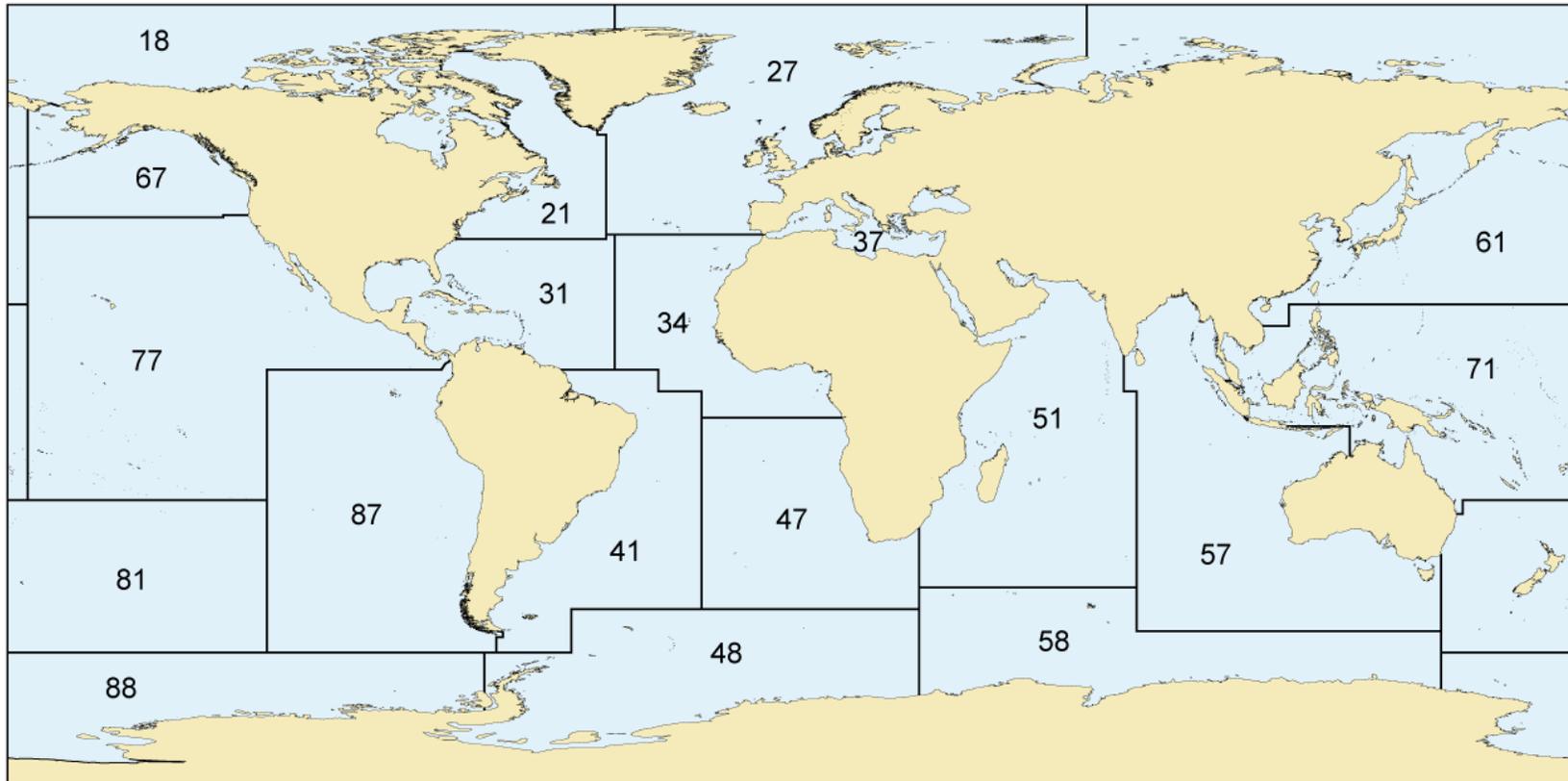
Kailola *et al.* 1993). In the Northern Territory, a test fishery began in 2000 to catch *C. mosaicus* in the estuarine western section of the Gulf of Carpentaria, with a goal of expanding processing capacity to 300 tonnes annually (Field 1999); however, it remains unclear if this goal has been achieved. Fishing of *C. mosaicus* was also proposed in Queensland, outlined in a 2006 report (DEH 2006). Developmental permits were issued in 2006 for a total of 800 tonnes, divided between Moreton Bay (200 tonnes), Tin Can Bay (200 tonnes), and the Gulf of Carpentaria (400 tonnes). However, it remains unclear if any of this allowable catch was ever caught, and the export permit for the fishery is currently expired.

Catches reported by FAO for Australia appear to be reasonably accurate, with a few exceptions. As usual, the reported taxon is incorrect (*Rhopilema* spp. instead of *Catostylus mosaicus*), and the reported FAO area where fishing occurs is strangely 58, 'Indian Ocean, Antarctic', rather than 57, 'Indian Ocean, Eastern' (Figure 6).

3.3.2. Bahrain

Bahrain apparently began fishing jellyfish around 2003 or 2004 (Mohammed 2008; FAO 2015a). The target species is suspected to be *Catostylus perezii*, as this species is abundant in the Persian Gulf and Arabian Sea (Gul & Morandini 2013; Gul *et al.* 2015), is the target of fisheries in nearby Pakistan (Gul *et al.* 2015), and resembles the

Figure 6. Major FAO areas



jellyfish being processed in photographs from Bahrain (see Mohammed 2008). Apparently, part of the motivation to start a jellyfish fishery was to reduce stings to fishers targeting finfish stocks, as well as to prevent them “scaring off fish” (Mohammed 2008). The method used to catch jellyfish has not been reported, but fishing appears to be done by fishers who traditionally targeted finfishes (and still do), with a jellyfish season from April to September (Mohammed 2008).

In 2007, a single processing company in Bahrain was reported to export 60 containers of processed jellyfish, each containing between 18 and 24 tonnes (Mohammed 2008). If an average of 21 tonnes per container is assumed, this is equivalent to 1,260 tonnes of processed jellyfish. As reported by Mohammed (2008), processed jellyfish is 15% of its wet weight if the product is bound for China, or 8% if bound for Japan. As the product is reportedly more popular in China, and since it is cheaper to produce the product with higher water content, it was assumed that two thirds of the product produced in 2007 was exported to China, with the remaining third exported to Japan. This equates to 10,850 tonnes of jellyfish caught by Bahrain in 2007, which is much larger than the 1,759 tonnes reported by FAO for Bahrain in the same year. Interestingly, values quoted in the news article by Mohammed (2008) for exports of *processed* jellyfish for 2005 and 2006 match almost exactly those reported by FAO as landings. Therefore, it appears likely that the

values reported by FAO for jellyfish landings in Bahrain are actually for processed jellyfish, and were similarly scaled up.

Catches apparently declined in Bahrain in 2008, and although it has been suggested that this could be due to turbidity from land reclamation (Mohammed 2008), other speculation points to the same processes having positive effects for jellyfish by keeping predatory turtles away from the coast (Anonymous 2008a). According to FAO (2015a), catches have continued to fluctuate since, with a relatively larger catch in 2012. Bahrain's jellyfish fishery appears to be persisting, with variable catches.

3.3.3. *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., a scyphozoan 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 & Gunn (1985) present details for 11 dip-net and 2 seine fishing cruises conducted between August and November in the northern Strait of Georgia. The total catch was 2.82 tonnes, which was then processed using 3 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.

On Canada's east coast, jellyfish frequently interfere with active and passive fishing gears, making a targeted fishery for jellyfish desirable (DFA 2002a). As such, a test fishery was implemented to understand the methods and costs involved in producing jellyfish, and to evaluate the potential market (DFA 2002b). An estimated 49 tonnes of jellyfish were caught over a period of 2 weeks in September 2002 in Newfoundland's Trinity Bay; however, only about 1 tonne was retained, with the rest being released at sea (DFA 2002a). 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. About 1.1 tonnes of jellyfish were processed and samples were sent to China, Taiwan, and Florida, U.S.A. for market testing (DFA 2002a). Due to a lack of demand for semaeostome jellyfish, as well as unrefined handling and processing techniques, the test fishery was discontinued.

3.3.4. *China*

China has the longest history of fishing for jellyfish, dating back at least 1,700 years (Omori & Nakano 2001), and is the world's largest producer of jellyfish. China is also the only country that farms jellyfish in aquaculture ponds (You *et al.* 2007), as well as releasing juvenile medusae into the wild as part of a hatchery program (Dong *et al.* 2009; Tian *et al.* 2016). Jellyfish grown in aquaculture operations were not included as part of this analysis; however, production has averaged just over 50,000 tonnes annually for the period 2003-2014 (FAO 2016) and may increase in the future if catches of the primary species from the wild continue to decline (see below). There have been seasonal bans on trawling in Liaodong Bay in the Bohai Sea since the 1980s with the intention of protecting polyp beds; however, some trawling is allowed at certain times of year which may damage polyps and their habitat (Ye 2006). The primary species of interest in China is *Rhopilema esculentum*, as it is the most in demand and the most valuable. However, declines in abundance, presumably due to overfishing (Dong *et al.* 2014), along with increasing demand for jellyfish, have resulted in the targeting of other species, including the giant jellyfish, *Nemopilema nomurai*. China does report jellyfish catches to FAO; however, these appear to be restricted to *R. esculentum*. In addition, catches appear to be

underreported in some years, resulting in dramatic underestimates for jellyfish landings in China, and hence globally.

R. esculentum is targeted in nearly all of coastal China, including in the Bohai, Yellow, East China, and South China Seas. Marine biologist Jack Rudloe travelled to China in 1995 to learn about jellyfish fishing and processing in support of establishing a fishery for cannonball jellyfish *Stomolophus meleagris* in the U.S.A. (J. Rudloe, Gulf Specimen Marine Laboratory, pers. comm., April 2014). While visiting cities including Qingdao, Weihai, Yantai, and Laizhou, he learned that many men and women travelled from the south coast of China and followed the migrating blooms of *R. esculentum*, catching and processing them at different locations along the way. In addition, a fleet of 200 government-issued 50-foot wooden boats with diesel engines fished the Gulf of Bohai everyday. Fishers left in the morning and travelled 6 hours to reach the fishing grounds. Trawls or set-nets were fished overnight for another 6 hours, and then catches were rushed back to the docks in order to meet afternoon processing schedules. Omori (1981) also reports information on fishing grounds and seasons in Chinese waters. You *et al.* (2016) describe a dramatic increase in the number of fishing boats in Liaodong Bay in recent decades, with a concomitant reduction in the length of the jellyfish fishing season. Prior to the 1980s, there were hundreds of boats and the season lasted approximately two

months. This changed to several thousand boats in the 1980s, with a season of 1-2 weeks. By the 1990s, there were 8-9 thousand boats with a season lasting only 2-3 days. Today, there are more than 10 thousand boats fishing in Liaodong Bay, resulting in a derby fishery that usually catches all of the available jellyfish in a matter of hours. Consequently, this has led to regular instances of illegal fishing (You *et al.* 2016; also see 2.4 *Management*).

Landings reported to FAO extend back to 1970, and averaged about 25,000 tonnes through the 1970s and 1980s. Dong *et al.* (2014) present a useful summary of *R. esculentum* in Chinese waters, along with catch statistics dating back to 1957, gleaned from several sources including China Fishery Statistical Yearbooks. Up until 1997, the statistics presented are very consistent with those reported by FAO. However, for the period from 1997-2006, it appears that statistics reported by FAO were curiously underreported by approximately 15%. A more startling discrepancy emerged with the publication by Li *et al.* (2014), which reports landings of *R. esculentum* from 1980 to 2012. For the period 1980-1990, it appears that landings reported by FAO were for *processed* jellyfish, rather than wet weight. As such, landings reported for this period are only 15% of what they should be. Put another way, these values are underestimated by more than 600%. Values reported by FAO for the 1970s, and by Dong *et al.* (2014) for the 1960s and late 1950s are of the same

order of magnitude as those for the 1980s. Therefore, it is likely that all values reported before 1991 are likely for processed jellyfish, and represent only 15% of the true catch. Adopting this assumption, we find that catches of jellyfish in Chinese waters have fluctuated between about 100,000 and 300,000 tonnes since 1950. While this assumption is obviously very significant if it ultimately proves to be false, it seems justified given that contemporary landings exceed these values, and there is a long history of fishing for jellyfish in China. Indeed, there are even indications that these scaled-up values may be underestimates, as Kingsford *et al.* (2000) notes that one report claims a peak jellyfish catch in China of 700,000 tonnes in a single year. As yet, that figure remains unconfirmed by other sources. There are also other major discrepancies in Chinese catch statistics for jellyfish. For example, FAO (2015a), Dong *et al.* (2014), and Li *et al.* (2014) all report landings of approximately 96,000 tonnes in 1991. In contrast, You *et al.* (2016) report a catch of 296,050 tonnes in 1991 for Liaodong Bay alone. As this value could not be verified, the more conservative estimate was adopted; however, this is yet another example illustrating that the reconstruction herein likely represents a minimum estimate, and landings of jellyfish may be much higher in some years.

