

ISSN 1198-6727



Fisheries Centre  
Research Reports  
*2011 Volume 19 Number 5*

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CHANGING JELLYFISH  
POPULATIONS:  
TRENDS IN LARGE MARINE  
ECOSYSTEMS

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Fisheries Centre, University of British Columbia, Canada

# CHANGING JELLYFISH POPULATIONS: TRENDS IN LARGE MARINE ECOSYSTEMS

by

Lucas Brotz

*Fisheries Centre Research Reports 19(5)*  
*105 pages © published 2011 by*

*The Fisheries Centre,  
University of British Columbia  
2202 Main Mall  
Vancouver, B.C., Canada, V6T 1Z4*

*ISSN 1198-6727*

Fisheries Centre Research Reports 19(5)  
2011

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*A Research Report from the Fisheries Centre at UBC*

*Fisheries Centre Research Reports 19(5)*  
*105 pages © Fisheries Centre, University of British Columbia, 2011*

FISHERIES CENTRE RESEARCH REPORTS ARE ABSTRACTED IN THE FAO AQUATIC SCIENCES AND FISHERIES ABSTRACTS (ASFA)  
 ISSN 1198-6727

## DIRECTOR'S FOREWORD

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This report, based on the Master's thesis of the author, represents the first analysis of jellyfish populations to supplement, in a rigorous fashion, scientific datasets with anecdotal observations. This allowed a global picture to emerge, the results of which confirm the previous disturbing suspicion that jellyfish populations are increasing in many coastal ecosystems around the world.

Jellyfish can have profound and costly impacts on human activities and marine ecosystems. For instance, it is reported that massive quantities of moon jellyfish (*Aurelia* sp.) and Nomura's giant jellyfish (*Nemopilema nomurai*) have been invading the coastal waters of the western and southern Korean peninsula more frequently in recent times, resulting in estimated economic damages for both the fisheries and aquaculture sectors in the country of USD 265 million per year (Young-Sang Suh, National Fisheries Research & Development Institute, Republic of Korea, pers. comm.). This, together with the possibility that humans may be responsible for some of the increases in jellyfish abundance, means that studies like this have important policy implications.

Jellyfish are understudied organisms, and this report does a decent job of estimating the recent population changes on a global scale, despite a scarcity of data. But the study also highlights the fact that there are vast areas of the planet where we know nothing about the jellyfish community. Looking at the results of this study, I would suggest that it is time researchers and policy-makers started paying more attention to these increasingly abundant creatures in the world's coastal waters.

U. Rashid Sumaila, Director

UBC Fisheries Centre



## ABSTRACT

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Although there are various indications and claims that jellyfish have been increasing at a global scale in recent decades, a rigorous demonstration to this effect has never been presented. As this is mainly due to the scarcity of quantitative time series of jellyfish abundance from scientific surveys, an attempt is presented here to complement such data with non-conventional information from other sources. This was accomplished using the analytical framework of fuzzy logic, which allows the combination of information with variable degrees of cardinality, reliability, and temporal and spatial coverage. Data were aggregated and analysed at the scale of Large Marine Ecosystem (LME). Of the 66 LMEs defined thus far, which cover the world's coastal waters and seas, trends of jellyfish abundance after 1950 (increasing, decreasing, or stable/variable) were identified for 45, with variable degrees of confidence. Of those 45 LMEs, the majority (28 or 62%) showed increasing trends. These changes are discussed in the context of possible sources of bias and uncertainty.

## INTRODUCTION

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### *Definition of ‘Jellyfish’*

Throughout this analysis, the term *jellyfish* (used interchangeably with *jellies*) refers to gelatinous zooplankton including medusae of the phylum Cnidaria (scyphomedusae, hydromedusae, cubomedusae, and siphonophores) and planktonic members of the phylum Ctenophora. Thaliaceans of the order Salpida – pelagic tunicates known as salps – will also be included due to their gelatinous nature, pulsed life cycles, and apparent response to changing oceanic conditions (Loeb *et al.* 1997; Atkinson *et al.* 2004; Lee *et al.* 2010). Pyrosomes and doliolids could arguably be included in such a definition of jellyfish as well. However, time series data on these organisms are especially sparse, and this dearth of information prevented their inclusion in the analysis.

Other gelatinous zooplankton such as appendicularians, mollusks, and chaetognaths are not included due to their different size, life history, ecological role, carbon-to-weight ratio, and the fact that they are generally not considered jellyfish (*e.g.*, definitions in Mianzan and Guerrero 2000; Graham and Bayha 2007; Richardson *et al.* 2009).

Pleustonic jellyfish, such those belonging to the genera *Physalia*, *Porpita*, and *Velella*, have also been excluded because their local distribution is heavily influenced by wind patterns (Mackie 1974). As such, locations reporting these species are frequently implicated in claims of “unprecedented” blooms and mass beach strandings lacking a historical context.

The term *jellyfish* will be used to refer to both single and multiple species. This is a common practice in the literature, as opposed to the less colloquial, but possibly more accurate *jellyfishes*. Combined, there are roughly 1500 species of pelagic cnidarians, ctenophores, and thaliaceans that have been described (Purcell *et al.* 2007), and likely thousands more that have yet to be discovered.

### *Problem Statement*

While many jellyfish populations fluctuate with climatic cycles (Purcell 2005), recent evidence suggests that jellyfish may also be synanthropic, *i.e.*, benefiting from human interactions with the oceans, and thus may be increasing globally (Mills 2001; Purcell *et al.* 2007; Pauly *et al.* 2009b; Richardson *et al.* 2009). However, a lack of long-term datasets in most ecosystems makes abundance trends uncertain, and the links with human impacts tend to be correlative or anecdotal. While previous global reviews of jellyfish populations (*e.g.*, Mills 2001; Purcell *et al.* 2007; Chudnow 2008) show evidence of numerous localized increases, the perceived global, or even widespread, increase in jellyfish still lacks a rigorous foundation. As such, the goal of this study will be to establish an analytical framework that will facilitate the comparison of trends in jellyfish populations around the globe in order to determine whether or not they are indeed changing, as well as the extent of any such changes. To compensate for the lack of available scientific datasets on jellyfish, this framework must be designed in such a way to include a wide variety of information that covers different temporal and spatial scales. In addition, this information will have variable degrees of reliability, and as such, the relative strength of any conclusions stemming from the analysis must be captured.



## *Challenges of Studying Jellyfish Populations*

Establishing abundance trends for jellyfish is difficult due to a number of factors. There is a dearth of historical information on jellyfish, as they were usually damaged or not recorded when caught in routine bottom-trawl or zooplankton surveys (Pugh 1989; Hay 2006). In fact, the latter often used gear designed to either exclude jellyfish from plankton samples (*e.g.*, Heinle 1965) or were based on methodologies which explicitly recommended their removal before analysis (*e.g.*, Dovel 1964; Burrell and van Engel 1970). For example, a classic manual on zooplankton sampling published by UNESCO (1968) mentions jellyfish only once, to dismiss them, *i.e.*, “Gelatinous organisms and other animals [...] will occur in the catches and these must be considered separately from the main sample.”

Moreover, jellyfish are difficult to sample even when targeted (Omori and Hamner 1982; Pierce 2009). As a result of their neglect in routine surveys and marine samples in general, jellyfish were perceived as a bothersome, but unimportant component of marine ecosystems (Pauly *et al.* 2009b), which then justified their further neglect. Despite recent advances in research and understanding of jellyfish ecology at local scales, such knowledge is rarely used to evaluate possible causes or consequences of jellyfish blooms at larger scales, or to make predictions (Purcell 2009).

Jellyfish are also understudied due to their peculiar life cycles, which can result in extremely high variability in abundance, peaking in the form of ‘blooms’ (Mills 2001; Purcell *et al.* 2007; Boero *et al.* 2008; Dawson and Hamner 2009; Hamner and Dawson 2009). All cubozoans, as well as many hydrozoans and scyphozoans have a bipartite life history, consisting of a sessile polyp phase and a planktonic medusa phase. Herein, many polyps reproduce asexually through the process of strobilation, producing multiple ephyrae which join the zooplankton community (Arai 1997) and rapidly grow to become medusae (Palomares and Pauly 2009). For some species, the polyps may asexually bud more polyps or form dormant cysts capable of resisting harsh environmental conditions (Arai 2009). These characteristic life history traits make jellyfish uniquely suited to high variability environments as they can survive when conditions are unfavourable and rapidly reproduce when conditions become favourable again (Boero *et al.* 2008; Richardson *et al.* 2009). Siphonophores, ctenophores, and salps lack a polyp phase, but can also reproduce rapidly under favourable conditions (Alldredge and Madin 1982; Purcell *et al.* 2007). Such varied reproductive strategies make it extremely difficult to assess jellyfish populations. Indeed, even if few surveys have been conducted to quantify medusa abundance, very little, if anything, is known about their polyps (Mills 2001).

Although jellyfish have become increasingly popular in public aquaria in recent years, most jellies are difficult to culture due to the fact that they will not survive in traditional fish tanks, but rather require different tank designs and equipment (Widmer 2008). As such, jellyfish have also been understudied in the laboratory.

The lack of jellyfish population datasets that cover large temporal and spatial scales limits the conclusions that can be drawn about jellyfish on a global scale. To compensate for this in the present analysis, methods were adopted and designed to allow for the inclusion of a wide variety of input types, including anecdotal data.

## *Impacts of Jellyfish Blooms*

In recent years, more attention is being paid to jellyfish, especially as they directly interfere with human activities (reviewed by Purcell *et al.* 2007; Richardson *et al.* 2009), *i.e.*, through: stings (beach closures, tourism impacts, injuries, deaths); clogging intakes (coastal power plants, mining operations, shipping, military operations, aquaria); interference with fishing (clogged and split nets, spoiled catch, stung

fishers, damaged gear, capsized boats); aquaculture (fish deaths, pens fouled by polyps); and marine biological surveys (*e.g.*, interference with trawls and acoustic surveys). Although such events are generally not included in the analysis (see Data Selection), they may result in untold millions of dollars in losses (*e.g.*, Graham *et al.* 2003; Kawahara *et al.* 2006; Anonymous 2007b). Preventative measures are also increasing, and threats from jellyfish stings have spawned the development of new products for prevention and treatment of envenomations, including swim nets ([www.nojellyfish.com](http://www.nojellyfish.com), Provenzano *et al.* 1983), stinger suits ([www.stingersuits.com](http://www.stingersuits.com)), post-sting gel ([www.stingmate.com](http://www.stingmate.com)), and first aid kits ([www.bodyquip.net/Jellyfish\\_Sting\\_jellyfix.html](http://www.bodyquip.net/Jellyfish_Sting_jellyfix.html)). A lotion combined with sunscreen to prevent jellyfish stings has also been developed ([www.buysafesea.com](http://www.buysafesea.com)) which has been shown to be effective for some species (Kimball *et al.* 2004; Boulware 2006) but not others (Burnett 2005).

Jellyfish can also have ecosystem impacts that are difficult to quantify, such as indirect effects on fisheries resources via: predation of zooplankton, predation on fish eggs and ichthyoplankton, and as a vector for parasites (reviewed by Purcell and Arai 2001). These effects may be dramatic, such as in the Black Sea, where intense competition by the invasive ctenophore *Mnemiopsis leidyi* has been blamed for the collapse of the anchovy (*Engraulis encrasicolus*) fishery (Kideys 1994), although overfishing is more likely (Niermann 2004). In fact, it was probably a combination of these two factors, neither of which are likely to be able to effect such a severe stock collapse individually (Oguz *et al.* 2008). In any case, mesozooplankton, ichthyoplankton, and fish eggs all declined following the *M. leidyi* blooms, and the collapse of the anchovy stocks affected higher trophic levels of the Black Sea food web (Shiganova *et al.* 2004a). Consumption rates support the notion that blooms of jellyfish may have massive predation potential, making them capable of collapsing entire zooplankton populations (Niermann 2004). Similar effects have also been observed in Kiel Bight, where mesozooplankton and larval herring abundance were reported to be significantly lower during years of high *Aurelia* abundance (Möller 1984; Schneider and Behrends 1994). Examples such as the Baltic and Black Seas illustrate that jellyfish blooms have the potential to modify the entire zooplankton community and trophic structure of ecosystems (Behrends and Schneider 1995; Purcell *et al.* 2001b; Shiganova *et al.* 2004a).

Predation effects due to large blooms of jellyfish can also ripple through multiple trophic levels, affecting primary production (*e.g.*, Pitt *et al.* 2007; Kideys *et al.* 2008) and microbial processes (*e.g.*, Hansson and Norrman 1995; Condon *et al.* 2011). The role of jellyfish blooms in biogeochemical cycles is uncertain, but may be very significant (*e.g.*, Billett *et al.* 2006; Condon *et al.* 2011). In addition, jellyfish are potentially good indicators of ecosystem and climatic changes (Hays *et al.* 2005; Hay 2006).

Despite recent alarm, jellyfish are a natural presence in healthy ecosystems and have been blooming for hundreds of millions of years (Hagadorn *et al.* 2002; Young and Hagadorn 2010). Jellyfish have many important ecological functions. Recent investigations and calculations demonstrate that jellyfish likely play an important role in the mixing of ocean layers (Katija and Dabiri 2009; Leshansky and Pismen 2010). In addition, jellyfish are food for more than 100 fish species, as well as dozens of species of sea birds, sea turtles, and parasitic amphipods (Pauly *et al.* 2009b). Medusae may also serve as a food source for benthic and even sessile animals, including adult crabs (Towanda and Thuesen 2006) and solitary corals (Alamaru *et al.* 2009). Jellyfish can also serve as refugia habitat for many species of fish (Purcell and Arai 2001), and may carry a variety of associated organisms. Such associations may be parasitic (amphipods), commensal (crabs and shrimp), or even mutualistic (crabs) (Towanda and Thuesen 2006). Dolphins have also been observed using jellyfish for several playful behaviours (*e.g.*, Turner 2009; Edwards 2011), presumably for skill development; however, such activities are not well understood. Regardless, it is clear that these relationships provide only a glimpse of the complex interactions between jellyfish and other fauna in the marine realm.

Some jellyfish also benefit humans, notably as food (Hsieh *et al.* 2001), and potentially for use in drugs (Sugahara *et al.* 2006; Ohta *et al.* 2009). Products derived from jellyfish have also been used for animal feed, fertilizers, cement additives, processed foods, and cosmetics. However, it can be a challenge to make these products economically viable, and the use of jellyfish for such purposes is still very small compared to the harvesting of jellyfish for direct human consumption. The discovery, isolation, and development of a fluorescent protein from jellyfish led to a revolution in biotechnology (Zimmer 2005) and a Nobel Prize (Coleman 2010). However, such proteins are now synthesized in the laboratory. A deeper investigation of jellyfish mechanics has also inspired the development of new medical devices (Anonymous 2010g) and has informed the design of more efficient underwater vehicles (Dabiri 2011), with possible applications for the U.S. Navy (Walter 2011). Unfortunately, it appears such benefits are minor compared to the direct and indirect negative consequences of jellyfish blooms.

### *Invasive Species*

Invasive species of jellyfish have been reported in numerous locations around the globe. In some cases, their presence has dramatic ecological and economic consequences. In addition, it is likely that far more invasions have occurred than have been documented due to incomplete treatment, unusual life histories, and species crypsis (Holland *et al.* 2004; Dawson *et al.* 2005; Graham and Bayha 2007). The unique life history of many jellyfish is important to their invasiveness in a variety of ways (Graham and Bayha 2007). Inconspicuous benthic stages make detection and monitoring of invasions difficult. Without prior detection, a large bloom of invasive jellyfish could appear suddenly, but may actually represent an established polyp colony. As well, invasions can occur through either ballast water (planulae, medusae) or hull fouling (polyps). Many jellyfish polyps and cysts are resistant to harsh conditions (Boero *et al.* 2008; Arai 2009) and may therefore have an increased chance of surviving transport to new ecosystems. The ability of numerous jellyfish to reproduce asexually suggests that a successful invasion could occur from a single benthic organism. Indeed, examples exist where representative samples taken from large blooms of invasive jellyfish are all the same sex (*e.g.*, Graham *et al.* 2003), potentially indicating just such an event. Invasive species of jellyfish will be identified and discussed throughout this analysis, which will help to illuminate the global extent of invasions.

## MATERIALS AND METHODS

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### *Large Marine Ecosystem Approach*

In order to examine and compare changes in jellyfish populations, data were stratified by *Large Marine Ecosystem* (LME). First introduced at the 1984 annual meeting of the American Association for the Advancement of Science (AAAS), the LME framework defines boundaries based on ecological criteria rather than economic or political criteria (Sherman and Hempel 2009). LMEs may extend from nearshore areas, including river basins and estuaries, out to the seaward boundaries of continental shelves or coastal currents (Sherman and Tang 1999). When defining the physical extent of the LME boundaries, four ecological parameters are considered, *i.e.*, bathymetry, hydrography, productivity, and trophic relationships. These ecological measures are highly inter-related and each LME is defined by a distinct combination of factors. LMEs can range from 150,000 km<sup>2</sup> to more than 5 million km<sup>2</sup>. To date, 66 LMEs have been described in terms of these parameters (see [www.seaaroundus.org](http://www.seaaroundus.org)). As the majority of recently reported changes in jellyfish populations around the globe occur in coastal waters or semi-enclosed seas (Mills 2001; Purcell *et al.* 2007), the LME framework provides a suitable stratification scheme for examining these changes.

### *1950 Baseline*

In order to examine changes in jellyfish populations, a baseline must be selected. For the purposes of this analysis, changes were only considered if they occurred after 1950, notably because this was the first year for which the newly founded Food and Agriculture Organization of the United Nations (FAO) published its annual compendium of global fisheries catches (which now include jellyfish), part of an effort by the United Nations to “quantify the world” (Ward *et al.* 2004). The past 60 years have also seen a dramatic increase in the global human population, along with concomitant impacts on marine environments around the globe (Halpern *et al.* 2008). In addition, many of the changes reported in jellyfish populations are from recent decades (Mills 2001; Purcell *et al.* 2007) and thus a 1950 baseline provides the contrast required for comparison and testing of such reports. Finally, many of the anthropogenic factors that have been suggested as causes of recent increases in jellyfish populations are quantifiable after 1950, notably because many are derived from FAO data (*e.g.*, Watson *et al.* 2004) and have been re-expressed at the LME scale (*e.g.*, Maranger *et al.* 2008; Pauly *et al.* 2009a).

### *The Jellyfish Chronicles*

The data used in this analysis were aggregated into *chronicles*. Each chronicle consists of one or more pieces of supporting evidence and has an associated *Abundance Trend* and *Confidence Index* (which is calculated from scores for spatial, temporal, and reliability components). These chronicles were aggregated by LME and then combined using rule sets and a fuzzy expert system to generate a *Jellyfish Index* for each LME. Details for all chronicles included in the analysis are found in Appendix A.

Multiple pieces of evidence covering similar temporal and spatial scales were included as one chronicle. Only data that referred to changes (or lack thereof) over several years or greater were included. Therefore, isolated references to “lots of jellyfish” or “more jellyfish than last year” would not qualify for inclusion due to low temporal coverage, whereas a reference to “more jellyfish in recent years” would be included. The same rationale applied for decreases, relatively stable populations, or those showing high variability.

Increasing or decreasing trends were reported to occur only if they were sustained. Thus, a population of jellies showing a prolonged increase followed by a similar decrease was classified as “stable/variable” (see Abundance Trend). Chronicles with no recent data (post-2000) were given a lower temporal score to reflect the uncertainty of whether the identified trend has continued or not (see Scoring Chronicles).

### *Data Selection*

While all direct commentary or measurements indicating changes (or lack thereof) in jellyfish populations over several years or more were included in the analysis, indirect evidence was not. Such indirect evidence includes impacts of jellyfish on human activities such as sting events, clogging of intake pipes for power generation, shipping or mining operations, as well as interference with aquaculture operations. Although changes in the frequency of these events may indicate changes in jellyfish populations (Purcell *et al.* 2007), they can also be a consequence of changes in sampling effort. For example, a jellyfish bloom that interferes with an industrial operation may actually represent a stable jellyfish population if the industrial operation is new to the region, rather than an actual increase in the jellyfish population (Mills 2004). Therefore, isolated interference events with industrial operations have been excluded from the analysis.

Individual events related to direct interference of fishing activities were also excluded. However, an exception was made for information that referred to the changing frequency of such events, as it is assumed to be a strong indication of a change in jellyfish abundance. For example, fishers in some locations reported catching an increasing amount of jellyfish bycatch over years or decades (*e.g.*, Uye and Ueta 2004). As fishers generally have a keen understanding of the marine environment, such statements are assumed to be reliable. In addition, it is unlikely that these fishers have dramatically increased their effort over these time frames. In fact, it is expected they would improve their ability to avoid catching jellyfish over time (*e.g.*, Kendall 1990; Matsushita and Honda 2006; Nagata *et al.* 2009), and therefore any increases in bycatch are likely the result of increased jellyfish populations.

As mentioned, sting data were generally not included in the analysis, as it is also problematic due to a number of factors. An increase in the number of people participating in marine activities can be assumed to increase encounter rates (Macrokanis *et al.* 2004). In addition, data showing an increase in sting events may simply be a reflection of increased reporting (Gershwin *et al.* 2010). As such, an increase in sting events may not necessarily represent an increase in the amount of jellyfish present. Conversely, awareness and education campaigns, as well as the use of jellyfish deterrents or countermeasures, can lead to a decrease in sting events without a concomitant reduction of the jellyfish population (Gershwin *et al.* 2010). Therefore, sting data has been excluded from the analysis, except where it may reveal temporal changes (*e.g.*, increase in the stinger season) or spatial changes (*e.g.*, increased distribution of jellyfish).