Catches of *R. esculentum* appear to have declined rapidly in the mid-1970s, which has been attributed to overexploitation (Dong *et al.* 2014). This led to extensive

research on the culturing of *R. esculentum*, and in 1984, juvenile medusae were released in the waters of Liaodong Bay with the hopes of enhancing the stock. This hatchery program has continued each year, and has since expanded to include the release of hundreds of millions of juvenile medusae into the coastal waters of Liaoning and Shandong Provinces (Dong *et al.* 2014).

While the hatchery program has likely helped to enhance catches of *R. esculentum* in Chinese waters (Dong *et al.* 2014), another rhizostome, the giant jellyfish *Nemopilema nomurai*, has increasingly been a target for fishers in recent years. This species appears to have increased in abundance in the Yellow and East China Seas in the last decades (Yoon *et al.* 2008; Dong *et al.* 2010). Industrialized fishing for *N. nomurai* reportedly began around 2000, with catches averaging about 125,000 tonnes until 2008 (J.-H. Cheng, East China Sea Fisheries Research Institute, pers. comm., Nov. 2013). Catches since 2009 have exceeded 200,000 and even 300,000 tonnes in some years, with the most dramatic catch of more than half a million tonnes in 2013 (Li *et al.* 2014). Combined with the catch of *R. esculentum*, this means that China landed more than 750,000 tonnes of jellyfish in 2013. Curiously, catches of *N. nomurai* do not appear to be reported to FAO at all.

There are also other species of jellyfish targeted for food in China, including *Lobonema smithi*, *Lobonemoides gracilis*, *Rhopilema hispidum*, and *Cyanea nozakii* (see

Tables 1 and 2 for sources); however, the catches of these species are presumably quite small in comparison to the two aforementioned species.

3.3.5. *Ecuador*

In 2013, Chinese dealers began promoting the possibility of catching, processing, and exporting 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. In 2014, an astounding 78,000 tonnes of jellyfish were landed (most of which was caught in February and March), processed, and exported to China, Japan, and Thailand (M. Perciado, Instituto Nacional de Pesca, pers. comm., Jan. 2015). If such significant landings are maintained, it would catapult Ecuador to being the 3rd largest producer of jellyfish worldwide (Table 5). 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 in 2014, as processing facilities were shuttered due to a lack of environmental oversight. Many processing plants remained closed in 2015 as they did not acquire the necessary permits, and the catch for 2015 was reduced to 9,135 tonnes as buyers turned their attention to importing jellyfish from Mexico (E. Laaz,

Instituto Nacional de Pesca, pers. comm., Aug. 2016). It would seem that the future scale of Ecuador's jellyfish fishery remains to be determined.

3.3.6. Honduras

In 2007, samples of a species of *Stomolophus* (likely *S. meleagris*) were caught along the Atlantic coast of southern Honduras (near Cauquira) using small boats with dip-nets to test for exploitation potential. Ultimately, fishing grounds off Nicaragua were selected for a test fishery in 2008 instead of Honduran waters (see 3.3.15 *Nicaragua*). This was primarily due to the fact that the region of Honduras is not easily accessible by road, and any processing equipment and supplies have to be brought into the port by boat. Such logistics proved to be inefficient for a product that is relatively low-value, and therefore the future potential of a jellyfish fishery in Honduras remains uncertain. However, FAO does report a catch of 50 tonnes for Honduras in 2013, so perhaps some of the processing capacity concerns have been addressed.

3.3.7. India

India is yet another country that has been catching jellyfish for decades, but is absent from FAO jellyfish catch statistics. Fishers in numerous coastal states have been actively involved in catching jellyfish including Tamil Nadu, Andhra Pradesh, Odisha, and West Bengal. Fisheries for jellyfish have also been explored in the

Arabian Sea along India's west coast, including the states of Karnataka and Gujarat, and likely others.

Several species of jellyfish were initially reported to be targeted for processing and export from India, including *Rhizostoma* sp. (Chidambaram 1984) and *Aurelia* sp. (Govindan 1984). However, it is now believed that *Crambionella stuhlmanni* is the primary species being exported (Kuthalingam *et al.* 1989; CMFRI 2009; Mohan *et al.* 2011), with *Lobonema smithi* also being targeted or caught and sold as bycatch (Murugan & Durgekar 2008). In addition, *Rhopilema esculentum* is reported from Indian waters (Panda & Madhu 2009), so it is likely that this valuable species is also being exploited.

India's jellyfish fishery presumably began in the 1980s. In 1984, at least 21 tonnes of processed jellyfish were exported from India (Chidambaram 1984). This was primarily in response to requests from the Japanese External Trade Organisation (JETRO), which toured India in February 1984 and offered to import "any amount" of jellyfish from India (Govindan 1984). This was a welcome proposition, as jellyfish were a persistent nuisance to fishers in India due to clogged nets, spoiled catch, fouled gear, and stings (Govindan 1984; James *et al.* 1985; Kuthalingam *et al.* 1989). Several other countries were also reported to import jellyfish from India in the 1980s

including Thailand, Hong Kong, and Singapore (Chidambaram 1984; Kuthalingam *et al.* 1989).

Exports from India to Japan continued sporadically through the 1980s, 1990s, and 2000s, with the annual tonnage of processed jellyfish product ranging from zero to hundreds of tonnes (Omori & Nakano 2001; S.-I. Uye, Hiroshima University, pers. comm., Oct. 2012). However, India's total catch of jellyfish was more likely in the hundreds of thousand of tonnes at its peak in the mid-2000s. The 2004 Handbook of Fisheries Statistics from the Government of India (Anonymous 2005) indicates that between 2000 and 2004, production of jellyfish commodities ranged between 7,723 and 30,866 tonnes, with an annual average of 22,515 tonnes. As the commodity is reported as "Jellyfish, dried, salted or in brine" it was assumed that these values represent semi-dried, processed jellyfish. As such, the values need to be scaled up to obtain the original wet weight of the catch. Without knowing a specific scaling factor for the species and processing method used, a conservative value of 4 was used (see *3.1.2 Scaling factor*).

Even the limited statistics from the government Handbook are expected to be underestimates of India's total jellyfish catch due to non-reporting from many states. For example, in 2000 and 2001, only the state of Gujarat reported landings of jellyfish, whereas the totals for 2002 and 2003 include landings from Andhra

Pradesh, Karnataka, and West Bengal. Jellyfish are also caught in other states, such as Odisha (Anonymous 2007) and Tamil Nadu (Kuthalingam *et al.* 1989). Therefore, the true magnitude of India's jellyfish catch is likely much higher in some years. Murugan & Durgekar (2008) report a catch of 7 million tonnes of jellyfish from the Gulf of Mannar in 2007 alone; however, this figure is assumed to be erroneous as it dramatically eclipses the entire global catch of jellyfish. Attempts to obtain clarification of the estimate were unsuccessful, and therefore it was ignored in the catch reconstruction.

The rapid expansion of jellyfish fisheries in India in the 2000s appears to have resulted in some conflict in the region. Processing facilities are often makeshift tents or huts that are temporary or abandoned between jellyfish fishing seasons (Kuthalingam *et al.* 1989). Magesh & Coulthard (2004) chronicle how the number of these huts quickly grew in the early 2000s, resulting in tension between stakeholders. As middlemen from different regions and countries moved in to erect the huts, local fishers felt left out of the industry and unable to benefit from the export of jellyfish. Suspected pollution from the effluent of the processing huts exacerbated the situation further, and in some cases, huts were destroyed. The tension peaked after rapid expansion and very large landings in 2003. In a twist of fate, the fishery in Tamil Nadu was completely wiped out by the devastating

tsunami in 2004 (CMFRI 2009). Depending on the circumstances, processing of jellyfish can be an important supplementary employment for fishers, and it has been reported that more than one third of all fishers operating motorized boats in Tamil Nadu were seasonally involved in the processing of jellyfish (Swathilekshmi 2011).

As with most jellyfish fisheries, landings in India are highly variable. As such, years with high catches are often referred to as “unusual.” Examples include 2003 in Tamil Nadu (CMFRI 2009), 2007 in Andhra Pradesh (CMFRI 2007), and 2009 in Tamil Nadu (CMFRI 2009; Mohan *et al.* 2011). Interestingly, in 2009, fishers in northern Tamil Nadu targeted only the oral arms, disposing of the bells at sea (Mohan *et al.* 2011).

Information on jellyfish fisheries along India’s west coast is even sparser. In Jakhau, Gujarat, about 75 *odis* (fiberglass boats with inboard engines) were engaged in gillnet fishing for jellyfish in 2010 (CMFRI 2010). Each boat has a capacity of approximately 1 tonne per day, and there are two fishing seasons each year (April-May and November-December). Landings from one season in 2010 in Jakhau were approximately 800 tonnes, up from 250 tonnes in 2009 (CMFRI 2010).

There are also suggestions that exploitation of jellyfish in India is negatively affecting olive ridley sea turtles (*Lepidochelys olivacea*) by reducing their prey

(Anonymous 2007; 2008b). This can also lead to conflicts of interest regarding the mandates of different government departments (Murugan & Durgekar 2008).

More recently, it appears that many processing facilities for jellyfish in India have closed due to a lack of buyers for the exported product (T. Vaidyanathan, University of British Columbia, pers. comm., Aug. 2015). Fishers continue to catch large amounts of jellyfish as bycatch, especially in shore seines. However, whereas this bycatch was formerly processed and exported in the 2000s, it is now typically discarded. It is unclear how much the country's landings of jellyfish have declined, as there were reportedly still processing facilities in some regions as recently as 2010 (*e.g.*, CMFRI 2010); but it is assumed that recent catches in India are likely an order of magnitude lower than the peak in the mid-2000s.

3.3.8. Indonesia

Indonesia is one of the world's largest producers of jellyfish behind China and Thailand, and targets jellyfish in many locations (see Figure 3). There is a long history of jellyfish capture in Indonesia, with annual catches extending back to 1950, when fisheries statistics were first tabulated (FAO 2015a). Despite this history, catches of jellyfish in Indonesia are highly variable, with landings ranging in the hundreds of tonnes in some years all the way up to a peak of 123,000 tonnes in 1995. While this variability is likely a reflection of abundance, it may also have to do with

cultural misunderstandings and stakeholder relationships. Rudloe (1992) reported a lack of trust between the Indonesian sellers and Chinese buyers, and noted that “shipments of processed jellyfish sometimes have good product on top of the batches and poor quality on the bottom.”

Indonesia reports jellyfish catches for both of its FAO areas (57, ‘Indian Ocean, Eastern’ and 71, ‘Pacific, Western Central’; see Figure 6). However, there are other sources of data that indicate the reported catch statistics are not accurate in some years. For example, the Southeast Asian Fisheries Development Center (SEAFDEC) has published Fishery Statistical Bulletins since 1978. While jellyfish catch statistics are not available for every Southeast Asian country for every year, there are numerous years where either catch statistics or export statistics (or both) are available (see SEAFDEC 2015). Data on production of processed jellyfish are also available from FAO for some years (see FAO 2015b). While export data was rarely used in this analysis due to the possibility of importing and re-exporting, the export statistics reported by SEAFDEC are identical to those reported as production of processed jellyfish by FAO for the years where they are given. Therefore, it is reasonable to assume that the export statistics reported by SEAFDEC for the period 1976-1990 represent jellyfish that were caught and processed in Indonesia. A recent publication by Asrial *et al.* (2015a) also indicates that catches in Saleh Bay, Sumbawa

Island have exceeded 30,000 tonnes since 2010, an amount larger than the catches reported by FAO in some years for the entire country, further suggesting underreporting.

Numerous species of jellyfish are targeted in Indonesia. According to Kitamura & Omori (2010), *Lobonemoides robustus* is caught in the Strait of Malacca along the east coast of Sumatra from Medan to Lampung and Bangka Island. This species is also targeted in the Makassar Strait off southeastern Kalimantan (Indonesian Borneo) and along the north coast of the island of Java. The estuarine *Acromitus hardenbergi* is caught in Sumatra in Tanjung Balai. Fishing for jellyfish also occurs along Java's southern coast (Nishikawa *et al.* 2009). A newly described species, *Crambionella helmbiru*, is fished in Karangbolong and Cilacap from August to November (Mujiono 2010; Nishikawa *et al.* 2015). Further east, *Crambione mastigophora* is targeted near Prigi and Muncar (Omori & Nakano 2001; Kitamura & Omori 2010), as well as in Selah Bay, Sumbawa Island from October to December (Asrial *et al.* 2015a; b). *Rhopilema hispidum* is also fished along the north (near Cirebon) and south (near Kotabaru) coasts of Java, as well as southeastern Borneo. Fishing for jellyfish has also been reported from Bacan Island for a yet to be described species known as the 'Semi-China type,' which is said to be similar to *Rhopilema esculentum*, but smaller (Omori & Nakano 2001; Kitamura & Omori 2010). Several other locations in

Indonesia have reportedly caught jellyfish in the past, such as Nusa Tenggara, West Sumatra, and Sulawesi (SEAFDEC 2015); however, these areas were not marked explicitly on Figure 3, as specific locations where jellyfish are caught within these regions could not be determined. Typical gears include dip-nets and drift nets (Nishikawa *et al.* 2009) that are fished from outboard-powered boats with crews of 2 to 5 and capacities of 1 to 5 tonnes (Mujiono 2010).

3.3.9. Iran

Details of the jellyfish fishery in Iran are virtually nonexistent. Catches are reported by FAO (2015a) starting in 2010, with landings averaging 3,451 tonnes annually between 2010 and 2012. Target species are unknown; however, *Catostylus perezii* is suspected to be the primary species targeted in neighbouring Pakistan (Gul *et al.* 2015), and possibly Bahrain, so it is likely that *C. perezii* is also caught in Iran. López-Martínez & Álvarez-Tello (2013) report 300 tonnes of processed jellyfish products exported to China from Iran in 2012, which likely represents the majority of Iran's catch.

3.3.10. Japan

Japan has a long history of targeting jellyfish, but has never explicitly reported jellyfish catches to FAO. Omori (1981) notes that there are records of jellyfish fishing in the Seto Inland Sea dating back to the late 1800s. Omori (1978) reported that

Nemopilema nomurai is sometimes caught off the Hokuriku coast in the Sea of Japan, and that *Rhopilema esculentum* is occasionally caught along the coasts of western Japan. Omori (1981) also reports jellyfish fishing in Wakasa Bay, Mutsu Bay, as well in the Sea of Japan off Tōhoku. Most of these reports are from the 1970s, and it remains unclear if Japan continues to fish for jellyfish in these regions today. The Japanese sea nettle, *Chrysaora pacifica*, has also reportedly been caught for food in Japan (Morikawa 1984).

One region where fishing for jellyfish has persisted is the Ariake Sea, the largest bay in the southern island of Kyūshū. Catches primarily consist of *Rhopilema esculentum* and to a lesser extent, *Rhopilema hispidum* (S.-I. Uye, Hiroshima University, pers. comm., Sept. 2012). Historically, catches were estimated to total about 1,000 tonnes per year (Morikawa 1984), but processing in the region became more industrialized in 1977 as jellyfish began to bloom in much higher abundances, and catches of 18,000 and 10,000 tonnes followed in 1978 and 1979 respectively (Omori 1981). However, soon after 1979, jellyfish populations in the Ariake Sea returned to lower abundances, and a few hundred tonnes were caught each year and sold in the local fish market (S.-I. Uye, Hiroshima University, pers. comm., Sept. 2015). Similar conditions persisted for several decades until 2011, when large jellyfish blooms

again led to increased capacity and landings exceeding 10,000 tonnes annually to at least 2013.

Due to the recent increased proliferation of *Nemopilema nomurai* in the region (Kawahara *et al.* 2006b; Uye 2008), one would expect that this species is also being caught in Japan. While demand for *N. nomurai* appears to be relatively low in the Japanese market, there have been recent attempts to develop them as an additive to various foods such as candy, cookies, and ice cream (Anonymous 2006; Simpson 2009). Despite this, there are no available records for landings of *N. nomurai* in Japan.

Notwithstanding the fact that Japan produces and exports jellyfish, it also imports jellyfish in even greater quantities. From the late 1980s through the 1990s, imports of jellyfish to Japan averaged about 10,000 tonnes of processed product annually (Omori & Nakano 2001). Through the 2000s, the average dropped slightly to around 8,000 tonnes annually (Information Office, Tokyo Customs House, data courtesy of S.-I. Uye, Hiroshima University, Oct. 2012).

3.3.11. Korea (Republic of)

The Republic of Korea, also known as South Korea and hereafter referred to as Korea, does not explicitly report catches of jellyfish to FAO. However, Omori (1981) reports that fishing for jellyfish occurred historically in southwestern Korea, near

Mokpo, insinuating that fishing for jellyfish in Korea may actually extend back for centuries, rather than just decades. However, no additional information is readily available on the timing or scale of this fishery. More recent fishing for jellyfish in Korea also occurs along the southwestern coast near Muan and Gunsan (Omori 1981) as well as further north near Ganghwa and Ganghwado islands in Incheon (C. Han, National Fisheries Research and Development Institute, pers. comm., Oct. 2015). Ullah *et al.* (2015) identified the species as *Rhopilema esculentum*. Fishing typically occurs between September and November (Omori 1981). Catches appear to be relatively small compared to other Asian countries, with an average of 31 tonnes of processed jellyfish products produced annually between 1988 and 2011 according to trade production statistics (FAO 2015b). However, López-Martínez & Álvarez-Tello (2013) report 600 tonnes of processed jellyfish products exported to China from Korea in 2012, suggesting that Korea's jellyfish catches may be in the thousands of tonnes, rather than hundreds.

3.3.12. Malaysia

Malaysia is one of the world's largest producers of jellyfish behind China, Thailand, and Indonesia. Interestingly, in some locations in Peninsular Malaysia, edible jellyfish are available year-round (Yusoff *et al.* 2010; Khong *et al.* 2016), which is relatively rare. FAO catch statistics for Malaysia start in 1981; yet Rudloe (1992) as

well as Omori & Kitamura (2011) reported that commercial fishing for jellyfish actually started in 1969. However, Nishikawa *et al.* (2009) and Yusoff *et al.* (2010) indicate that fishing for jellyfish was introduced by the Japanese as early as the 1940s in Penang, and spread to Bagan Datoh by the 1950s. Khong *et al.* (2016) also state that the “jellyfish fishery in Malaysia is a century-old industry that has been carried on for at least three generations.” It is difficult to estimate catches through the 1950s and 1960s, but operations were presumably small, with landings in the hundreds of tonnes. Catches reported by the Southeast Asian Fisheries Development Centre (SEAFDEC) extend back to 1976; however, there are indications that these values may be underestimates. For example, SEAFDEC (2015) reports a catch of 441 tonnes of jellyfish for Malaysia in 1979, whereas Omori (1981) reports a catch of 3,400 tonnes for Malaysia in the same year. Ironically, SEAFDEC (2015) also reports exports of 604 tonnes of *processed* jellyfish by Malaysia in the same year, which suggests that the estimate by Omori (1981) is probably accurate. Regardless, capture statistics reported for Malaysia by FAO (2015a) and SEAFDEC (2015) are consistent after 1982, suggesting accuracy, with the exception of accounting for illegal, unregulated, and unreported catches (IUU).

Fishers in Malaysia catch jellyfish in both the Indian and Pacific Oceans (see Figure 3). The major fishing grounds and target species are outlined by Kitamura & Omori

(2010). *Lobonemoides robustus* is targeted in the Straits of Malacca off the Malaysian Peninsula, mainly between Bagan Datoh and Kuala Selangor, as well as near Klang. The estuarine *Acromitus hardenbergi* is also caught near Bagan Datoh, Teluk Intan, and the island of Pangkor, often using set-nets to take advantage of the tidal currents (Nishikawa *et al.* 2009). At least one other unidentified species of jellyfish known as the 'Semi-China type' is also caught in the Straits of Malacca, with fishing grounds near Penang and Teluk Intan (Omori & Nakano 2001). *Rhopilema hispidum* is targeted on the southern peninsula near Kukup, Johor (Nishikawa *et al.* 2009; Khong *et al.* 2016) where the oral arms are often discarded at sea (Yusoff *et al.* 2010). Fishing for jellyfish also occurs along the eastern peninsula near Kota Bharu (Omori 1981) and Terengganu, although catches there are reportedly highly variable, with the market being nearly saturated in 1986, followed by very low production in the years following (Rudloe 1992).

Jellyfish are also caught in Malaysian Borneo, with several locations in Sarawak. In fact, the relatively large catch reported by Malaysia in 1997 of more than 50,000 tonnes may have been due primarily to catches from Sarawak, which were apparently 49,665 tonnes that year (Abu Talib *et al.* 2003). Detailed information on jellyfish fisheries in Sarawak is presented by Rumpet (1991) based on visits to the region in 1998. Interviews with jellyfish fishers suggested a possible decline in catch

per unit effort (CPUE) through the 1980s, suspected to be due to a combination of factors including increased demand incentivising more fishers, as well as lower abundances of jellyfish. The primary target species, known as the 'white type,' is generally caught in Southern Sarawak and is suspected to be *L. robustus* (Kitamura & Omori 2010; Rizman-Idid *et al.* 2016). A secondary species, the 'red type,' is mostly caught further north near Matu in the Division of Mukah, and is potentially *Rhopilema esculentum* (Omori & Nakano 2001; Rizman-Idid *et al.* 2016). The primary gears used to catch the white type are scoop nets, hooks, and trawl nets, while the red type is often targeted using drift nets, bag nets, set-nets, and trawl nets (Rumpet 1991). *Lobonema smithi* is also targeted in Malaysia, although apparently not at commercial scale (Khong *et al.* 2016).

3.3.13. Mexico

Development of Mexico's jellyfish fishery began in 2000 in the Gulf of Mexico off the state of Tabasco, targeting cannonball jellyfish *Stomolophus meleagris*. However, the fishery shifted to the Gulf of California in 2001, principally to the shallow coastal waters along the state of Sonora. A summary of the fishery is provided by López-Martínez & Álvarez-Tello (2013). Average annual catches are 10,000 to 15,000 tonnes, but may vary from 1,000 tonnes to a peak of more than 30,000 tonnes in 2015. The fishery started relatively small, with about 70 small boats ('*pangas*'), each with a

crew of 2 or 3 fishers dip-netting for jellyfish. 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 1,000 *pangas* fished for jellyfish, with the season lasting only 5 days. In response, additional management measures and enforcement are currently being investigated and implemented, and while catches continue to remain relatively large, the future of Mexico's jellyfish fishery remains uncertain.

3.3.14. Myanmar

Available information on Myanmar's jellyfish fishery is scant. FAO (2015a) reports catches commencing in 1995 and continuing to the present, with a mean annual catch of just over 2,000 tonnes. However, in 2005, FAO reports the exact same value for the wet weight of jellyfish caught – 1,976 tonnes – as it does for exports of semi-dried processed jellyfish from Myanmar (FAO 2015a; b). FAO export and catch data appear to be more reconcilable for 2008-2011, although export data from SEAFDEC (2015) suggests exports were 30-80% higher than production for the period 2002-2006. The possibility of importing and re-exporting is possible, and as such, only the more conservative capture values reported by FAO (2015a) and SEAFDEC (2015) were used in the catch reconstruction.

At least several species of jellyfish are caught in Myanmar. *Lobonemoides robustus* is targeted in the Bay of Bengal, both in the north in Rakhine State and in the south near Myeik (Kitamura & Omori 2010). *Crambionella annandalei* is targeted near Sittwe, where *Rhopilema hispidum* also occurs (Omori & Nakano 2001).

3.3.15. Nicaragua

In 2008, 205 tonnes 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 tonnes. Fishermen used dip-nets with a 2-inch mesh size. Bells and oral arms were processed separately, yielding 57 tonnes 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 660 tonnes and 1,955 tonnes of jellyfish were caught in 2013 and 2014 respectively (J. Álvarez-Tello, Centro de Investigaciones Biológicas del Noroeste, pers. comm., May 2015).

3.3.16. Pakistan

Pakistan is yet another nation that does not explicitly report its jellyfish catches to FAO. Data is scant; however, the government handbook of fisheries statistics (MFD 2012) does report catches for the period 2007-2009 with an average annual catch of 1,663 tonnes. While this is only for one of two targeted species, it is the primary species. Although *Rhizostoma pulmo* and *Catostylus mosaicus* were previously reported as the target jellyfish species in Pakistan (Tahera & Kazmi 2006; Muhammed & Sultana 2008), it now appears that these were misidentifications, and the target species are in fact *Catostylus perezii* and *Rhopilema hispidum*, with the former being caught in much larger quantities (Gul & Morandini 2013; 2015).

Gul *et al.* (2015) discuss what little information is available regarding the jellyfish fishery in Pakistan. *C. perezii* is fished in Baluchistan, while *R. hispidum* is fished in Sindh province. Gill nets and set-nets are the typical gears used. It is unclear when the jellyfish fishery in Pakistan began, but currently at least 8 to 10 companies regularly process jellyfish there. In contrast with jellyfish fisheries in some other countries, the fishery in Pakistan primarily only uses the subumbrellar portions of the jellyfish, with the bell typically being discarded at sea. It is suspected that Pakistan's jellyfish fishery is growing, as López-Martínez & Álvarez-Tello (2013) report 1,600 tonnes of jellyfish product exported to China from Pakistan in 2012.

3.3.17. *Philippines*

Fishing for jellyfish in the Philippines presumably began in the mid-1970s, as both FAO and SEAFDEC first report catches beginning in 1976. The catch statistics reported by both organizations are virtually identical; however, SEAFDEC reports exports from the Philippines that are an order of magnitude higher than the catches (hundreds of tonnes versus tens of tonnes respectively). While the possibility of re-exporting exists, FAO (2015b) reports nearly identical exports as well as the same values for production of semi-dried jellyfish, indicating that the actual wet weight landings are likely at least 4 times higher than indicated by the exports (see 3.1.2 *Scaling factor*), and much higher than the catch values reported. This suggests that catches in some years are probably in the thousands of tonnes, a full two orders of magnitude higher than reported. When production statistics of processed jellyfish were available, they were scaled up to estimate the wet weight of the catch; however, due to the high variability of the catches, in years with no export statistics, only the reported catches were used in the catch reconstruction.