### *Abundance Trend*

Each chronicle was assigned an *Abundance Trend* of increasing (+1), decreasing (-1), or stable/variable (0). This was identified by considering changes of integrated biomass, which is affected by both abundance and presence. Therefore, increases (or decreases) in any of overall biomass, frequency of occurrence, or duration of occurrence were all considered to be indications of an increase (or decrease). As such, more frequent blooms, larger blooms, longer-lasting blooms, and range expansions (and their converses) are all included. When there was knowledge of multiple species over similar scales, the overall biomass of jellyfish within the ecosystem was considered. In addition, small, non-abundant hydromedusae were scored lower due to the fact that they are less likely to affect the overall biomass of jellyfish in the ecosystem.

Supporting evidence for each chronicle consisted of either qualitative or quantitative information. Chronicles with qualitative data as their primary source were classified based on the description of the jellyfish population in question (Table 1). For chronicles with quantitative records, such as multi-year datasets with values for relative abundance or biomass, a general linear regression analysis was performed. If the slope of the linear regression (abundance against time) was positive and significantly different from zero ( $p < 0.05$ ), the dataset was considered to represent an increase. Conversely, a significant negative slope constituted a decrease. If the slope of the linear regression was not statistically significant, the dataset was classified as stable/variable (for further discussion regarding the classification of trends, see Defining an ‘Increase’).

**Table 1.** Abundance Trend Rule Set.

Abundance Trend	Change	Definition
-1	Decrease	Decrease in overall biomass, relative abundance, frequency of occurrence or duration of occurrence
0	Stable/variable	Stable or no obvious trend
1	Increase	Increase in overall biomass, relative abundance, frequency of occurrence or duration of occurrence

### Scoring Chronicles

Each chronicle was scored according to a set of rules based on temporal coverage (*Time Score*, Table 2), spatial coverage (*Space Score*, Table 3), and reliability (*Reliability Score*, Table 4). Reliability for invasive species was scored differently (see Identifying Invasive Species). These scores were used as inputs for calculating the overall *Confidence Index* of each chronicle (see Fuzzy Expert System).

**Table 2.** Time Score Rule Set.

Time Score	Definition
Low	Multiyear trend <5 years; recent and unrepeated bloom that has not occurred previously; unclear timeframe; no recent data (post-2000)
Medium	Short tem (5-9 years)
High	Medium term (10-14 years)
Very high	Long term ( $\geq 15$ years)

**Table 3.** Space Score Rule Set.

Space Score	Definition
Low	Singular location or small region within LME (<200 km wide)
Medium	Large region or two disparate locations within LME (>200 km apart)
High	Three or more disparate locations within LME; wide-scale sampling in at least half of LME
Very high	Wide-scale sampling of LME

**Table 4.** Reliability Score Rule Set.

Reliability Score	Definition
Low	Lifeguard or NGO commentary; species unlikely to contribute significantly to biomass; high uncertainty; documented anthropogenic polyp habitat
Medium	Marine professional commentary ( <i>e.g.</i> , fisher)
High	Marine scientist commentary; synthesized knowledge; ‘bookend’ ( <i>i.e.</i> , non-continuous) scientific data
Very high	Scientific data of numerous or dominant species; well-documented frequency of blooms

## Identifying Invasive Species

Invasive species were considered to represent those that have been declared as non-indigenous by experts. The presence of invasive species of jellyfish was assumed to represent an increase in jellyfish biomass (*Abundance Trend* = 1). With this assumption, it is clearly important to understand if an invasive species is truly established, as some invaders can appear briefly in a particular area and may not be detected thereafter. Knowledge of such events was assumed to represent no change in a jellyfish population (*Abundance Trend* = 0), rather than an increase, as the excess biomass due to the invader presumably vanishes if the species is no longer detected. However, it should be noted that the possibility of repeated detection persists in these cases due to potential establishment by cryptic polyps or successive invasions, as is likely with *Phyllorhiza* sp. in the South Brazil Shelf LME (see LME #15).

The possibility also exists that invasive species of jellies could cause a reduction in native jellyfish biomass. However, no evidence of such an event was found, except possibly in the Mediterranean Sea (see LME #26). In the case of the Black Sea, where invasion by the ctenophore *Mnemiopsis leidyi* coincided with a decline of the native *Aurelia* population, there still appears to be a long-term increase in *Aurelia* abundance (see LME #62).

Chronicles that pertained to invasive species were scored similarly to other chronicles on the basis of time and space, but differently for reliability. The contribution to an increase in jellyfish biomass due to an invader was weighted by the *Invasive Reliability Score* in order to provide a more accurate estimate of the total change in jellyfish biomass (Table 5). The assumptions and weighting factors were designed with the intention of avoiding an overemphasis due to invasive species. Nonetheless, it should be noted that the invasive jellyfish accounted for in this review represent a conservative estimate, as it is likely that far more invasions have occurred than have been documented due to incomplete treatment, unusual life histories, and species crypsis (Holland *et al.* 2004; Dawson *et al.* 2005; Graham and Bayha 2007).

Invasive species were separated for analysis, allowing assessment of their contribution to the results. Consistent with the baseline selected for the analysis, species that invaded regions prior to 1950 were excluded.

**Table 5.** Invasive Reliability Score Rule Set.

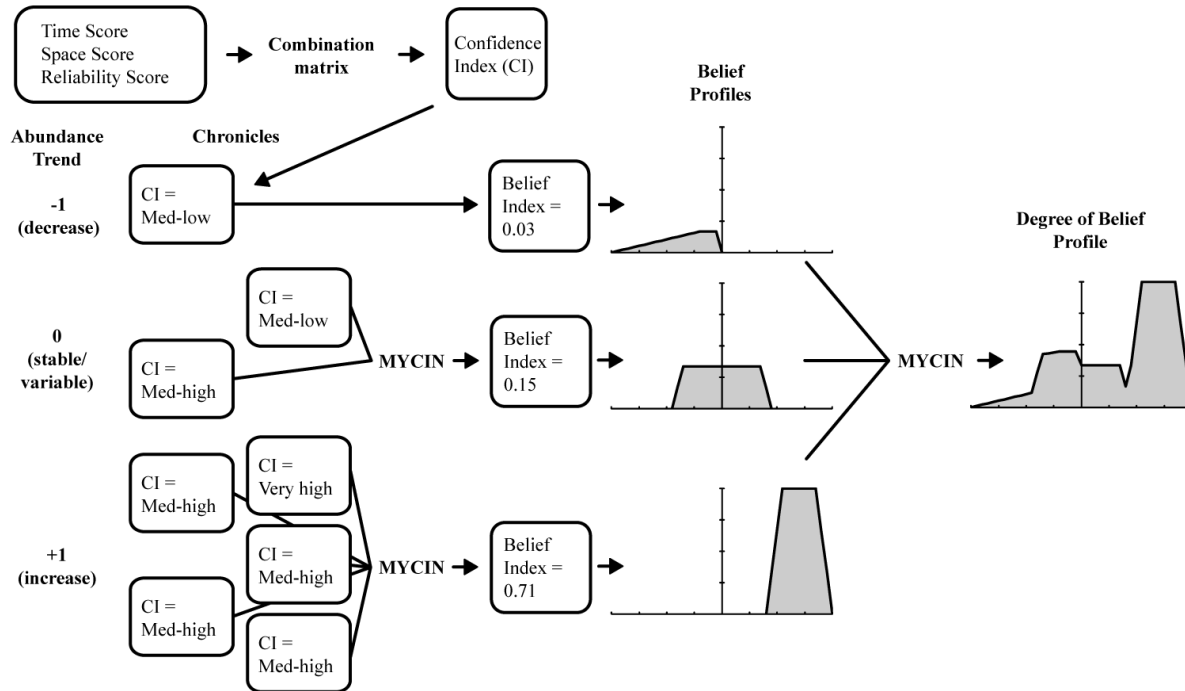
Reliability Score	Definition
Low	Uncertainty of invasiveness or species is unlikely to contribute significantly to biomass ( <i>e.g.</i> , small hydromedusae)
Medium	Documented invasive species or newly-blooming species (without knowledge of other species in ecosystem) or unsuccessful establishment <sup>a</sup>
High	Thriving invasive species
Very high	Known dominant species

<sup>a</sup> *Abundance Trend* = 1 in all invasive cases except for unsuccessful establishment (where *Abundance Trend* = 0 and *Invasive Reliability Score* = *Medium*)

## Fuzzy Expert System

Scores and chronicles were combined using a series of rule sets and fuzzy logic (see Figure 1 for a schematic diagram of the fuzzy expert system used in the analysis, using the North Sea LME as an example). Fuzzy set theory, originally developed by Zadeh (1965), is now firmly established in engineering and science (*e.g.*, Lee 1990; van der Werf and Zimmer 1998; Cheung *et al.* 2007). Fuzzy models are increasingly being used for ecological applications (Jørgensen 2008), and a review of such models in ecosystem studies is available in Adriaenssens *et al.* (2004). Fuzzy set theory allows the representation of variables according to a gradation or degree of membership, rather than the classic *true* and *false*

membership of conventional Boolean sets. In addition, fuzzy logic allows a conclusion to be reached with an associated gradation or degree of belief. As such, fuzzy set theory and logic provide an ideal system for combining information of variable cardinality and confidence.



**Figure 1.** Schematic diagram of the fuzzy expert system used in the analysis of jellyfish population trends by LME, with the North Sea LME represented as an example.

Variables with differing degrees of confidence were combined using the ‘MYCIN’ method, an asymptotic accumulation of the degree of belief, after Buchanan and Shortliffe (1984). This knowledge accumulation method is not affected by the order in which evidence is combined, and can be defined as:

$$\text{Degree of belief}_{n+1} = \text{Evidence}_n + [(1 - \text{Evidence}_n) * \text{Evidence}_{n+1}]$$

where Degree of belief<sub>n+1</sub> is the membership in the conclusion after combining the membership from Evidence<sub>n</sub> and Evidence<sub>n+1</sub>. The membership for any number of pieces of evidence can thus be combined to yield a final membership (i.e., degree of belief) in the conclusion.

The three scores for each jellyfish chronicle (*Time Score*, *Space Score*, and *Reliability Score*) were combined using a fuzzy rule set, or combination matrix, to yield a *Confidence Index* (Table 6). The combination matrix used treats all three scores equally, and therefore represents all possible combinations of scores. Thus, each chronicle has an associated *Abundance Trend* representing the direction of change for the jellyfish population in question, and a *Confidence Index* representing the degree of belief. For details for all chronicles included in the analysis, see Appendix A.



**Table 6.** Score Combination Matrix

Score A	Score B	Score C	Confidence Index
Low	Low	Low	Low
Low	Low	Medium	Low
Low	Low	High	Medium-low
Low	Low	Very high	Medium-low
Low	Medium	Medium	Medium-low
Low	Medium	High	Medium
Low	Medium	Very high	Medium
Low	High	High	Medium
Low	High	Very high	Medium-high
Low	Very high	Very high	Medium-high
Medium	Medium	Medium	Medium
Medium	Medium	High	Medium-high
Medium	Medium	Very high	Medium-high
Medium	High	High	Medium-high
Medium	High	Very high	High
Medium	Very high	Very high	High
High	High	High	High
High	High	Very high	High
High	Very high	Very high	Very high
Very high	Very high	Very high	Very high

Within each LME, chronicles that had the same *Abundance Trend* were combined to yield a *Belief Index*. This was derived by converting the *Confidence Indexes* for each chronicle into a membership (degree of belief) according to Table 7, and subsequently combining these memberships using MYCIN.

**Table 7.** Membership Rule Set.

Confidence Index	Degree of Belief (per chronicle)
Low	0.0156
Medium-low	0.0313
Medium	0.0625
Medium-high	0.1250
High	0.2500
Very high	0.5000

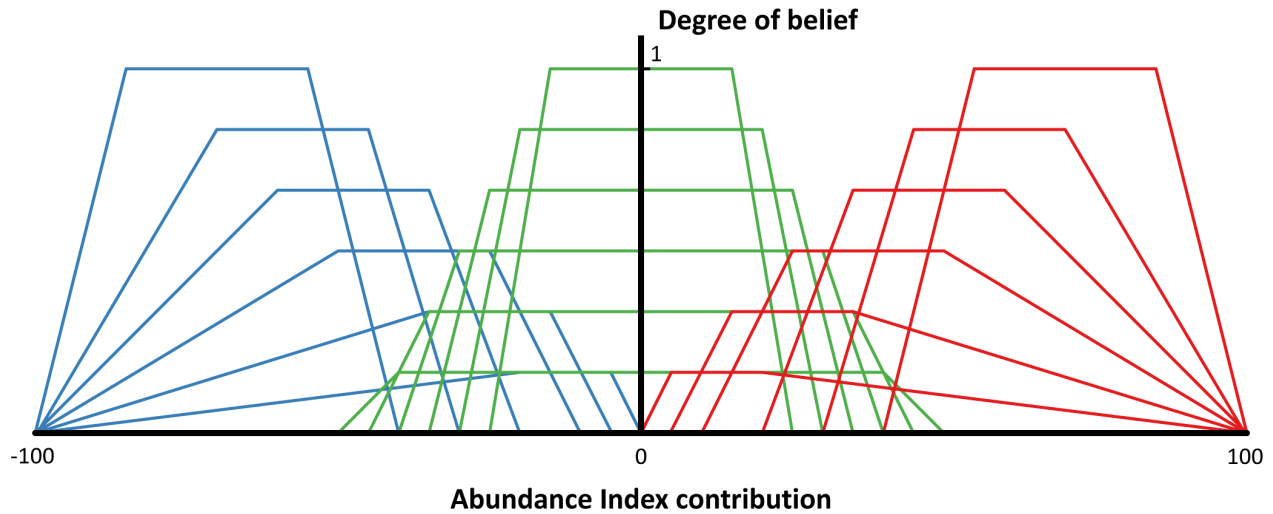
The resulting *Belief Indexes* for each *Abundance Trend* were used to select an appropriate *Belief Profile* according to Table 8.

**Table 8.** Belief Profile Selection Rule Set.

Belief Index	Belief Profile
0	None
0.01 – 0.09	Low
0.10 – 0.19	Medium-low
0.2 – 0.34	Medium
0.35 – 0.49	Medium-high
0.60 – 1	Very high

The *Belief Profiles* used in the fuzzy expert system are membership functions designed to represent the degree of belief over a continuous scale of -100 to +100, with negative scores representing declining jellyfish populations and positive scores representing increasing populations (Figure 2). These asymmetrical *Belief Profiles* therefore provide a representation of the accumulated evidence for each particular trend, including both the quantity and the relative certainty of the evidence. Within each LME,

one profile was selected for each *Abundance Trend*, as long as there was supporting evidence (*i.e.*, *Belief Index* > 0). Thus, an LME could have 1, 2, or 3 profiles as inputs for the fuzzy expert system, depending on whether or not there were chronicles supporting each *Abundance Trend*.



**Figure 2.** Belief Profiles used for inputs in the fuzzy expert system (*blue*=decrease, *green*=stable/variable, *red*=increase).

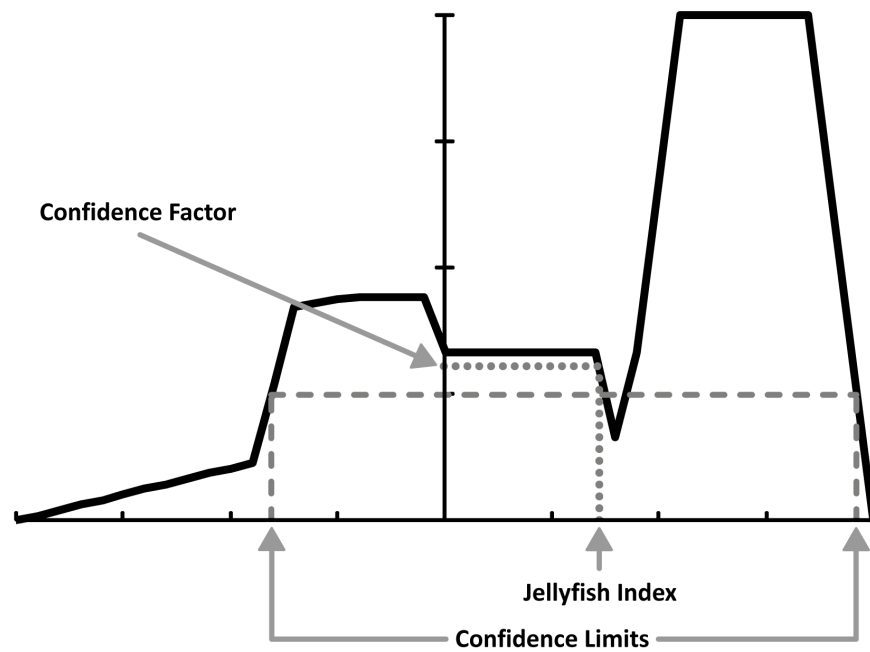
The *Belief Profiles* were combined using the MYCIN method to yield a final *Degree of Belief Profile* for each LME. This profile contains information about the evidence within each LME over all *Abundance Trends*. To calculate a final *Jellyfish Index*, the centroid-weighted method (Cox 1999) was used to ‘defuzzify’ the final profile (Figure 3).

### Uncertainty

The confidence in the *Jellyfish Index* was quantified by the degree of belief at the centroid value (the *Confidence Factor*) and the associated values at *Degree of Belief* = 0.25 (the *Confidence Limits*). The difference between the *Confidence Limits* is defined as the *Confidence Interval* (Figure 3). If a particular profile did not reach a *Degree of Belief* = 0.25 due to lack of evidence (*e.g.*, Gulf of California LME), the upper and lower limits of the confidence interval were selected where the degree of belief falls to zero. Using these two measures of uncertainty (the *Confidence Factor* and the *Confidence Interval*) provides information about both the strength of the data within an LME and how consistent the observed trend is (if any). In a sense, these can be interpreted similar to measures of ‘accuracy’ and ‘precision’. That is to say, a high *Confidence Factor* represents a robust conclusion, and hence can be interpreted as accurate. Similarly, a small *Confidence Interval* would indicate that the chronicles included in a particular LME exhibit similar trends, and are therefore precise. The combination of these two measures ultimately defines the overall confidence in the *Jellyfish Index* for each LME, and thus a *Confidence Quotient* is defined, equal to the *Confidence Factor* divided by the *Confidence Interval*. Conclusions with a *Confidence Quotient* > 1 were classified as *high certainty*, while those with a *Confidence Quotient* < 1 were classified as *low certainty*.

Based on the *Belief Profiles* used in the analysis (Figure 2), *Jellyfish Indexes* could range from a minimum of -70 to a maximum of +70. LMEs with a *Jellyfish Index* of greater than +10 were classified as increases, while those with a *Jellyfish Index* less than -10 were classified as decreases. LMEs with a *Jellyfish Index*

between -10 and +10 were classified as stable/variable, indicating they did not show an increasing or decreasing trend. These thresholds were chosen in order to ensure there was sufficient evidence to suggest a trend.



**Figure 3.** Degree of Belief Profile for the North Sea LME.

## RESULTS

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A total of 138 chronicles were included in the analysis, distributed unevenly over 45 LMEs. Of the 45 LMEs, 28 (62%) showed increasing trends, while only 3 (7%) showed decreasing trends. The remaining 14 LMEs (31%) were classified as stable/variable, showing neither increasing nor decreasing trends (Figure 4).

Out of the 28 LMEs exhibiting increases, 10 were classified as high certainty (*Confidence Quotient* > 1), and 18 were classified as low certainty (*Confidence Quotient* < 1). Of the 14 LMEs with stable/variable trends, 4 were of high certainty and 10 were of low certainty. The Humboldt Current LME was the only system to exhibit a decrease associated with a high certainty.

The results are similar when normalized by area. Accounting for the size of the LMEs, 21% of the total area included represented regions with increases of high certainty, while increases of low certainty represented 45%. Stable/variable regions represented 28% of the total area included, while the remaining 6% was associated with decreases.

Results for all LMEs, including invasive species and excluding overfishing of jellyfish are shown in Table 9, and a map of the results is presented in Figure 4. The *Belief Indexes* used for each LME in the analysis are included in Appendix B. When examined separately, these *Belief Indexes* illustrate the degree of evidence for chronicles based on native species compared to those based on invasive species, as well as those representing overharvesting of jellyfish.

### *Effects of Invasive Species*

Invasive species were separated from the analysis in order to examine their impact on the results (for results with native species only, see Table 10). Invasive species of jellyfish were reported in 21 LMEs. In eight of those LMEs, the inclusion of invasive species had a negligible contribution to the results, and did not affect the *Jellyfish Index*.

By contrast, the inclusion of invasive species can be considered responsible for the conclusion of low certainty increases in four LMEs (Gulf of Mexico, Southeast U.S. Continental Shelf, Caribbean Sea, and Baltic Sea), as the exclusion of invaders changed the classification of these LMEs from increasing to stable/variable. Similarly, invaders can be considered responsible for the low certainty increase reported in the East Brazil Shelf LME, as there were no data for native species. The Insular Pacific-Hawaiian LME exhibited an increase due to native species; however, the inclusion of invasive species increased the certainty of the conclusion to high. In the remaining LMEs, the inclusion of invasive species increased the *Jellyfish Index* by variable amounts, but did not alter the conclusions.

Several invasive species of jellyfish from disparate taxonomic groups were reported in numerous locations, including scyphozoans *Aurelia* spp. and *Phyllorhiza punctata*; hydrozoans *Blackfordia virginica*, *Maeotias marginata*, and *Turritopsis* spp.; as well as the infamous ctenophore *Mnemiopsis leidyi*.