Important fishing grounds in the Philippines include San Miguel Bay in southern Luzon Island as well as Carigara Bay off Samar Island. Jellyfish are also targeted around Palawan Island, with fisheries along the east coast of the island as well as Malampaya Sound and near Port Barton. Fisheries in all of these locations are

presumably for *Lobonemoides robustus* (Omori & Nakano 2001; Kitamura & Omori 2010). *Lobonema smithi* has also been reported as a target species (e.g., PCAMRD 2008); however, it is likely that these specimens are also *Lobonemoides robustus* (Kondo *et al.* 2014). Over 1,500 people benefit from jellyfish fishing in Malampaya Sound alone (more than 10% of the population in the region), including fishermen as well as women and children involved in processing (PCAMRD 2008). However, reports in the late 2000s suggested that overfishing had led to a decline of jellyfish in the area, and fishing for jellyfish was suspended in October 2008 in Malampaya Sound as Japanese importers focused more on jellyfish from Indonesia, where catches are larger and shipping costs are lower (PCAMRD 2008; Kitamura & Omori 2010). Jellyfish are likely targeted in many more regions in the Philippines than are indicated in Figure 3, such as Mindanao (SEAFDEC 2015); however, specific locations of where additional jellyfish are caught could not be readily determined.

3.3.18. Russian Federation

Information on the recent development of a jellyfish fishery in Russian waters is chronicled by Yakovlev *et al.* (2005). Prior to 1999, the jellyfish *Rhopilema esculentum* was rare along the Primorsky Coast. However, in 1999, *R. esculentum* arrived in Peter the Great Gulf in large abundances, presumably carried there by shifting currents, as other rare marine species started showing up around the same time as well. As

R. esculentum is the most valuable jellyfish in Asia, a few firms began catching and processing *R. esculentum* in Peter the Great Gulf for export to China. According to Yakovlev *et al.* (2005), 2,000 tonnes were landed in 2000, followed by 346 tonnes in 2001. These values are in contrast with FAO statistics, which report no catch in 2000, and a catch of 142 tonnes in 2001. According to FAO, catches in Russia have continued since 2003 at < 1,000 tonnes annually.

3.3.19. Sri Lanka

Sri Lanka is yet another country catching jellyfish that is not found in FAO's jellyfish catch statistics. Sri Lanka began catching and exporting jellyfish no later than 1986 (Anonymous 1986). By 2008, the fishery had grown to the point where nearly 20,000 fishers targeted jellyfish, with export values in the millions of U.S. dollars (Naalir 2008). There appears to be considerable controversy over the jellyfish fishery in Sri Lanka, with environmentalists expressing concern over ecological impacts, overfishing of jellyfish, and a lack of regulation; while the Minister of Fisheries supports the economic benefits of exporting processed jellyfish to China (Perera 2008).

Fishing grounds are reportedly near Panama and Komariya in the Ampara District, and in the Kirinda area in the Hambantota District (Perera 2008). In 2009, one of the two primary target species was identified as belonging to the genus *Crambionella*

(NARA 2010). Catch statistics are not readily available; however, an article in 2008 indicated that “more than 100 to 150 tons of jellyfish are processed daily” for “only a few weeks of the year” (Perera 2008). If an average of 125 tonnes is assumed to be processed daily for 21 days, it can be estimated that Sri Lanka catches approximately 2,625 tonnes of jellyfish annually. To estimate the catch, this amount was scaled linearly from zero between 1985 and 2008, and carried forward from 2008. This estimate for recent catches is also consistent with the figure reported by López-Martinez & Álvarez-Tello (2013) of 800 tonnes of processed jellyfish product exported to China from Sri Lanka in 2012.

3.3.20. Thailand

Thailand is the world’s second largest producer of jellyfish, behind China. Jellyfish are caught both in the Pacific (Gulf of Thailand) and the Indian Ocean (Andaman Sea). Catches in the Pacific were first reported by FAO in 1970, with catches from the Indian Ocean following in 1978 (FAO 2015a). However, Soonthonvipat (1976) noted in the mid-1970s that Thailand was targeting jellyfish both in the Gulf of Thailand and the Andaman Sea, and wrote at the time that these activities began “only within the past decade.” Initially, the product was exported solely to Japan; however, production for both domestic markets and export to several countries increased rapidly (Soonthonvipat 1976). Unlike many countries, total catches reported for

Thailand appear to be consistent between FAO (2015a) and SEAFDEC (2015), with the exception of 2010, where landings reported by the latter were three times that of the former (110,000 and 37,133 tonnes respectively). However, in several years, the production of processed jellyfish reported by FAO (2015b) is higher than what would be expected from the reported catch. While the possibility of re-exports exists, this is unlikely to account for the differences in the values, and the catches are assumed to be underreported by FAO in those years.

In addition to the commercial jellyfish fisheries in Thailand that are primarily exporting catches to other countries in Asia, it is likely that jellyfish are also targeted in Thailand by artisanal and subsistence fisheries for local use. Estimates for these sectors have been made by Teh *et al.* (2015), and were included in the reconstruction. Estimates of foreign illegal fishing of jellyfish in Thai waters were also borrowed from Teh *et al.* (2015); however, as jellyfish are likely not caught in direct proportion to other fished groups, only 50% of the foreign fishing estimates for Myanmar and Malaysia were used in order to remain conservative.

A large proportion of the jellyfish catch in Thailand is suspected to be *Cephea cephea*; however, this has yet to be verified. Both *Lobonemoides robustus* and *Rhopilema hispidum* are presumably caught in the Gulf of Thailand near Rayong and Samut Sakhon (Omori & Nakano 2001; Kitamura & Omori 2010). *L. robustus* is also targeted

in the Andaman Sea near Ranong and Phuket. The estuarine *Acromitus hardenbergi* is caught at the mouth of the Trat River, in both Nong Khan Song and Tha Phrik (Kitamura & Omori 2010). Soonthonvipat (1976) indicated that the targeted species in Thailand is *Rhopilema esculentum*; however, this has not been confirmed by updated studies of edible jellyfish species in Southeast Asia, where the taxonomy is still considerably confused (Omori & Kitamura 2004; Kitamura & Omori 2010). Fishing for jellyfish has also been reported near Songkhla, further south in the Gulf of Thailand (Rudloe 1992).

Interestingly, Soonthonvipat (1976) suggested that there seemed to be a decline of jellyfish in the Andaman Sea as early as the 1970s, but noted that “the question regarding overfishing of jellyfish could not be answered.” Rudloe (1992) reported that there is some government regulation of jellyfish fisheries in Thailand, including closure of the fishery during the last several weeks of the season to allow for spawning.

3.3.21. Turkey

Turkey began catching jellyfish in 1984 and continued until 2006, which is the last year with reported landings. Catches over this time period ranged from zero to 4,000 tonnes, with an annual average of approximately 1,200 tonnes. Catches reported by FAO appear to agree with those from Turkey’s State Institute of Statistics, with the

latter providing a spatialized breakdown of the catches. For the years where spatial data could readily be obtained, the majority of the landings came from the Eastern Black Sea (46%) and the Marmara Sea (31%), with a smaller proportion of the catches coming from the Mediterranean Sea (11%), the Western Black Sea (7%), and the Aegean Sea (4%).

Information on this jellyfish fishery is scant, but it is suspected that the targeted species was *Rhizostoma pulmo* (Ozer & Celikkale 1998; Omori & Nakano 2001; Ozer & Celikkale 2001). The markets for Turkish jellyfish are unclear. Like jellyfish fisheries in most countries, much of the product may have been exported to Asia; however, it is also suspected that some of the product was used to feed farm animals such as chickens (Hsieh & Rudloe 1994; CIESM 2010).

3.3.22. U.S.A.

In the southeastern United States of America, both along the Atlantic coast and in the Gulf of Mexico, cannonball jellyfish or 'jellyballs' (*Stomolophus meleagris*) have traditionally been a nuisance for shrimp fishers and power plants, but are now commercially exploited. There have been numerous attempts to establish fisheries for *S. meleagris* in the U.S.A., with varying degrees of success. The first attempt was reportedly in Medart, Florida in the 1970s for export to Taiwan; however, the venture failed, partially due to the reluctance of fishers to provide the product

(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 U.S. 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. In addition, jellyfish were considered a nuisance to swimmers, shrimp fishers, and power plants. The initial report concluded that a jellyfish fishery could be developed in Florida; however, several challenges would have to be overcome including economic viability, processing knowledge, labour costs, and pollution from processing facilities. An additional challenge proved to be the size of the product. Cannonball jellyfish rarely exceed 19 cm in bell diameter, but jellyfish products fetching the highest prices 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.

In 1993, a small amount (~1 tonne) of jellyfish were caught in the Atlantic near Fernandina Beach, Florida, processed, and sent to potential buyers in Asia (Jones & Rudloe 1995). While the overall quality of the jellyfish was rated high, the darker colour of Atlantic cannonball jellyfish was not preferred. Several additional samples were then produced by various parties in 1993 and 1994 using cannonball jellyfish from the Gulf of Mexico, which are whiter in colour. After some success, approximately 15-30 tonnes were caught, processed, and shipped to Korea. Challenges for the fishery continued, including higher labour costs and an unfamiliarity with the species in Asia. In 1995, catches exceeding 90 tonnes were caught using seine gear. Through the 1990s, a jellyfish fishery in Florida did not expand due economics (Bynum 2003); however, jellyfish have reportedly been caught near the Florida panhandle, and then transported to Georgia for processing (Bridges 2008). Nonetheless, fishing of jellyfish in Florida waters continues, with boats operating out of both Apalachicola and Port Saint Joe, with a combined annual catch of approximately 1,100 tonnes.

The state of Georgia has also established a small jellyfish fishery. It 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 are shrimpers that

occasionally convert their boats to fish for jellyfish, and are reportedly thankful for their newfound opportunity (Bynum 2003; Landers 2011). The jellyfish fishery in Georgia transitioned from an experimental to a recognized fishery in 2013, and continues to operate at processing capacity with the possibility of future expansion. FAO statistics for the U.S.A. show an average of 574 tonnes of jellyfish landed annually for the period 1999-2013; however, the processing capacity in Georgia alone is reported to be on the order of 450 tonnes per week (Bland 2014). Indications are that exports exceed 1,000 tonnes of semi-dried product annually, suggesting average annual landings of roughly 4,000 tonnes (Anonymous 2014; Nobel 2014). This makes jellyfish the 3rd largest fishery in Georgia by weight, behind shrimp and blue crab (Page 2015). Most fishing occurs between November and May in federal waters adjacent to Doboy Sound (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 due to concerns over pollution from processing facilities. Proposals have been put forth in Beaufort and Colleton Counties, with capacities in excess of 2,000 tonnes per week (Bland 2014). While approximately 6 tonnes of jellyfish were apparently landed and processed at a temporary facility in 2014, these operations have ceased pending further review (Moody 2014; Murdock 2014).

There was also a historical fishery for jellyfish in Washington State's Puget Sound, but instead of targeting jellyfish for food, this 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 harvested from Puget Sound since the 1990s, as GFP is now synthesized in the laboratory. However, during the course of researching the luminescent proteins of *A. victoria*, it has been estimated that a total of 1 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 tonnes, or 2 tonnes 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 past 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, Canada can form extensive blooms with occasional densities of 1-2 medusae/m³ (pers. obs.).

3.3.23. Vietnam

Vietnam is yet another country known to catch jellyfish but remains absent from FAO's jellyfish statistics. The jellyfish fishery began in the early 1990s, introduced by Chinese importers (Nishikawa *et al.* 2009). Details on the jellyfish fisheries of northern Vietnam, especially those in the Gulf of Tonkin near Thanh Hoa, were investigated by Nishikawa *et al.* (2008) through interviews with processing plant owners and fishers, field sampling, and examination of local statistics. As with most jellyfish fisheries, large interannual variations were reported. Fishing for jellyfish can be very profitable for fishers in Vietnam, as well as their families that assist with pre-processing on beaches. Despite a short fishing season of less than 2 months, income from jellyfish may support fishers for the rest of the year. Nishikawa *et al.*

(2008) estimate that 800,000 to 1,200,000 individual medusae may be caught each year in the Thanh Hoa region alone. In addition, the authors report statistics for 2 major government-run processing companies, one for 1995 to 2005 and the other for 2000 to 2005, with combined mean annual exports of approximately 4,500 tonnes of semi-dried product. The values can be conservatively scaled up (see 3.1.2 *Scaling factor*) to provide a minimum estimate of Vietnam's jellyfish catches since 1995. Of course, the estimated values are likely underestimates, as there are additional private companies that do not report their exports (Nishikawa *et al.* 2008). For example, four enterprises in Quang Ninh province were found to be illegally discharging wastewater into the UNESCO World Heritage Site of Ha Long Bay in 2013 in connection with jellyfish processing (Anonymous 2013); however, the relative scale of these operations remains unclear.

Thanh (2011) reports that the town of Diem Dien in Thai Binh province, which accepts jellyfish caught from neighbouring provinces such as Quang Ninh, Hai Phong, and Nam Dinh, processes approximately 15,000 tonnes of jellyfish annually. It is unclear how much overlap there is between the figures reported by Nishikawa *et al.* (2008) and Thanh (2011). As such, only the values reported by Nishikawa *et al.* (2008) were used in the catch reconstruction. However, the reported values are encouragingly of similar magnitude, and serve to highlight that Vietnam has

emerged as a major player in the global jellyfish market. To extrapolate jellyfish production beyond 2005, a linear regression model was used, which generally reflects the pattern of apparent growth in Vietnam's jellyfish landings between 1995 and 2005, based on the available minimum estimates.