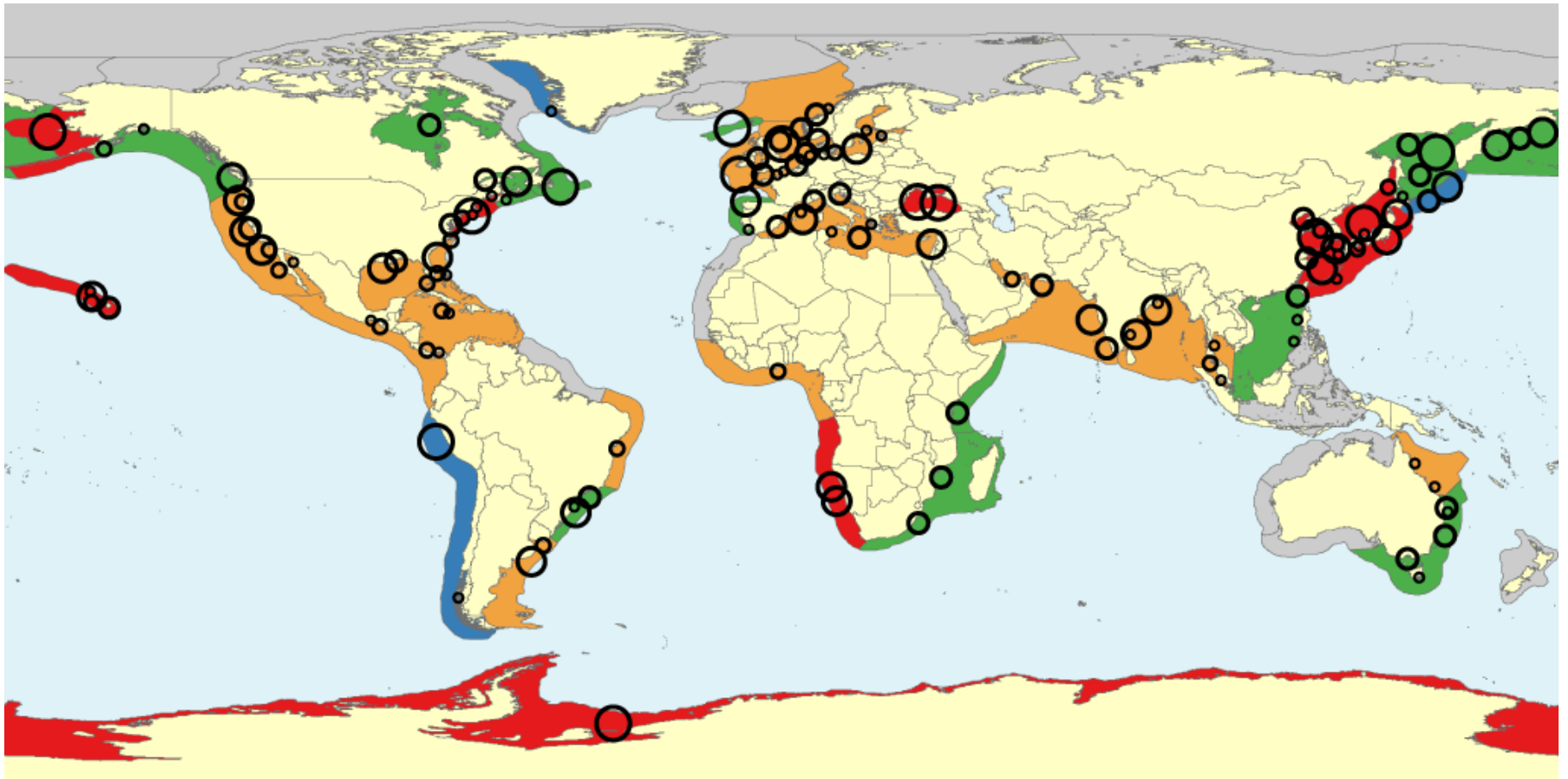
### *Effects of Jellyfish Overexploitation*

Interestingly, several of the chronicles that were classified as decreases in the analysis (*Abundance Trend* = -1) concerned jellyfish species that have been harvested for food, science, or unique proteins, and have

subsequently declined, possibly as a result of overfishing. However, only four chronicles had a primary source of evidence that directly attributed a decrease to overexploitation. As such, these chronicles were treated separately in the analysis (Table 11). In the Arabian Sea LME, the inclusion of overfishing of jellies reduced the *Jellyfish Index* sufficiently to alter the trend conclusion from increasing to stable/variable (both conclusions of low certainty). Including of overfishing of jellyfish for the Bay of Bengal LME resulted in no change to the *Jellyfish Index*. The South China Sea and East Central Australian Shelf LMEs showed a reduced *Jellyfish Index* when overfishing of jellies was included; however, this reduction was not sufficient enough to classify these LMEs as decreases, and are therefore still classified as stable/variable (*Abundance Trend* = 0). Thus, it can be said that in the majority of locations where overfishing of jellyfish could be identified, it did not alter the conclusions of the analysis.

**Table 9.** Results of analysis of jellyfish population trends by LME including both native and invasive species.

LME ID	LME Name	Trend Conclusion	Conclusion Certainty	Jellyfish Index	Confidence Quotient	Confidence Factor	Lower Limit	Upper Limit	Interval
1	East Bering Sea	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50
2	Gulf of Alaska	Stable/variable	Low	7.06	0.80	0.58	-35.00	37.24	72.24
3	California Current	Increase	Low	25.55	0.63	0.73	-31.25	85.00	116.25
4	Gulf of California	Increase	Low	35.87	0.13	0.13	0.00	100.00	100.00
5	Gulf of Mexico	Increase	Low	14.13	0.75	0.65	-35.00	51.25	86.25
6	Southeast US Continental Shelf	Increase	Low	14.13	0.75	0.65	-35.00	51.25	86.25
7	Northeast US Continental Shelf	Increase	High	52.52	1.58	0.83	43.75	96.25	52.50
8	Scotian Shelf	Stable/variable	High	0.00	1.07	0.67	-31.25	31.25	62.50
9	Newfoundland-Labrador Shelf	Stable/variable	High	0.00	1.54	0.83	-27.00	27.00	54.00
10	Insular Pacific-Hawaiian	Increase	High	54.84	1.13	0.67	25.63	85.00	59.37
11	Pacific Central-American Coastal	Increase	Low	41.74	0.77	0.30	12.50	51.25	38.75
12	Caribbean Sea	Increase	Low	13.60	0.81	0.31	3.00	41.26	38.26
13	Humboldt Current	Decrease	High	-42.80	1.26	0.71	-91.00	-34.50	56.50
14	Patagonian Shelf	Increase	Low	47.90	0.87	0.50	17.50	75.00	57.50
15	South Brazil Shelf	Stable/variable	Low	7.06	0.80	0.58	-35.00	37.24	72.24
16	East Brazil Shelf	Increase	Low	35.87	0.13	0.13	0.00	100.00	100.00
18	West Greenland Shelf	Decrease	Low	-35.87	0.13	0.13	-100.00	0.00	100.00
21	Norwegian Sea	Increase	Low	41.74	0.70	0.27	12.50	51.25	38.75
22	North Sea	Increase	Low	35.89	0.22	0.30	-40.67	96.25	136.92
23	Baltic Sea	Increase	Low	14.13	0.75	0.65	-35.00	51.25	86.25
24	Celtic-Biscay Shelf	Increase	Low	36.94	0.44	0.56	-37.50	91.00	128.50
25	Iberian Coastal	Stable/variable	Low	7.06	0.80	0.58	-35.00	37.24	72.24
26	Mediterranean Sea	Increase	Low	43.95	0.22	0.30	-37.50	96.25	133.75
28	Guinea Current	Increase	Low	35.87	0.13	0.13	0.00	100.00	100.00
29	Benguela Current	Increase	High	54.84	1.15	0.67	26.63	85.00	58.37
30	Agulhas Current	Stable/variable	Low	0.00	0.71	0.50	-35.00	35.00	70.00
31	Somali Coastal Current	Stable/variable	Low	0.00	0.44	0.33	-37.50	37.50	75.00
32	Arabian Sea	Increase	Low	14.13	0.75	0.65	-35.00	51.25	86.25
34	Bay of Bengal	Increase	Low	14.57	0.52	0.58	-37.24	75.00	112.24
35	Gulf of Thailand	Increase	Low	35.87	0.13	0.13	0.00	100.00	100.00
36	South China Sea	Stable/variable	Low	8.86	0.56	0.44	-37.50	40.67	78.17
40	Northeast Australian Shelf	Increase	Low	35.87	0.13	0.13	0.00	100.00	100.00
41	East Central Australian Shelf	Stable/variable	Low	0.00	0.71	0.50	-35.00	35.00	70.00
42	Southeast Australian Shelf	Stable/variable	Low	8.86	0.56	0.44	-37.50	40.67	78.17
47	East China Sea	Increase	High	70.00	1.90	1.00	43.75	96.25	52.50
48	Yellow Sea	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50
49	Kuroshio Current	Increase	High	35.34	1.13	0.67	25.63	85.00	59.37
50	Sea of Japan	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50
51	Oyashio Current	Decrease	Low	-14.13	0.75	0.65	-51.25	35.00	86.25
52	Sea of Okhotsk	Stable/variable	High	6.25	1.55	0.86	-27.00	28.56	55.56
53	West Bering Sea	Stable/variable	Low	-7.49	0.40	0.50	-75.00	51.25	125.25
60	Faroe Plateau	Stable/variable	High	0.00	1.54	0.83	-27.00	27.00	54.00
61	Antarctic	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50
62	Black Sea	Increase	High	70.00	1.90	1.00	43.75	96.25	52.50
63	Hudson Bay	Stable/variable	Low	0.00	0.44	0.33	-37.50	37.50	75.00



**Figure 4.** Map of population trends of native and invasive species of jellyfish by LME. *Red* = increase (high certainty); *orange* = increase (low certainty); *green* = stable/variable; *blue* = decrease, *grey* = no data. Circles represent discrete chronicles with relative sizes reflecting the *Confidence Index*. Circle locations are approximate, as some were shifted to avoid overlap; the circle for the Antarctic LME summarizes circumpolar observations.

**Table 10.** Results of analysis of jellyfish population trends by LME including native species only (effects of invasive species excluded; only those LMEs that had invasive species are shown).