Regarding the target species, *Lobonemoides robustus* is presumably caught near Nha Trang and in Cam Ranh Bay in southern Vietnam, as well as near the island of Phu Quoc in the Gulf of Thailand. Further north, *Rhopilema hispidum* is targeted in the Gulf of Tonkin, near Thanh Hoa and Haiphong (Omori & Nakano 2001; Kitamura & Omori 2010). *Rhopilema esculentum* is also caught in northern Vietnam, albeit in much lower abundances than *R. hispidum* (Nishikawa *et al.* 2009). Gears may include dip-nets and drift gill nets, and other species of jellyfish may also be caught as bycatch, including *Cyanea*, *Chrysaora*, and *Sanderia* spp.; however, these non-target species are not processed for export (Nishikawa *et al.* 2009).

3.3.24. Other countries

As mentioned, FAO reports jellyfish catches for the Falkland Islands (Malvinas), Namibia, and the United Kingdom. However, these countries and territories are not known to have jellyfish fisheries and it is likely that the reported catches are in fact discarded bycatch from other fisheries. Indeed, the FAO fishing areas reported for jellyfish catches by the United Kingdom are not part of the United Kingdom's

Exclusive Economic Zone (EEZ), namely 41, 'Atlantic, Southwest' and 48, 'Atlantic, Antarctic' (see Figure 6). In addition to the countries discussed above, a number of other nations have been reported to export jellyfish. For example, North Korea, Hong Kong, Singapore, and Taiwan all exported jellyfish to Japan in the 1980s and 1990s (Omori & Nakano 2001). Cambodia can also be added to this list for a solitary export to Japan in 2001 (S.-I. Uye, Hiroshima University, pers. comm., June 2014). However, it is unclear if these countries caught the jellyfish in question in their own waters, or if they are simply re-exports.

Given the expanding jellyfish fisheries in Middle-Eastern countries such as Iran, Bahrain, and Pakistan, it seems likely that there may also be fisheries for jellyfish in the United Arab Emirates (U.A.E.), Saudi Arabia, and Oman. Unfortunately no information on jellyfish fisheries in these countries is readily available, other than the fact that López-Martinez & Álvarez-Tello (2013) report that 1,000 tonnes of processed jellyfish was exported to China from the U.A.E. in 2012. Due to the possibility of re-exports, this account was not included in the reconstruction; however, this may be evidence that yet another country is developing a jellyfish fishery.

Lychnorhiza lucerna has also been investigated as a possible fishery in Argentina (Schiariti 2008), and numerous specimens have been caught around the Río de la

Plata along the northern coast of Buenos Aires province. These catches have been processed by scientists and fishers in order to investigate the quality of the product. As *L. lucerna* interferes with tourism as well as fisheries for finfish and shrimp in the region (Schiariti 2008; Nagata *et al.* 2009), there is interest in targeting this species. However, this is considerable uncertainty regarding how much jellyfish can be produced from the area on a consistent basis. As buyers from Asia necessitate a minimum to be involved, this uncertainty has heretofore prevented the fishery from developing. Until significant investment is made to overcome the ecological and economic knowledge gaps, a jellyfish fishery in Argentina will likely remain undeveloped.

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 sennaeostome, 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 operations, desalination plants, tourism, and other industries (Quiñones *et al.* 2013; Mianzan *et*

al. 2014), signifying that many would welcome a targeted fishery in the area. Similarly large abundances of *C. plocamia* also occur in northern Chile, suggesting that if a fishery were to be established in Peru, expansion to Chile would also be a possibility (Palma 2011).

Norway also explored the possibility of exploiting the mesopelagic *Periphylla periphylla* (Wang 2007). Despite dramatic increases in abundance of this species in a number of Norwegian fjords (Brotz 2011), a commercial jellyfish fishery has not developed.

Javenech, a pharmaceutical company in France, lands approximately 3 to 4 tonnes of *Rhizostoma plumo* annually from the Bay of Biscay for processing into collagen. *Rhizostoma octopus* is also commercially exploited for high-grade medical collagen in Wales, United Kingdom using gill nets with a mesh size of 5 × 5 cm. The unregulated fishery began in 2014, with landings of 4.3 tonnes in 2015 (Elliott *et al.* 2016). Currently, these two fisheries are assumed to be the only commercial-scale operations fishing jellyfish for a use other than human consumption.

4. Growth of jellyfish in Mexico's Gulf of California

Understanding the growth and mortality of fish populations is essential for predicting how stocks will respond to fishing pressure, and thus for incorporation in ecosystem models and the implementation of regulations to ensure sustainable fisheries. Traditionally, estimates of growth were most often made using age-based methods, whereby the age of captured fishes were estimated by examining their otolith structures (or less often scales), which exhibit annual growth markings. However, such markings are less evident in tropical fishes, as seasonality is less pronounced in the tropics. These methods are also not applicable to most marine invertebrates, such as jellyfish, which lack otoliths and often do not live beyond one year. Some cubomeduse exhibit daily growth markings in their statoliths (*e.g.*, Ueno *et al.* 1995; Gordon *et al.* 2004; Gordon & Seymour 2012); however, such markings have not been identified in other taxonomic classes of jellyfish. As a result, past studies of jellyfish growth tend to lack standardized methods, instead reporting instantaneous growth rates in terms of percent growth, making comparison within and between species virtually impossible (Palomares & Pauly 2009). Thankfully, size-based methods, which examine the lengths or weights of a sample of animals, have also proven to be effective, and are often much easier to implement than age-based methods.

Medusae of *Stomolophus meleagris* were examined from Mexico's Gulf of California, where there is an expanding fishery for them. Data were analyzed in order to identify growth patterns, which will help inform fisheries management decisions and contribute to the understanding of how stocks will respond to fishing pressure.

4.1. Length-frequency analysis and the ELEFAN software

The ELEFAN software, short for Electronic Length-Frequency Analysis, was developed by Dr. Daniel Pauly more than 30 years ago and was recently updated as a stand-alone application in the open-source programming language R (see Pauly & Greenberg 2013). The primary inputs of ELEFAN are length-frequency (L/F) data, which are then used to estimate parameters of the von Bertalanffy Growth Function (VBGF), namely the asymptotic length L_{∞} and the curvature of the growth curve K . The standard, non-seasonal VBGF (see von Bertalanffy 1938) takes the form:

$$L_t = L_{\infty} \cdot (1 - e^{-K(t-t_0)})$$

where L_t is the predicted length at age t , L_{∞} is the asymptotic length (roughly corresponding to the maximum length in the population in question), K is the curvature parameter of dimension time^{-1} that expresses how fast L_{∞} is approached, and t_0 is the (usually negative) age at which size = 0.

There is a concern that jellyfish size is not always related to age. In fact, jellyfish may exhibit degrowth under adverse environmental conditions, such as poor food availability (*e.g.*, Hamner & Jenssen 1974; Frandsen & Riisgard 1997; You *et al.* 2007; Lilley *et al.* 2014). However, as the medusae included in this analysis are relatively young, they are expected to exhibit continued growth over the study period. Of course, all models are wrong (Box 1976), but length-frequency analysis has proven to be an informative and useful tool for studying jellyfish growth patterns (Palomares & Pauly 2009).

4.2. Sampling of *Stomolophus meleagris*

The Gulf of California, also known as the Sea of Cortés, is a productive and variable body of water separating the Mexican mainland and the Baja California Peninsula (22-32° N and 105-107° W). It is approximately 1,130 km long and 80-209 km wide (Lluch-Cota *et al.* 2007). The peninsular shoreline is mostly rocky with sandy stretches and virtually no riverine input, while in contrast the continental shore is characterized by long sandy beaches, muddy bays, and large coastal lagoons with considerable freshwater input. The shelf is wider along the continental shore (Figure 7), and the depth of the Gulf increases towards its mouth. The environment in the Gulf of California is strongly seasonal, with most rainfall occurring during the summer and fall (Salinas-Zavala *et al.* 1993). Fishing is the most important human

activity in the Gulf, with a variety of fisheries including both highly industrialized pelagic and coastal artisanal fleets. The most important targeted taxa include shrimp, small pelagic fishes such as sardines, herring, and anchovies, as well as squids and tunas (Lluch-Cota *et al.* 2007). As discussed, there is also a rapidly developing fishery for cannonball jellyfish *Stomolophus meleagris* since 2001 (see 3.3.13 Mexico).

S. meleagris has a polymorphic life cycle including fertilized egg and planula, as well as various polypoid and medusoid phases (Calder 1982; Figure 1). Small medusae typically appear in the coastal lagoons in the Gulf of California in December, suggesting that polyps are likely located in the lagoons. The medusae grow rapidly through December, January, and February, and are then targeted by the fishery in March through to April or May after migrating out of the lagoons. Medusae appear to be virtually nonexistent between June and November (Álvarez-Tello *et al.* 2016).

Individual *S. meleagris* medusae were collected by handheld trawl nets in 2014, 2015, and 2016 by members of the Instituto Nacional de Pesca. Most samples were taken near Guaymas, including in the Las Guásimas coastal lagoon (Figure 7) using a 2 m long trawl net with 50 × 50 cm square steel frame opening and ¼-inch stretched mesh. The date, time, latitude, longitude, and water temperature were also recorded for each sample. In 2016, smaller medusae were also sampled from lagoons using

the same trawl gear with 1 mm mesh. Specimens were also measured each year from local processing plants. Individual bell diameters were measured using a vernier caliper. More than 20,000 individual medusae were sampled in total.

Figure 7. Map of the Gulf of California in Mexico; dark blue indicates shelf (< 200 m); black circle indicates approximate location of Guaymas and Las Guásimas coastal lagoon



4.3. Analysis and results

All samples were pooled to create a Wetherall Plot (Wetherall 1986), which can provide an estimate of L_{∞} by examining the differences between the mean and maximum values of L within a sample. Using all of the sample data, the Wetherall Plot yielded an estimate of $L_{\infty} = 18.4$ cm (Figure 8). Samples from December 2015 – March 2016 were binned into biweekly increments and used to generate a length-frequency plot (Figure 9), which appears to represent two distinct cohorts. These data, representing more than 5,000 individual specimens, were selected given that the sampling method used targeted small medusae and would be useful for estimating growth parameters. ELEFAN was then used to estimate the goodness-of-fit based on various values of K (Figure 10), suggesting an estimate of $K = 3.7$ year⁻¹. Values of K can vary widely for jellyfish, from as low as 0.45 year⁻¹ for some specimens of *Aurelia aurita* to as high as 4.69 year⁻¹ for selected *Phyllorhiza punctata* (Palomares & Pauly 2009). Even within a genus, K may range from less than 1 year⁻¹ to nearly 4 year⁻¹, as is the case for *Aurelia* spp. (Palomares & Pauly 2009). Therefore, the estimate of $K = 3.7$ year⁻¹ for *S. meleagris* suggests rapid growth, and appears to reasonably represent the observed growth patterns in the population (Figure 11).

Figure 8. Weatherall Plot using ELEFAN with $L_{\infty} = 18.4$ cm

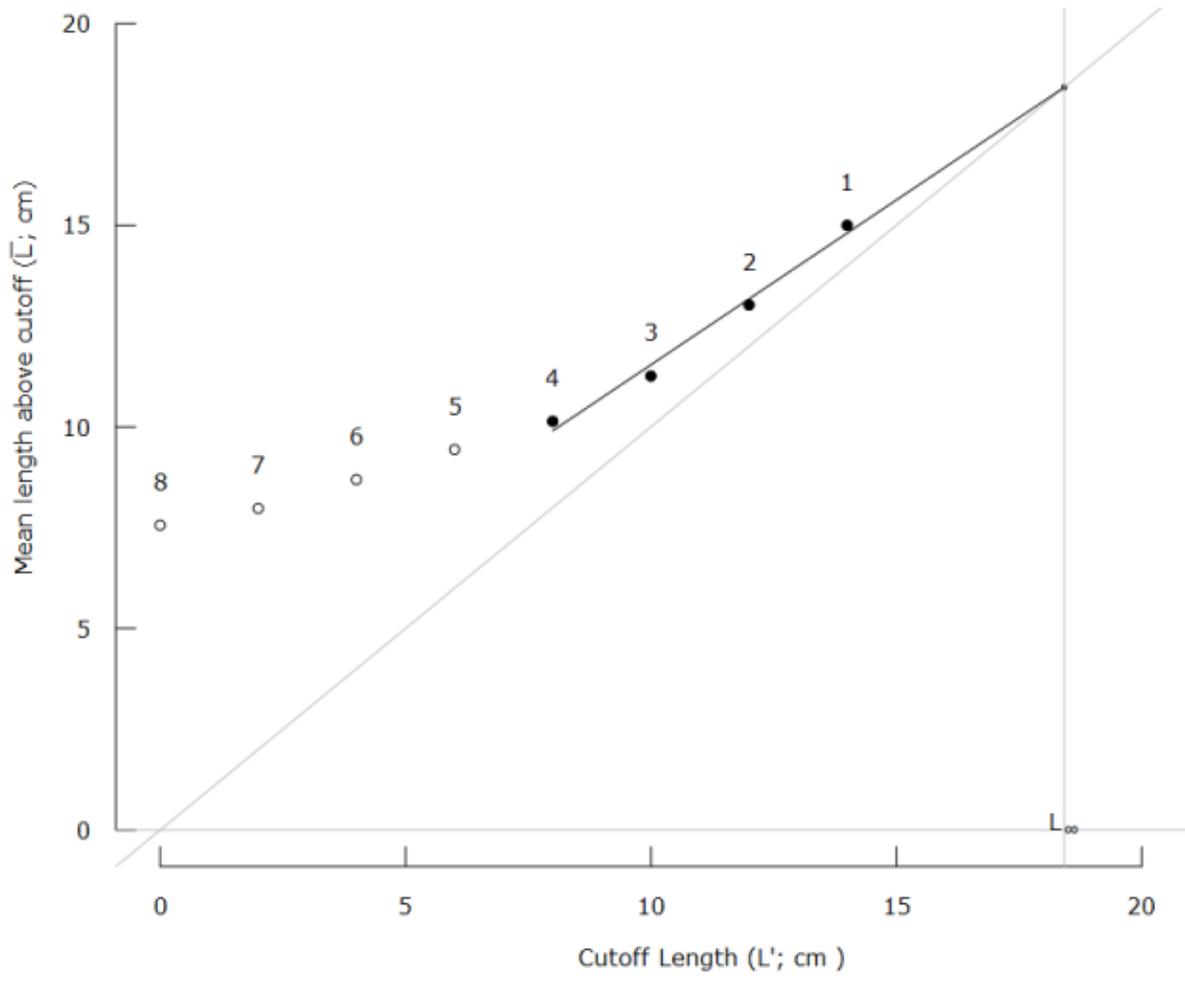


Figure 9. L/F data plot for *S. meleagris* sampled Dec. 2015 - April 2016 appearing to show two distinct cohorts of medusae