LME ID	LME Name	Trend Conclusion	Conclusion Certainty	Jellyfish Index	Confidence Quotient	Confidence Factor	Lower Limit	Upper Limit	Interval
3	California Current	Increase	Low	19.82	0.73	0.78	-31.25	75.00	106.25
5	Gulf of Mexico	Stable/variable	Low	7.06	0.80	0.58	-35.00	37.24	72.24
6	Southeast US Continental Shelf	Stable/variable	Low	7.06	0.80	0.58	-35.00	37.24	72.24
7	Northeast US Continental Shelf	Increase	High	52.52	1.58	0.83	43.75	96.25	52.50
10	Insular Pacific-Hawaiian	Increase	Low	47.90	0.87	0.50	17.50	75.00	57.50
11	Pacific Central-American Coastal	Increase	Low	35.87	0.09	0.09	0.00	100.00	100.00
12	Caribbean Sea	Stable/variable	Low	0.00	0.17	0.17	-50.00	50.00	100.00
13	Humboldt Current	Decrease	High	-61.84	1.47	0.83	-91.00	-34.50	56.50
14	Patagonian Shelf	Increase	Low	47.90	0.87	0.50	17.50	75.00	57.50
15	South Brazil Shelf	Stable/variable	Low	0.00	0.71	0.50	-35.00	35.00	70.00
16	East Brazil Shelf	No data							
21	Norwegian Sea	Increase	Low	41.74	0.70	0.27	12.50	51.25	38.75
22	North Sea	Increase	Low	35.89	0.22	0.30	-40.67	96.25	136.92
23	Baltic Sea	Stable/variable	Low	0.00	0.71	0.50	-35.00	35.00	70.00
25	Iberian Coastal	Stable/variable	Low	0.00	0.71	0.50	-35.00	35.00	70.00
26	Mediterranean Sea	Increase	Low	31.02	0.54	0.66	-37.50	85.00	122.50
42	Southeast Australian Shelf	Stable/variable	Low	8.86	0.56	0.44	-37.50	40.67	78.17
47	East China Sea	Increase	High	70.00	1.90	1.00	43.75	96.25	52.50
48	Yellow Sea	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50
49	Kuroshio Current	Increase	High	35.34	1.13	0.67	25.63	85.00	59.37
62	Black Sea	Increase	High	61.84	1.47	0.83	34.50	91.00	56.50

**Table 11.** Results of analysis of jellyfish population trends by LME with effects of jellyfish overfishing added (only those LMEs with jellyfish overharvesting are shown).

LME ID	LME Name	Trend Conclusion	Conclusion Certainty	Jellyfish Index	Confidence Quotient	Confidence Factor	Lower Limit	Upper Limit	Interval
32	Arabian Sea	Stable/variable	Low	7.19	0.61	0.54	-37.24	51.25	88.49
34	Bay of Bengal	Increase	Low	14.57	0.52	0.58	-37.24	75.00	112.24
36	South China Sea	Stable/variable	Low	0.00	0.41	0.33	-40.67	40.67	81.34
41	East Central Australian Shelf	Stable/variable	Low	-7.06	0.69	0.50	-37.24	35.00	72.24



## DISCUSSION

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This study represents the first rigorous demonstration that jellyfish populations appear to be increasing in coastal ecosystems worldwide, as previously suggested (Mills 2001; Purcell *et al.* 2007; Pauly *et al.* 2009b; Richardson *et al.* 2009). Of the 45 LMEs included in the analysis, 28 (62%) showed increasing trends, while only 3 (7%) showed decreasing trends. The remaining 14 LMEs (31%) were classified as stable/variable, with no obvious trend. These results suggest that while increases of jellyfish populations are not universal, they are both numerous and widespread. Regarding the 21 LMEs that were not included, most were from the Arctic (11), Australia (4), and the South Pacific (3). Therefore, the results represent extensive spatial coverage of the world's coastal ecosystems. While only 33% of the conclusions are of high certainty, the majority of those (10 of 15) were in LMEs that showed increasing trends. In addition to demonstrating that jellyfish populations are increasing in numerous ecosystems around the world, this also underscores the fact that information on jellyfish abundance is poor over much of the globe. Thus, we must strive to learn more about these fascinating and important creatures, especially given the fact that they seem to be one of the few groups of organisms that appear to be benefiting from the continued anthropogenic impacts on the world's biosphere.

### *Defining an 'Increase'*

Information used in the analysis was weighted by time, space, and reliability in order to reflect the relative contribution to a change in jellyfish populations within each LME. As a consequence of the methods used and the inclusion of anecdotal data, the results reflect the degree of belief that any particular jellyfish population has changed or not, rather than the magnitude of those changes. Therefore, observations of 'more' jellyfish may not necessarily mean there are truly 'more jellyfish' if the observations are not normalized by effort. Nonetheless, it is expected that these factors are correlated, as changes of larger magnitude are assumed to be more noticeable and thus have more supporting evidence. Only after accepting this assumption should this analysis be considered to reflect real 'increases' and 'decreases'.

Jellyfish populations are extremely variable on both temporal and spatial scales due to their peculiar ecology (see Challenges of Studying Jellyfish Populations). Thus, even LMEs showing pronounced increases in jellyfish populations with 'high certainty' may also experience dramatic declines over short timescales. For example, the trend in the East Bering Sea LME is classified as an increase due to the results of a regression analysis, but jellyfish in the Bering Sea declined dramatically after 2000 (Brodeur *et al.* 2008b). Despite this decline, jellyfish abundance in this LME appears sustained above the levels observed in the 1980s, and the increase remains significant (see LME #1 – East Bering Sea). Other long-term studies also show high variability, such as the 37-year dataset from Peru (Quiñones *et al.* 2010b). Jellyfish populations in that system appear tightly correlated with El Niño events; however, the data appear to exhibit a decline (see LME #13 – Humboldt Current). Even the well-documented increase in blooms of the giant jellyfish (*Nemopilema nomurai*) in East Asia is not persistent, as blooms do not occur every year (Uye *et al.* 2010). With these cyclical patterns of jellyfish populations, trends may turn out to be ephemeral, and an apparent long-term pattern may collapse with updated data. An example is the population of cannonball jellyfish (*Stomolophus meleagris*) in the southeastern United States, which appeared to show a decline over the last decade, but then rebounded strongly in recent years (see LME #6 – Southeast U.S. Continental Shelf). Clearly then, increases or decreases may actually represent a trend during only part of a cycle, and may reverse over a longer timeframe.

With such high variability, poor sampling frequency in either the past or present could dramatically affect the detection of true trends. To account for these concerns, attempts were made to ensure chronicles used

in the analysis were up to date wherever possible, thus reflecting changes to present day. As well, all chronicles were scored based on the time-span covered, and therefore information covering longer timescales had more influence on the results. On the contrary, those chronicles without up-to-date information were also given the lowest possible temporal score. Nonetheless, datasets of jellyfish abundance spanning multiple decades are sparse, and therefore the results only represent a rough estimate of true jellyfish population dynamics.

The fact that jellyfish are typically part of the zooplankton makes them vulnerable to changes in oceanic current patterns. The presence or absence of a bloom may be simply due to relocation, and thus an increase observed in one location may be concomitant with a decrease in another location. If the increase is observed but the decrease is not, one comes to the false conclusion that jellyfish have increased. Whenever there was evidence of such an explanation, the chronicle was not included. An example is a recent quote from of a fisher in Florida who said he was seeing more sea nettles (*Chrysaora* sp.) than in the preceding decades. However, it is possible that this was due to the relocation of a population that is normally observed elsewhere in the Gulf of Mexico (Spinner 2010). Even without knowledge of such events, the analysis is not overly sensitive to this pitfall, because only multi-year data from the same location were used. As chronicles were either up-to-date or scored with low reliability, increases due to spatial redistributions would have to be sustained. In addition, chronicles based on information over short time periods or from single locations were also scored lower, thereby minimizing the effect on the results.

There is also the possibility of a reporting bias, whereby newsworthy blooms or increases in jellyfish are reported, but absences and stable or declining populations are not. While this understandable bias is likely to overestimate increases, the methods used in this analysis were designed to minimize this effect. Episodic blooms were not included unless a temporal component of at least several years could be identified. In addition, as mentioned, these temporal components were scored based on their relative duration, ensuring that information covering longer time-spans had more influence on the results than information that spanned less than a decade. Interference events with human activities, which are typically newsworthy, also were not included unless the information was in a clear historical context (see Data Selection). Finally, all information was up to date wherever possible, ensuring any apparent trends were sustained. If updated and recent material could not be found, the chronicle in question was scored lower and therefore had less influence on the results. Finally, much of the anecdotal information used in the analysis was gleaned from targeted interviews. As numerous responses in these interviews indicated stable populations, they are assumed to represent a relatively unbiased source of information where scientific data are lacking.

### *Species Invasions*

Invasive species of jellyfish were reported in 21 of 45 LMEs found in this analysis (47% of the systems included). If uncertain and less significant invasions are also included, the number of LMEs with invasive species rises to 24 (53%). For the most part, invasive species were not responsible for the observed increases reflected in the results. However, the widespread detections demonstrate that jellyfish are truly global invaders of significant concern. Thriving populations of invasive jellyfish in systems like the Mediterranean and Black Seas should serve as warnings for other ecosystems around the globe, and it is likely that far more invasions have occurred than are reported (see Invasive Species).

## *Taxonomic Concerns*

The term ‘jellyfish’, according to the definition used here (see Definition of ‘Jellyfish’), refers to specimens from several phyla (Cnidaria, Ctenophora, and Chordata). Such organisms are obviously extremely distant phylogenetic relatives; therefore, grouping them under an umbrella term such as ‘jellyfish’ is problematic. First, the use of such an idiom ignores taxonomy. The changes evident in the results of this analysis should not only be viewed in their entirety, but also in the context of ecology and evolution. Without proper taxonomic resolution, a deeper and more meaningful understanding of the mechanisms and consequences involved may be unattainable (Haddock 2004). Second, using a broad category also runs the risk of inferring attributes of a larger group of organisms based only on a handful of species. Such ‘errors of commission’ (Dawson 2010) could inhibit robust conclusions if they are not made in the light of evolution. Generalizations concerning such a broad group of organisms will certainly have exceptions (Bayha and Dawson 2010), and we must be careful not to ignore these differences by focusing only on commonalities.

Despite these concerns, there is also value in generalized results. Notwithstanding their phylogenetic diversity, jellyfish share many similarities. As demonstrated in this analysis, one such similarity is a recent trend of increasing abundance. As such, raising awareness of the issues and developing a deeper understanding of the mechanisms involved should be priorities. Wherever possible, jellyfish included in this analysis were identified to species. Hopefully, this will facilitate analysis and discussion from both specific and general perspectives.

### *LME #1 – East Bering Sea<sup>1</sup>*

Knowledge of jellyfish abundance in this LME is unique due to a long-term dataset from the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (Brodeur *et al.* 1999; Brodeur *et al.* 2002; Brodeur *et al.* 2008a). This time series consists of bottom-trawl surveys beginning in 1975, with continuous annual measurements since 1979. Data were collected for 356 stations each summer, producing total biomass estimates for six geographic regions. Jellyfish were not identified to species for most of the record. However, recent taxonomic survey data suggest the biomass is primarily composed of *Chrysaora melanaster*, which is indigenous to the Bering Sea (Brodeur *et al.* 2002; Brodeur *et al.* 2008a). During the day, this species is found within a narrow depth range of 30-40 m (Brodeur 1998; Brodeur *et al.* 2002), suggesting that bottom-trawls would only catch jellyfish during deployment and retrieval. As such, this sampling method vastly underestimates the number of jellyfish present and does not allow for the calculation of estimates of absolute biomass. However, as sampling has been consistent throughout most of the study, the record does provide an index of relative abundance for which trends can be identified (Brodeur *et al.* 2002; Brodeur *et al.* 2008a).