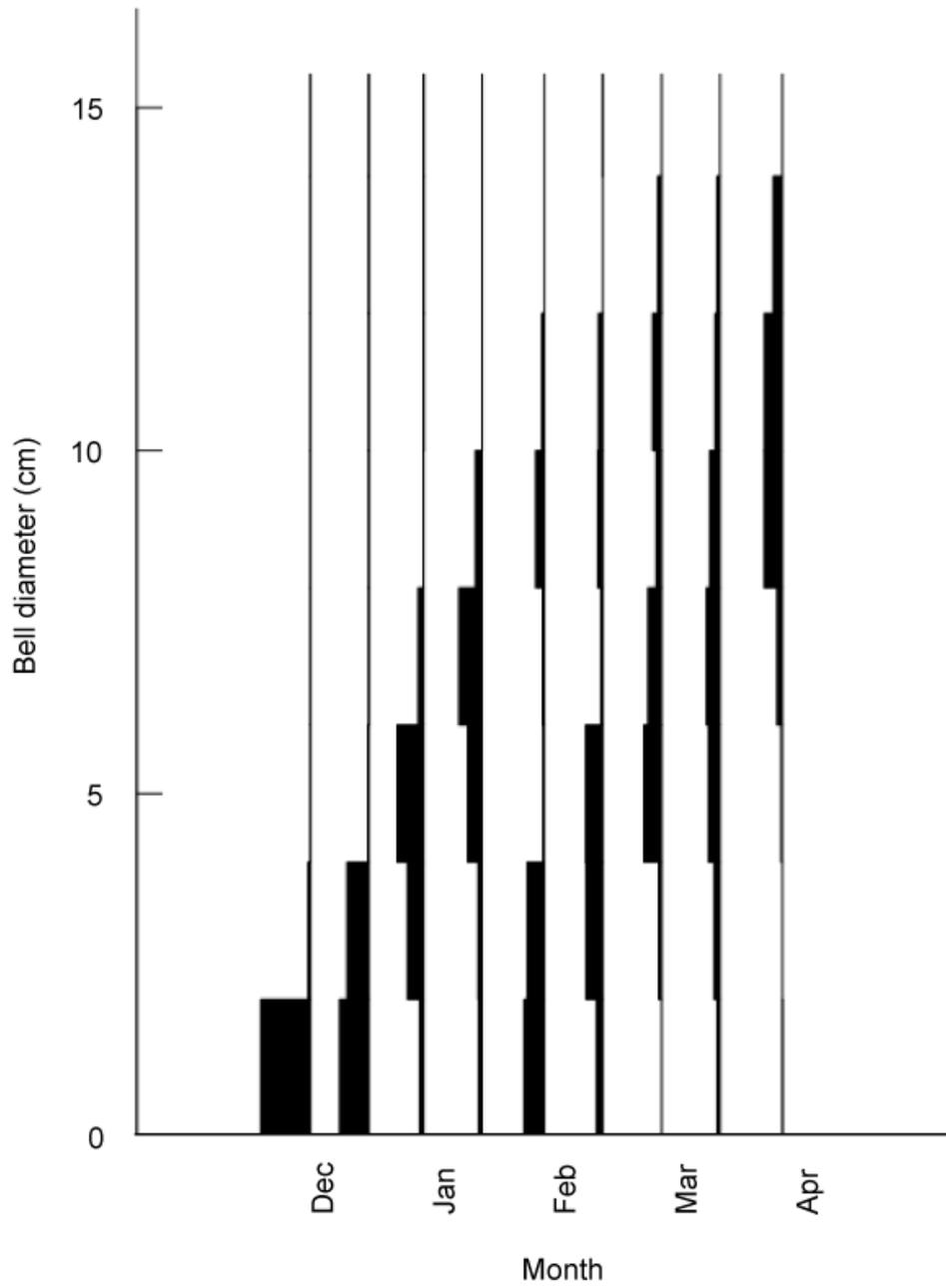


Figure 10. Response surface for the goodness-of-fit estimator using ELEFAN, suggesting an estimate of $K = 3.7 \text{ year}^{-1}$

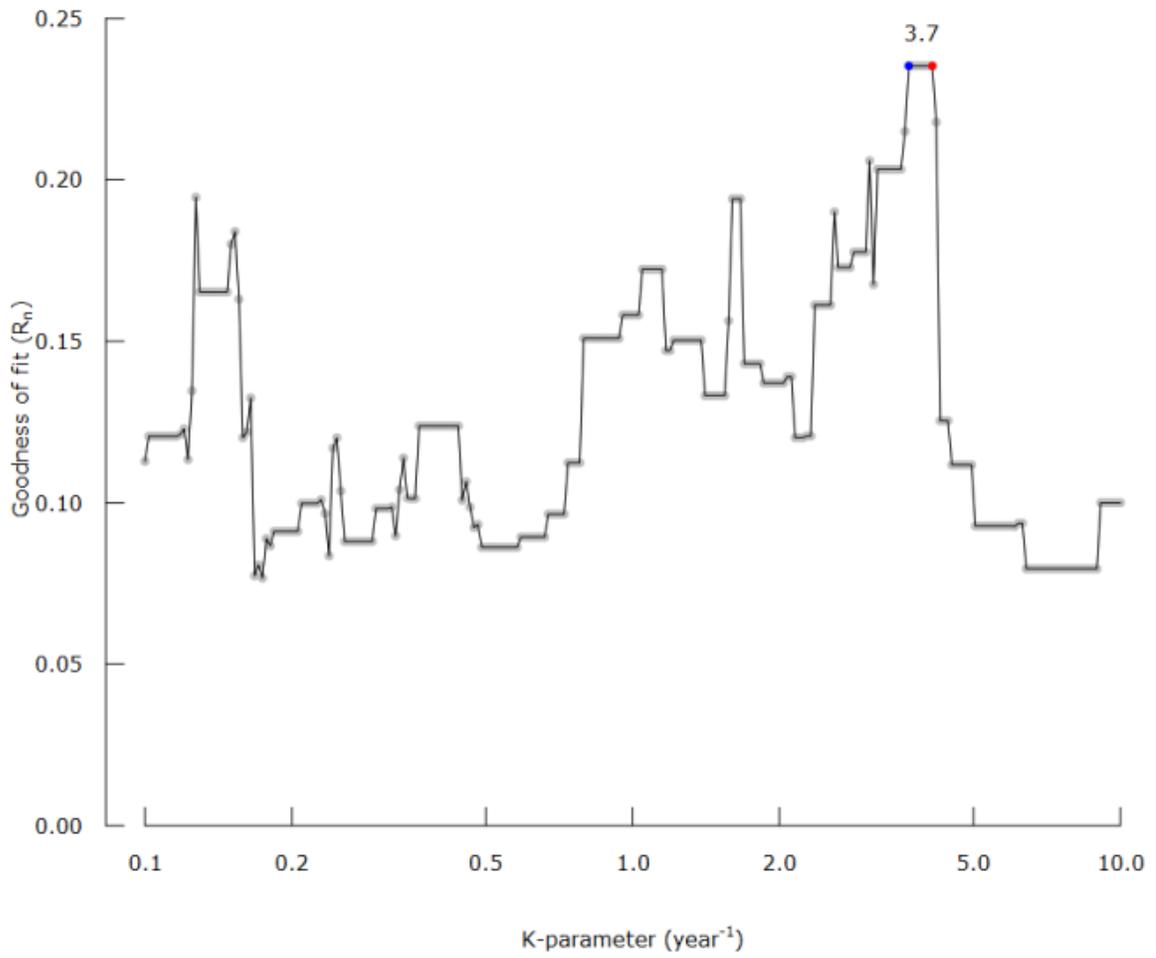
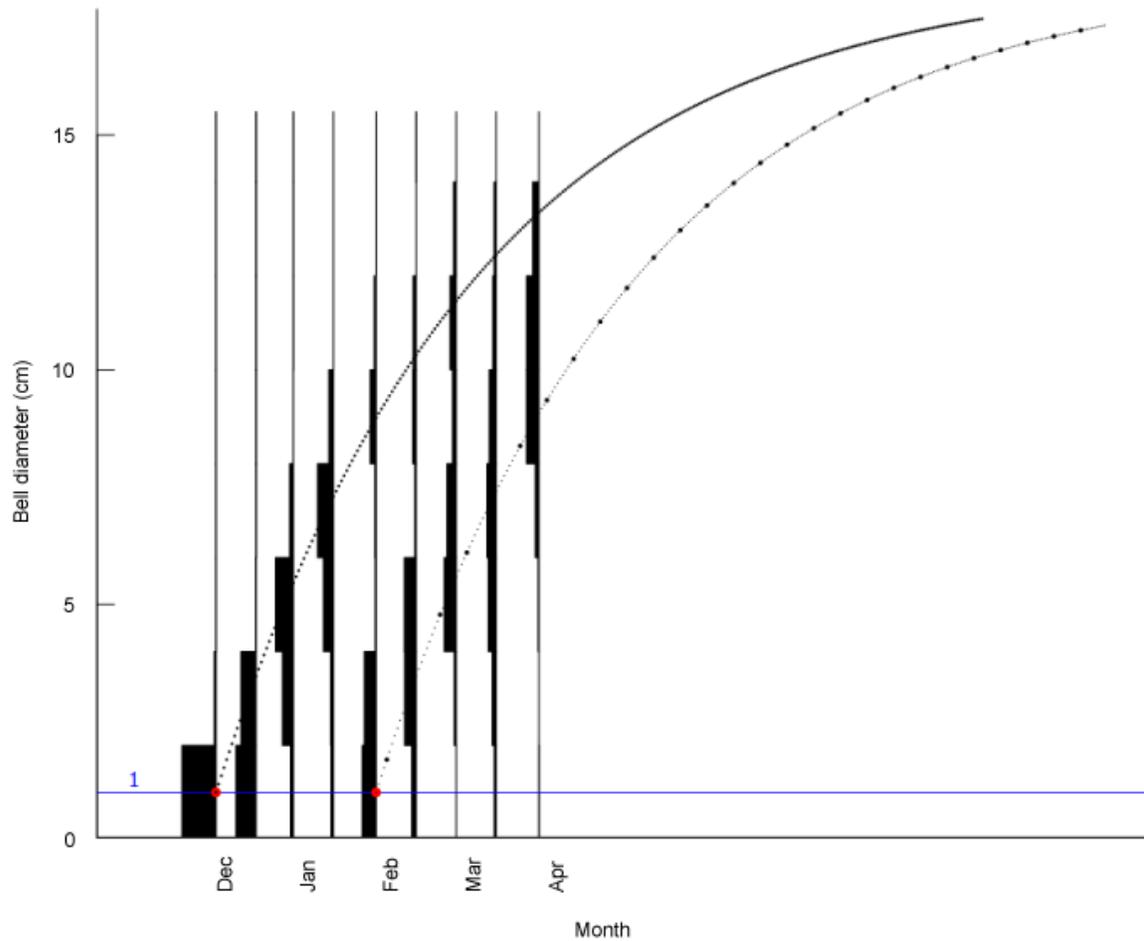


Figure 11. Growth curve fitting using ELEFAN for *S. meleagris* sampled Dec. 2015 – April 2016; $L_{\infty} = 18.4$ cm; $K = 3.7$ year⁻¹



In order to compare between different taxa, it is useful to compare values of K and W_{∞} , the asymptotic weight (rather than L_{∞}). This was accomplished by examining the length-weight relationship for *S. meleagris* (Figure 12). In total, 136 specimens