The Bering Sea time series shows a dramatic increase in jellyfish biomass throughout the 1990s with a peak in 2000, followed by a sharp decline (Brodeur *et al.* 2008a). Between 2001 and 2009, the population was variable but appeared to somewhat stabilize at levels below those of the 1990s, but above those of the 1970s and ‘80s. However, 2009 showed another increase to levels comparable to the mid-1990s (Decker *et al.* 2009). Linear regression over the entire dataset shows a significant increase ( $R^2 = 0.23$ ,  $p = 0.006$ ), indicating a variable but sustained long-term increase in jellyfish abundance in this LME since the 1970s.

The onset of both the rapid increase and decrease coincide with recent regime shifts in the Bering Sea (Brodeur *et al.* 2008a). In addition to the increase in biomass, the jellyfish from this dataset exhibited a significant range expansion beginning in 1991 (Liu *et al.* 2011). Distribution expanded northwesterly to

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<sup>1</sup> Numbers preceding each LME denote the identity (ID) used by the *Sea Around Us* Project database.

the middle of the shelf in the 1990s and into the shallow inner shelf during the year 2000 peak (see Fig. 4 in Brodeur *et al.* 2008a). The shift to the 1990s regime was characterized by warmer summertime sea surface temperature (SST) than the 1980s regime (Hunt *et al.* 2002), coinciding with a steep increase in jellyfish biomass. However, after the 1999 regime shift, the eastern Bering Sea showed even warmer summer SST and reduced winter ice coverage, which coincided with the precipitous decline in jellyfish (Brodeur *et al.* 2008a). Thus, it should be noted that warmer temperatures do not necessarily mean an increase in jellyfish (Brodeur *et al.* 2008a), as has been demonstrated for the majority of species investigated (reviewed in Purcell *et al.* 2007).

Correlations with biotic and abiotic factors varied over time and space, highlighting the fact that jellyfish population dynamics can be complicated and regional. As usual, virtually nothing is known about the field ecology of the polyps (Mills 2001; Brodeur *et al.* 2008a).

As the Bering Sea is relatively unpolluted, Brodeur *et al.* (2008a) suggest that the only probable causes for changes in jellyfish populations are climate and fishing. More specifically, the authors hypothesize that complex bottom-up changes affected the reproduction, survival, and growth of large jellyfish. While a correlation with regime shifts is evident, the association with fish and other marine populations is indiscernible (O'Harra 2004), and the current understanding of the ecosystem dynamics remains limited. With continued warming predicted for this LME, further northward range expansion of the jellyfish population is expected (Brodeur *et al.* 2008a).

## *LME #2 – Gulf of Alaska*

The National Marine Fisheries Service and the Alaska Department of Fish and Game have conducted small-mesh trawls in the Gulf of Alaska since 1953. These trawls were conducted mainly along the Alaskan Peninsula to identify concentrations of commercially exploitable shrimp. The standardization of trawling gear and methods in 1972 allows comparison of annual data. Anderson and Piatt (1999) compared catch per unit effort (CPUE) data for a wide variety of zooplankton from 6812 trawls over the period 1973-1996. Data presented for jellyfish (Scyphozoa) show low to moderate levels in the 1970s, a dramatic increase in biomass in the mid to late 1980s, and a moderate decline in the 1990s. With the fact that CPUE levels from the 1990s are on the order of 2 to 10 times higher than those of the 1970s, it can be said that jellyfish have increased in the region over this time period. Linear regression over the time series also reveals a significant, positive slope ( $R^2 = 0.42$ ,  $p < 0.001$ ). However, without recent data it cannot be concluded that this trend has continued so this chronicle is assigned a *Time Score = Low*. Due to a tight coupling between populations of many taxa with physical oceanographic conditions, the authors of this study argue that the Gulf of Alaska ecosystem is regulated to a large degree by 'bottom-up' processes. They also point out that the coherence of population trends for many ecologically disparate taxa (including both commercially exploited and non-targeted species) supports a common cause such as climate change. This powerful dataset, yet another from fisheries research, sheds light on the complex nature of jellyfish ecology and ecosystem dynamics. An updated version of the dataset should be of great interest to medusologists.

Canada's Department of Fisheries and Oceans (DFO) has been collecting zooplankton data off the British Columbia coast for decades. Regions studied include a survey transect known as 'Line P', which consists of 26 stations extending from the mouth of Juan de Fuca Strait to Ocean Station Papa, located at 50°N and 145°W. Zooplankton tows are collected from 150 m to the surface, typically three times per year. Surveys are also conducted over and offshore of the continental shelf of Vancouver Island, and in the Strait of Georgia (see below). However, most of these surveys will intentionally avoid large scyphomedusae, and may throw out samples that have chance encounters with large jellies (M. Galbraith, DFO, pers. comm., Nov. 2010). Combined measurements of ctenophores, hydromedusae, scyphomedusae, and

siphonophores show large interannual variations, but no obvious trend (*Abundance Trend* = 0) over the period 1983–2010 in all B.C. regions, including Line P, stations along the continental shelf off Vancouver Island, and further north toward Hecate Strait (data provided by Galbraith 2010).

Prince William Sound is the site of the 1989 ‘Exxon Valdez’ oil spill, and is home to a diverse ecosystem that depends largely on forage fish. Several projects were launched after the 1989 spill to assess the impact on forage fish, which included aerial and acoustic surveys, as well as seining and underwater video for target verification. Aggregations of *Aurelia labiata* were visible during these surveys conducted over three consecutive summers in the mid-1990s. Purcell *et al.* (2000) present their results for surveys from 1995, 1996, and 1997, where a total of 995 jellyfish aggregations were observed. Abundance of jellyfish in the aggregations followed a seasonal pattern, generally peaking in July and August of each year. Dramatic interannual variation in relative abundance was observed, with moderate density levels in 1995, a 2-fold increase in 1996, followed by low densities in 1997. The authors note that 1996 was characterized by deep mixing and also had high densities of zooplankton and hydromedusae. In contrast, 1997 was unusually warm due to a strong El Niño, and showed low densities of zooplankton and hydromedusae. This dataset was extended by an additional two years, when it was noted that in 1998, an even larger number of *Aurelia* aggregations were observed than for any of the three previous years (see Purcell 2003 and references therein) but were virtually absent in 1999 (Purcell *et al.* 2000). Further studies in Prince William Sound also showed high interannual variation in jellyfish populations (Purcell 2003), although may not be useful for identifying abundance trends as they did not include large aggregations of medusae.

At the southern end of this LME is a region known as the Salish Sea, consisting of the Georgia Strait, Puget Sound, and the Juan de Fuca Strait. Knowledge of jellyfish in this region is reasonably high, and provides an important example of the high variability of jellyfish populations across space and taxa. Mills (1981) presents seasonal distributions more than 50 species of jellyfish from Friday Harbor on San Juan Island, compiled over 4 years (1976–1980). No reference is made to interannual variations in abundance; however, seasonal distributions were noted to show “surprisingly little” variation between years. The author also notes numerous species of hydromedusa-producing polyps on the underside of dock floats and boat hulls around Friday Harbor, including *Bougainvillia ramosa*, *Sarsia* spp., and *Obelia* spp., which suggests artificial structures could be contributing to increased habitat for jellyfish polyps in this region. This idea is supported by a study from Purcell *et al.* (2009) of *Aurelia labiata* polyps under the floating docks at Cornet Bay Marina on Whidbey Island, Washington. This small marina has approximately 60 slips for recreational vessels. Studies from 15 sites within the marina over 3 years (2004–2006) show an average coverage of 58% by *A. labiata* polyps, with an average density of 9.3 cm<sup>-2</sup>. Extrapolating this density over the entire 685 m<sup>2</sup> of the floating docks suggests a colony of roughly 100 million individual polyps. In the first year of observation (2004), the number of discs per strobilating polyp averaged about 10, indicating that polyps have the potential to produce numerous ephyrae. The fraction of polyps that strobilated each year varied by site and date; however, strobilation was observed during all years. As the Cornet Bay Marina was originally constructed in the 1950s and expanded numerous times since, it can be said that this location has produced an increasing amount of artificial structure since its creation. With a colony of 100 million polyps, many of which can produce an average of 10 ephyrae, this anthropogenic habitat likely now contributes hundreds of millions of jellyfish to the ecosystem each year that otherwise would not be there. With the exception of a few aquaculture operations in other ecosystems, this is perhaps the most quantitative and well-defined example to date of how coastal development may contribute to increases in jellyfish populations. Such artificial habitat may be especially well-suited for jellyfish polyps, as they have been shown to prefer plastic substrates both in the laboratory (Holst and Jarms 2007; Hoover and Purcell 2009) and *in situ* at this site (Hoover and Purcell 2009). Floating docks may also provide a refuge from benthic predators of polyps, as they are unable to reach the floating substrate. During the course of the study, no large predators, such as nudibranchs, were observed under the floats.

Zooplankton surveys by Fisheries and Oceans Canada in Georgia Strait have recorded ctenophores, siphonophores, and medusae since 1991. Except for a couple of notable peaks in the late 1990s, jellyfish biomass data show no obvious trend between 1991 and 2006 in the surface layer (L. Li, UBC, pers. comm., Nov. 2010).

Hydromedusae were sampled in the spring over a 5-year period in 2 locations on the east coast of Vancouver Island in British Columbia (also a part of the Salish Sea). While the intent was to study the impact of *Aequorea victoria* on larval herring, densities of jellyfish were calculated for each year. Summarized in Purcell and Arai (2001), the data again suggest extreme interannual variation, with densities varying by up to three orders of magnitude from one year to the next. Physical data are also available from one of the sampling sites, with mean jellyfish densities showing a significant positive correlation with both temperature and salinity (Purcell 2005).

Another dataset of jellyfish abundance comes from Roscoe Bay, British Columbia, where measurements of the *Aurelia labiata* population have been taken periodically for 10 years. An index of relative abundance shows extreme interannual variation and no obvious trend (D. Albert, UBC, pers. comm., July 2010).

There are some indications that medusae populations have recently increased near Vancouver, British Columbia. Residents reported seeing unprecedented strandings of *Cyanea capillata* along beaches in 2008 (Sutherland 2008) and others have noticed apparent increases of *C. capillata* and *Aequorea* sp. in 2008 and 2009 (M. Neale, Van. Aqua., pers. comm., Oct. 2009). However, a dramatic change in jellyfish populations was observed in Indian Arm in summer 2010. In contrast to the previous two years, virtually no *C. capillata* were seen. However, *Aurelia labiata* were at their highest abundance in at least 10 years. Then, in 2011, an unusually cold spring resulted in a later-than-usual plankton bloom, and virtually no jellyfish were seen until very late in the season, when *A. labiata* and *C. capillata* began to increase in abundance (pers. obs.).