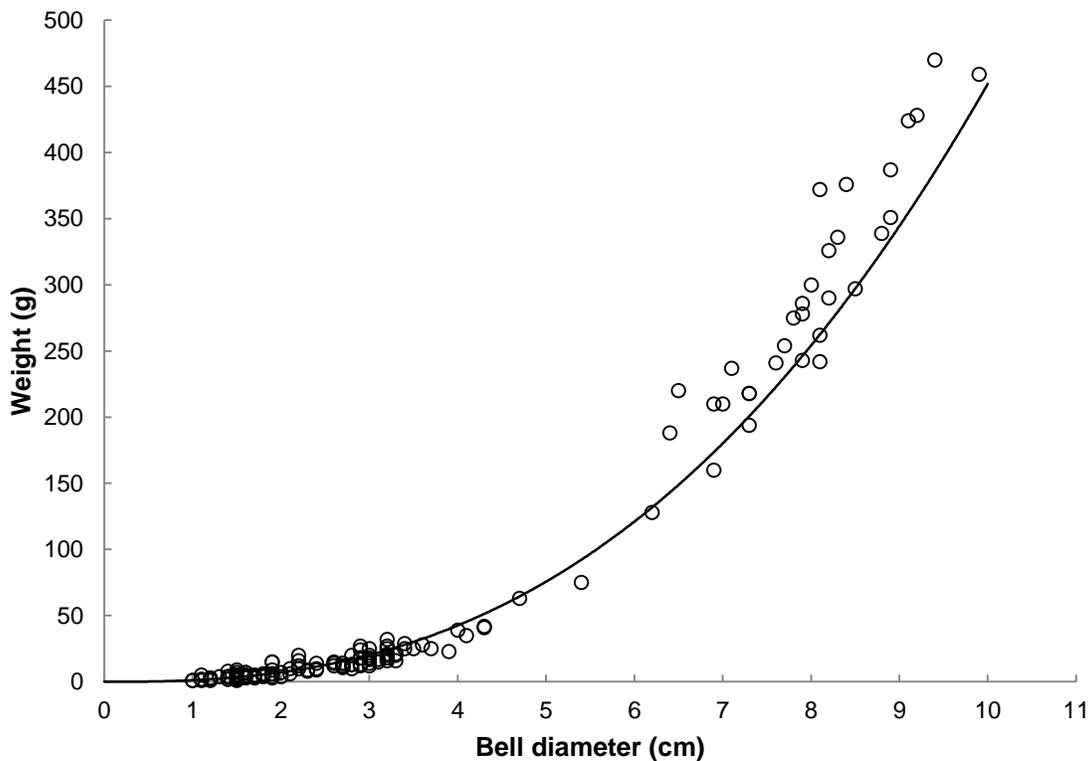
were measured for their length (L; bell diameter) and weight (W), which was then used to estimate parameters (a and b) of the length-weight equation:

$$W = a \cdot L^b$$

For *S. meleagris*, it was found that $W = 1.19 \cdot L^{2.58}$ which explained 95% of the variance.

The estimated value of $b = 2.58$ is consistent, although not equivalent, with that found by Álvarez-Tello *et al.* (2016) of $b = 2.8106$ for the same species. More samples of larger medusae in both studies might help to narrow the discrepancy.

Figure 12. Length-weight relationship for *S. meleagris*

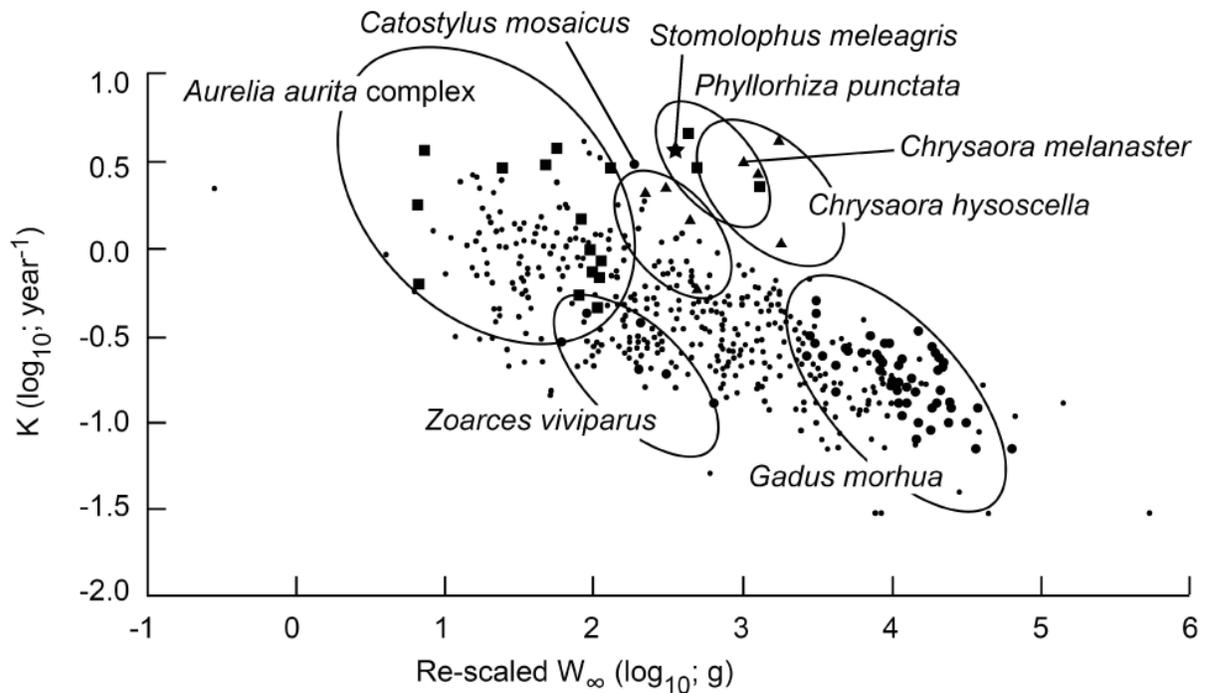


Using the derived parameters for the length-weight relationship, $L_{\infty} = 18.4$ cm can be converted to $W_{\infty} = 2.18$ kg. In order to compare with other taxa, such as fish, jellyfish can be normalized to the water content of fishes. *S. meleagris* is approximately 96% water (Hsieh *et al.* 1996), whereas fish typically have a mean water content of 75% (Palomares & Pauly 2009). As such, W_{∞} for *S. meleagris* can be re-scaled by the ratio of the dry weights, $25/4 = 6.25$, and thus $W_{\infty(\text{norm})} = 348$ g. Taking $\log_{10}(K) = 0.57$ and $\log_{10}(W_{\infty(\text{norm})}) = 2.54$, these values can then be compared with other taxa on an auximetric plot (Figure 13). As can be seen from Figure 13, *S. meleagris* grows similarly to *Phyllorhiza punctata*, which is a more rapid growth pattern than for fish (higher K for a given W_{∞}). This is in contrast with other jellyfish, such as the *Aurelia aurita* complex and *Catostylus mosaicus*, whose growth patterns tend to resemble those of small fishes (Palomares & Pauly 2009).

It was found that *S. meleagris* from the Gulf of California grow according to a pattern that can be described with VBGF parameters $K = 3.7 \text{ year}^{-1}$ and a maximum bell diameter of 18.4 cm. This is comparable to other large jellyfish, and exceeds the rate at which most fishes approach their maximum sizes, even when they are normalized for their differing water content. Using L/F analysis to estimate the growth parameters of *S. meleagris* demonstrates that a tool from fisheries science can be adapted for application to jellyfish. Such analyses are useful for understanding the

growth of jellyfish, which as mentioned, is important for understanding responses to fishing pressure though estimations of mortality. In addition, such studies may also help contribute to taxonomy and understanding of jellyfish evolution by comparing and contrasting the growth patterns observed across and between species. Indeed, we must continue to examine these understudied animals using all available tools, especially those that have already been evaluated and established in traditional fisheries science.

Figure 13. Auximetric plot of various fish (small circles) and jellyfish species including *Stomolophus meleagris*; based on Palomares & Pauly (2009)



5. Conclusions

All investigated aspects of jellyfish fisheries proved to be previously underestimated. This includes the number of countries that have explored fishing for jellyfish (at least 28) and the number of edible species (exceeding 35). The magnitudes of catches have been dramatically underestimated, with contemporary global landings exceeding 750,000 tonnes annually, and a global catch exceeding 1 million tonnes in 2013. These estimates are more than double the values published by FAO (2015a). Research and management of jellyfish fisheries is lagging far behind the expansion of the industry, despite the availability of traditional fisheries science methods such as length-frequency analysis, which can be applied to jellyfish.

While jellyfish are often perceived as a nuisance, they can also be a valuable commodity and are savoured as a delicacy in many places. Perhaps as awareness of jellyfish as human food continues to spread, perceptions of jellyfish will also change. From an Anglocentric point of view, since they are not truly “fish” (itself a paraphyletic term), there have been suggestions to step away from the moniker of “jellyfish” and instead refer to them as “jellies” or “gelatinous zooplankton.” However, given that some of the established tools available from fisheries science can be applied to jellyfish, perhaps it is time to put the “fish” back into “jellyfish,”

and include them in the realm of “fisheries.” Indeed, the global catches of jellyfish already eclipse those of many groups of taxa targeted by established fisheries, such as lobsters (Pauly & Zeller 2016a; miscellaneous marine crustaceans excluded). Moreover, despite the considerable information and research on the fishery for Antarctic krill (*Euphausia superba*) the catches presented herein are even greater, making jellyfish the largest zooplankton fishery on the planet. Clearly much more attention needs to be paid to research on jellyfish and their associated fisheries. After examining some of the peculiarities that characterize jellyfish fisheries, a number of management implications and research priorities emerge.

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. Given the extreme variability of jellyfish populations, 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, ecosystem-based management, and the protection of critical habitat, especially for polyps. Combined with economic drivers, concerns related to processing technologies (see below), as

well as minimizing bycatch and competition with species of concern (*e.g.*, Elliott *et al.* 2016), management of jellyfish fisheries will surely continue to be a challenge.

5.1. Research priorities

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);
- 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;

The development of processing technologies should also be a top priority, given both the environmental and human health concerns. Large quantities of effluent are

generated as a byproduct of jellyfish processing, which are too often not dealt with in an environmentally responsible way. As discussed, edible jellyfish may also 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 neurobehavioural toxicity and Alzheimer's disease (Perl & 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 & 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 delicious (*pers. obs.*). 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, subject to economic viability.

5.2. Sustainability and the future of jellyfish fisheries

While assessing the 'sustainability' of a system (or fishery) can be a complicated task (Costanza & Patten 1995; Shelton & Sinclair 2008), it is generally accepted that fisheries have rarely been sustainable (Pauly *et al.* 2002). If we consider a simplistic

definition of a sustainable fishery as one that produces consistent, sustained catches (or yields), it is interesting to consider jellyfish fisheries. Jellyfish populations are highly variable, even when they are not subject to exploitation (Brotz 2011). Therefore, it cannot be expected that catches would be consistent on short timescales of several years. However, the catch reconstruction herein makes it possible to evaluate whether or not catches are being sustained by inspecting the landings from countries that have been fishing for jellyfish for decades. Thailand has been catching jellyfish since the 1970s and has contemporary annual catches that can exceed 100,000 or even 200,000 tonnes in some years, comparable with historic maximum catches. Indonesia has also been targeting jellyfish for decades, and still has annual catches that usually exceed 20,000 tonnes, which although is not approaching maximal historic levels, is considerable nonetheless (for specific values, see *Appendix A*). A more recent example is Vietnam, which began catching jellyfish in the mid-1990s, and has been steadily increasing landings, which now exceed 50,000 tonnes annually. Of course, the 'sustainability' of the jellyfish fisheries in these countries could be masked by increasing geographic expansion, improved technology, or the fact that stocks may not be fully exploited. While these examples suggest that sustainable jellyfish fisheries might be possible, there are also examples that appear to be anything but. For example, overfishing of medusae is suspected to be the

primary cause for the decline of *Rhopilema esculentum* in China (Dong *et al.* 2014), suggesting that while the polymorphic life cycle of edible jellyfish (Figure 1) likely provides a buffer against overfishing, it should not be viewed as a total safeguard. Indeed, catches of *R. esculentum* continue to decline in China, despite bans on trawling in Liaodong Bay to protect polyp habitat (Ye 2006), as well as hatchery programs that rear and release hundreds of millions of juvenile medusae in coastal waters each year (see 3.3.4 *China*).

One of the few studies to evaluate the sustainability of a jellyfish fishery is presented by Asrial *et al.* (2015a) for Saleh Bay, Indonesia. A Gordon-Schaefer surplus production model was generated using catches and effort (number of scoop nets) since 2006. The authors determined that the maximum sustainable yield (MSY) for *Crambione mastigophora* in the region is 33,261 tonnes annually, with a maximum sustainable fishing effort (f_{MSY}) of 3,917 scoop nets and a corresponding catch per unit effort (CPUE) of 8.49 tonnes per net. Given that catches in the region have exceeded 30,000 tonnes since 2010 (Asrial *et al.* 2015a), the authors conclude that the jellyfish fishery in Saleh Bay is “fully exploited,” and effort is actually exceeding the sustainable level by 63%. As such, the authors recommend reducing the effort and catches in the region. Asrial *et al.* (2015a) also used a modified version of the RAPFISH technique (see Pitcher & Preikshot 2001) to evaluate the fishery based on a

number of bio-ecological, economic, technological, and social indicators. Their overall conclusion was that the jellyfish fishery can be classified as “quite sustainable,” which is neither the best nor worst possible ranking, and improvements could be made through management interventions.

While several jellyfish fisheries have a long history in Asia, those in the Western Hemisphere have only developed recently, with varying degrees of success. For example, jellyfish fisheries in the U.S.A. and Mexico have proven to be a boon for local fishers, whereas no market has yet developed for jellyfish from Argentina, Peru, or Canada. 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 1,400 species of jellyfish worldwide (Purcell 2012), but fewer than 40 of those have been documented as being consumed by humans (see 2.1.1 *Target species*). 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. While it is conceivable that consumption of scyphozoans 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 some countries – such as Canada and Peru – were not successful.

Secondly, attention must be paid to the processing of jellyfish. In order ensure economic success, specific details regarding the nuances of jellyfish processing should come from potential buyers, likely in Asia. As discussed, the method and materials used in the processing of jellyfish can vary greatly, so potential exporters need to work closely with buyers to deliver a suitable product. Jellyfish processing is typically labour intensive, so the time and effort required will have to be factored into the economics of any operation, especially in regions where labour costs are high. Jellyfish fisheries in the U.S.A. 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, the significant environmental and human health concerns regarding the contemporary use of processing chemicals needs to be addressed (see *5.1 Research priorities*). In addition, the development of alternative processing technologies could provide multiple benefits for jellyfish fisheries, including expansion beyond rhizostome species, reduction of costs, and the development of new markets.

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 meager, greatly limiting the advancement of research and development of management plans. 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 jellyfish fisheries. Fluctuations in market demand also present additional challenges, and it is clear that economic considerations will have to be added to the list of relevant concerns for jellyfish fisheries.

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. Indeed, the development of jellyfish fisheries for food and medicines has been proposed as a

possible strategy to deal with increasing jellyfish blooms (e.g., Purcell *et al.* 2007; Richardson *et al.* 2009). 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). Such an attitude can also serve to ignore the root causes of the problem. Increasing jellyfish blooms have been linked to numerous anthropogenic factors, such as overfishing, coastal development, shipping, global warming, and pollution (Purcell *et al.* 2007; Richardson *et al.* 2009; Duarte *et al.* 2013). If we simply adapt to a new normal instead of addressing and correcting the underlying causes, our baseline will shift (Pauly 1995), and ultimately, jellyfish may be the only seafood left. Even if a fishery for jellyfish can be developed, any stakeholders that end up profiting from such an endeavour will desire a sustained income, rather than seeing the resource eradicated, so we cannot simply fish away our jellyfish problems (Gibbons *et al.* 2016). 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.

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Appendix A – Reconstructed jellyfish landings by country, 1950-2013

Year	Total Est.	FAO	Aus.	Bahrain	Canada	China	Ecuador	Honduras	India	Indo.	Iran	Japan	Korea (S)
1950	216,887	300				215,487				300		1,000	
1951	218,287	1,700				215,487				1,700		1,000	
1952	218,487	1,900				215,487				1,900		1,000	
1953	218,487	1,900				215,487				1,900		1,000	
1954	218,687	2,100				215,487				2,100		1,000	
1955	218,687	2,100				215,487				2,100		1,000	
1956	218,787	2,200				215,487				2,200		1,000	
1957	218,687	2,100				215,487				2,100		1,000	
1958	311,567	2,200				308,267				2,200		1,000	
1959	248,620	2,100				245,420				2,100		1,000	
1960	392,274	2,100				389,073				2,100		1,000	
1961	102,667	2,800				98,767				2,800		1,000	
1962	183,573	2,900				179,573				2,900		1,000	
1963	99,873	3,000				95,773				3,000		1,000	
1964	138,880	3,100				134,680				3,100		1,000	
1965	178,187	3,500				173,587				3,500		1,000	
1966	367,040	3,800				362,140				3,800		1,000	
1967	145,367	3,600				140,667				3,600		1,000	
1968	85,707	3,800				80,807				3,800		1,000	
1969	267,003	4,200				260,380				4,200		1,000	
1970	348,804	59,100				337,333				6,000		1,000	
1971	118,137	24,500				106,667				6,000		1,000	
1972	121,681	24,600				110,667				5,300		1,000	
1973	476,771	129,900				388,000				4,800		1,000	
1974	152,901	24,900				147,120				432		1,000	
1975	127,316	26,985				114,060				5,507		1,000	
1976	73,401	36,763				34,207				8,886		1,000	
1977	203,187	95,619				77,687				8,886		9,500	
1978	132,212	68,158				24,293				7,440		18,000	
1979	174,244	70,314				86,447				5,744		10,000	
1980	72,025	12,249				59,920				5,896		311	
1981	173,321	52,561				119,773				12,352		311	

Year	Total Est.	FAO	Aus.	Bahrain	Canada	China	Ecuador	Honduras	India	Indo.	Iran	Japan	Korea (S)
1982	269,336	132,737				117,213				8,952		311	
1983	349,604	232,963				72,000				23,842		311	
1984	289,607	67,771			3	243,073			1,817	10,224		311	
1985	470,355	108,027				406,053			3,634	7,500		311	
1986	273,889	126,587				129,200			5,452	19,048		311	
1987	486,579	132,580				389,893			7,269	8,656		311	
1988	306,790	92,479				213,987			9,086	28,880		311	140
1989	335,909	103,662				232,960			10,903	22,672		311	
1990	338,358	75,219				261,160			12,720	7,668		311	4
1991	222,037	166,284				96,009			14,537	16,844		311	668
1992	424,700	353,838				228,459			16,355	10,440		311	204
1993	219,687	191,797				132,572			18,172	26,443		311	76
1994	292,694	213,221				113,354			19,989	16,152		311	128
1995	389,253	338,761	22			171,905			21,806	123,076		311	152
1996	398,827	326,850	22			265,325			23,623	17,080		311	244
1997	579,604	486,393	32			400,483			25,440	17,719		311	56
1998	604,281	464,423	23			430,784			27,258	8,176		311	60
1999	637,060	475,751	0			402,206			29,075	32,652		311	132
2000	794,493	467,512	0			459,869			30,892	29,516		311	100
2001	652,990	365,241	0			456,297			41,124	30,836		311	40
2002	720,782	344,815	5		1	413,113			164,756	60,096		311	32
2003	709,388	365,439	5			423,884			123,464	90,649		311	52
2004	546,825	190,933	5	1,300		330,716			123,464	18,396		311	16
2005	685,728	289,049	9	3,083		412,703			123,464	14,604		311	168
2006	778,676	345,424	1	362		356,692			109,281	8,172		311	24
2007	551,952	242,597	1	10,850		348,868			95,098	26,780		311	252
2008	782,385	396,402	14	1,354		361,626			80,915	6,800		311	68
2009	801,009	353,358	1	13,921		427,878			66,732	20,000		311	148
2010	688,383	271,474	1	329		326,322			52,549	30,519	7,918	311	172
2011	751,939	359,865	1	4,492		418,264			38,366	40,000	810	14,598	40
2012	868,181	332,950	2	58,767		543,126			24,183	32,115	1,625	13,958	2,400
2013	1,101,521	397,965	11	5,758		763,539		50	10,000	30,818	< 0.5	11,934	124

Year	Total Est.	FAO	Malay.	Mexico	Myan.	Nic.	Pakistan	Phil.	Russia	Sri Lanka	Thailand	Turkey	USA	Vietnam
1950	216,887	300	100											
1951	218,287	1,700	100											
1952	218,487	1,900	100											
1953	218,487	1,900	100											
1954	218,687	2,100	100											
1955	218,687	2,100	100											
1956	218,787	2,200	100											
1957	218,687	2,100	100											
1958	311,567	2,200	100											
1959	248,620	2,100	100											
1960	392,274	2,100	100											
1961	102,667	2,800	100											
1962	183,573	2,900	100											
1963	99,873	3,000	100											
1964	138,880	3,100	100											
1965	178,187	3,500	100											
1966	367,040	3,800	100											
1967	145,367	3,600	100											
1968	85,707	3,800	100											
1969	267,003	4,200	1,423											
1970	348,804	59,100	1,423								3,047			
1971	118,137	24,500	1,423								3,047			
1972	121,681	24,600	1,423								3,291			
1973	476,771	129,900	1,423								81,548			
1974	152,901	24,900	1,423								2,926			
1975	127,316	26,985	1,423								5,326			
1976	73,401	36,763	1,423					12			27,874			
1977	203,187	95,619	5,172					280			101,663			
1978	132,212	68,158	3,564					1,228			77,687			
1979	174,244	70,314	3,400								68,654			
1980	72,025	12,249	2,576					600			2,723			
1981	173,321	52,561	2,328					2,002			36,555			
1982	269,336	132,737	10,754					1,572			130,534			
1983	349,604	232,963	18,715					2,316			232,420			
1984	289,607	67,771	18,000					91			14,303	1,785		
1985	470,355	108,027	12,997					5			38,136	1,719		
1986	273,889	126,587	15,853					34		114	101,076	2,802		

Year	Total Est.	FAO	Malay.	Mexico	Myan.	Nic.	Pakistan	Phil.	Russia	Sri Lanka	Thailand	Turkey	USA	Vietnam
1987	486,579	132,580	25,737					88		228	54,394	3		
1988	306,790	92,479	27,195					55		342	24,974	1,821		
1989	335,909	103,662	42,036					86		457	25,311	1,173		
1990	338,358	75,219	20,530					64		571	34,222	1,109		
1991	222,037	166,284	12,094					1,956		685	78,933			
1992	424,700	353,838	15,623					2,404		799	149,542	564		
1993	219,687	191,797	16,293					1,012		913	23,114	781	1	
1994	292,694	213,221	10,138					600		1,027	130,159	814	23	
1995	389,253	338,761	7,692		1,812			2,496		1,141	52,263	487	90	6,000
1996	398,827	326,850	19,902		3,426			604		1,255	56,131	904		10,000
1997	579,604	486,393	53,811		1,412			112		1,370	67,559	900		10,400
1998	604,281	464,423	11,802		432			139		1,484	106,564	1,750	5,100	10,400
1999	637,060	475,751	7,182		1,000			2,660		1,598	139,541	1,203	5,100	14,400
2000	794,493	467,512	9,036		1,000			1,736	2,000	1,712	233,414	900	5,100	18,908
2001	652,990	365,241	10,299	1,200	1,100			1,860	346	1,826	77,091	2,000	5,100	23,560
2002	720,782	344,815	6,648	8,000	1,300			450		1,940	46,330	500	5,100	12,200
2003	709,388	365,439	5,863	1,600	1,500			40	44	2,054	27,927	4,000	5,100	22,896
2004	546,825	190,933	4,041	8,000	1,700			23	53	2,168	26,952	1,000	5,100	23,580
2005	685,728	289,049	5,285	13,048	1,976			1,472	67	2,283	55,420	544	5,100	46,192
2006	778,676	345,424	4,909	15,172	2,000			92	79	2,397	238,348	1,017	5,100	34,719
2007	551,952	242,597	4,068	2,000	2,200		2,114	116	105	2,511	14,081		5,100	37,497
2008	782,385	396,402	5,846	6,752	2,410	205	1,756	17	81	2,625	266,232		5,100	40,274
2009	801,009	353,358	4,013	10,389	2,710		1,118	17	237	2,625	202,757		5,100	43,052
2010	688,383	271,474	5,249	16,887	3,180		1,663	19	312	2,625	189,398		5,100	45,829
2011	751,939	359,865	3,738	16,755	3,420		1,663	15	671	2,625	152,774		5,100	48,607
2012	868,181	332,950	11,980	20,988	3,690		6,400	13	698	2,625	89,126		5,100	51,385
2013	1,101,521	397,965	11,745	21,253	3,935	660	6,400	9	622	2,625	172,776		5,100	54,162

Appendix B – Supporting publications

Several of the publications using material extracted from this dissertation contain supporting information that was not included herein. These publications are available for download from the following links:

Brotz, L., A. Schiariti, J. López-Martínez, J. Álvarez-Tello, Y.-H.P. Hsieh, R.P. Jones, J. Quiñones, Z. Dong, A.C. Morandini, M. Preciado, E. Laaz, & H. Mianzan *in press*. Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Reviews in Fish Biology and Fisheries*.

<http://link.springer.com/article/10.1007/s11160-016-9445-y>

Brotz, L. 2016. Jellyfish fisheries – a global assessment, pp. 110-124 *in* D. Pauly & D. Zeller (eds.) *Global Atlas of Marine Fisheries: A Critical Appraisal of Catches and Ecosystem Impacts*. Island Press, Washington, D.C., U.S.A.

<https://www.islandpress.org/book/global-atlas-of-marine-fisheries>

Gibbons, M.J., F. Boero, & L. Brotz 2016. We should not assume that fishing jellyfish will solve our jellyfish problem. *ICES Journal of Marine Science* 73(4): 1012-1018.

<http://icesjms.oxfordjournals.org/content/73/4/1012.full>