*Aequorea victoria* was heavily harvested in Friday Harbor, Washington in order to extract and purify the proteins aequorin and green fluorescent protein (GFP). From the 1960s to the 1990s, between 25,000 and 125,000 *Aequorea* medusae were harvested nearly every year (Mills 2001). *Aequorea* sp. have since declined steadily in the region throughout the last two decades, with current abundances barely reaching the hundreds (Mills 2001, 2004). However, this does not appear to be the case in the southern part of Puget Sound, where populations of *Aequorea victoria* may actually be increasing (E. Thuesen, ESC, pers. comm., Nov. 2010). Mills (2001) has also noted a decline in *Polyorchis pencillatus* in this region, another species which has been collected for research purposes.

Such diverse examples of jellyfish population changes in the Salish Sea demonstrate the complexity of jellyfish population dynamics, even over small spatial scales. Changes over the last decade include increases in anthropogenic polyp habitat, declines of both harvested and non-harvested jellyfish, and recent blooms of other species. As this evidence does not demonstrate a consistent trend, this chronicle is labeled variable (*Abundance Trend* = 0) with high uncertainty (*Reliability Score* = Low).

#### Invasive Species in LME #2 – Gulf of Alaska

While not included as a separate chronicle due to the additional knowledge from the region and the likely small contribution to biomass of this species, established populations of the hydrozoan *Cladonema radiatum* have been reported from the Salish Sea (USGS 2011), and are suspected to be invasive.

### *LME #3 – California Current*

Plankton samples along the California coast have been collected and analysed by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) since 1949, and sampling continues today. Lavaniegos and Ohman (2007) present detailed results of select taxa for both the Central California (CC) stations and the Southern California (SC) stations for the period 1951-2005. Calyophoran siphonophores showed a significant increase in both CC and SC, whereas salps showed a significant decrease in SC only. To gain an overall picture of the gelatinous biomass from this dataset, a modified analysis was performed to include all members of Ctenophora, hydromedusa, siphonophora, and Salipida. As per Lavaniegos and Ohman (2003), pooled data from springtime night tows were used. Updated to 2006, data from CalCOFI (2010) show a significant increase in jellyfish density in SC, with 5 of the 6 highest abundances occurring in the last decade. Pooled samples for the Central Station were also available, although there is a gap in data collection from 1986 to 2002. In this region, salps show extreme peaks in 1961, 1980, and 1982. However, there is no trend in the overall data, as densities for 2003-2006 are on the order of those prior to 1986. As such, the two CalCOFI stations were treated as separate chronicles for the purposes of this analysis, with differing *Abundance Trends*.

Similar research has been conducted further south in this LME, off Baja California. Lavaniegos (2009) presents results for cruises conducted by the Mexican Research of the California Current program (IMECOCAL) for the period 1997-2007. Results were divided into two geographic areas – Northern Baja California (NBC) and Central Baja California (CBC). Results reveal that both tunicates (appendicularians, doliolids, salps, and pyrosomes) and “carnivores” (chaetognaths, siphonophores, medusae, ctenophores, and heteropods) showed a significant increase in NBC, whereas “carnivores” showed a significant increase in CBC and tunicates showed no significant trend. While these groups include many organisms that are classified as jellyfish in this analysis, they also include organisms that are not (see Definition of ‘Jellyfish’). Therefore, the results must be included with caution, as organisms such as chaetognaths are shown to be highly abundant taxa in this LME (Lavaniegos and Ohman 2007), and are possibly responsible for the observed trends. As such, data from this study are classified as an increase (*Abundance Trend* = 1) over the entire study area (*Space Score* = *Medium*), albeit with high uncertainty (*Reliability Score* = *Low*).

Numerous studies have also been conducted in Monterey Bay, located along the central Californian coast. The abundance and distribution of two hydromedusae were analysed using data from the Monterey Bay Aquarium Research Institute’s (MBARI) remotely operated vehicle (ROV). Presented by Raskoff (2001), the study encompasses 9 years of data (1990-1998) and includes two El Niño events (1991/1992 and 1997/1998). The El Niño events were clearly evident through a visualization of water masses entering the bay, using the calculation of spiciness<sup>2</sup>. Both of these events strongly affected the abundance and distribution of both hydromedusan species. *Mitrocoma cellularia* showed a sudden increase in abundance, as well as an increased depth range, during both El Niño events, while its abundance and range was much more limited in the time between events. Conversely, the abundance of *Colobonema sericeum* dropped to very low levels during the events, while it was found in high numbers between events. While the responses from these two species to the El Niño events are clearly dramatic, it remains unclear whether they are due to tolerance, reproduction, or transport.

A number of siphonophores have also been studied in Monterey Bay. Robison *et al.* (1998) present results for 257 ROV transects including over 10,000 observations of the physonect siphonophore *Nanomia bijuga*. The time series encompassed only three years of data and the authors found no significant differences in abundance between years. A similar sample of 295 ROV transects included 1755

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<sup>2</sup> The measurement of spiciness combines the dynamic interaction of temperature and salinity – low temperature, low salinity has a low spiciness, whereas warm, salty water has a high spiciness.

calycophoran siphonophores. Again, there was no significant difference in overall abundance over the three year study period (Silguero and Robison 2000). While these surveys show no obvious trend for hydromedusa and siphonophore populations through the 1990s, other populations of jellyfish in Monterey Bay appear to be changing. Irregular seasonality and increased duration of occurrence has been noted for several species in Monterey Bay (Tucker 2010). There is also suspicion that *Aurelia* populations have increased in Monterey Bay in recent decades (W.M. Graham, DISL, pers. comm., May 2010). Unfortunately, the data to verify such suspicions have not been published or released by MBARI, and the anecdotal data were offered with considerable caution and uncertainty. Given the high uncertainty and somewhat contrasting information, Monterey Bay is not included as a separate chronicle in the analysis, and jellyfish abundance in this LME is probably better estimated using the more robust datasets. Hopefully, the powerful dataset maintained by MBARI will see more analysis and publication of jellyfish data in the near future.

A series of sampling cruises were conducted in the spring and summer of 1981 off of the coasts of Oregon and southern Washington. While the primary goal of these cruises was to study juvenile salmonids, large volumes of jellyfish were also collected and analysed. Results are presented by Shenker (1984). A total of 263 purse seine sets were collected. However, several sets contained so many medusae that the net was split and the samples were lost. Scyphomedusae were “very abundant” throughout the survey, dominated by *Chrysaora fuscescens* which occurred in over 82% of all samples. Other scyphomedusae included *Aurelia* spp., *Cyanea capillata*, and *Phacellophora camtschatica*, which were all reported as “widely distributed, but abundant only in discrete locations.” Hydromedusae, including *Aequorea* spp. and *Eutonina indicans*, were also collected but were not quantified due to the fact that they were generally extruded through the seine mesh during net retrieval. *C. fuscescens* was found in relatively low densities in May, with much higher concentrations in June, July, and August, especially nearer to inshore stations. Calculated densities of collected samples ranged as high as 1.8 L of medusae per 100 m<sup>3</sup> and 50 mgCm<sup>-3</sup>, suggesting that *C. fuscescens* is a major component of the summer neritic plankton community in the northern California Current LME.

Two decades later, scyphomedusae were again sampled in the northern California Current LME. Suchman and Brodeur (2005) present results for cruises from Newport, Oregon to Crescent City, California as part of the US Global Ocean Ecosystems (GLOBEC) program. A total of 365 successful trawls were made over four cruises in June and August of both 2000 and 2002. Large medusae were widely distributed throughout the study area, with *Chrysaora fuscescens* being the dominant species. Other species of varying abundance included *Aurelia labiata*, *Phacellophora camtschatica*, and *Aequorea* sp. As usual, distribution was not even across sampling stations and varied by month and year. Highlighting the difficulty in quantifying abundance estimates for jellyfish, a large proportion of the total catch of each species was usually concentrated in relatively few stations. Actual abundance estimates were likely higher than those calculated (discussed in Suchman and Brodeur 2005). Correlation analysis of a variety of environmental variables showed that latitude, and either water depth or distance from shore explained the distribution of medusae on all cruises. As *C. fuscescens* is most abundant close to shore during the summer, it was suspected that it would inhabit primarily cold, upwelled water. While this was the case for the largest catches, *C. fuscescens* was actually found across a wide range of temperatures and salinities, with both variables proving to be poor predictors of habitat.

Calculations of maximum biomass concentrations for *C. fuscescens* were 64 mgCm<sup>-3</sup> in 2000 and 28 mgCm<sup>-3</sup> in 2002, comparable with Shenker’s (1984) estimate of 50 mgCm<sup>-3</sup> in 1981. The authors also note that triennial groundfish trawl surveys off the U.S. west coast since 1980 show no consistent trend in jellyfish abundance, other than declines during El Niño years. With no apparent trend from the fisheries surveys, as well as the similarity of the aforementioned biomass concentrations, the authors conclude that there is “no evidence that abundance or distribution of *C. fuscescens* has substantially changed over the



past 20 years off the coast of Oregon.” As such, this chronicle is rated as stable/variable (*Abundance Trend* = 0). However, Brodeur *et al.* (2008b) have suggested that habitat dynamics are changing to favour jellyfish over fish in this region due to the expansion of anoxic and hypoxic zones along the Oregon shelf. Chan *et al.* (2008) note that a five-decade dataset shows little evidence of hypoxia prior to 2000, but there have been recent increases in both the frequency and severity of hypoxic events along the shelf due to changes in winds that drive upwelling. In 2006, anoxia was observed at inner-shelf stations associated with the complete absence of all fish and near-complete mortality of macroscopic benthic invertebrates (Chan *et al.* 2008). As many jellyfish are tolerant of low-oxygen conditions and may outcompete fish in these situations (Purcell *et al.* 2001a), the California Current LME could see an increase in jellyfish in the years to come (Brodeur *et al.* 2008b).

### Invasive Species in LME #3 – California Current

There are reports from several locations in the California Current LME of invasions by jellyfish, likely due to translocation from shipping activities. Three species of invasive hydromedusae, all native to the Black Sea, have been observed in the San Francisco Estuary system (Mills and Rees 2000). *Maotias marginata* was first reported from in the scientific literature as being collected in 1992, followed by medusae populations in the thousands in 1993, indicating a probable establishment of at least several years prior (Mills and Sommer 1995). Other reports suggest that *M. marginata* may have been present in the San Francisco Bay estuary system as far back as 1959 (Mills and Rees 2000). Indeed, a recent analysis by Schroeter (2008) of otter trawl data from Suisun Marsh in the upper San Francisco Estuary from 1981 to 2005 confirms the presence of *M. marginata* back to the beginning of the dataset. The analysis also revealed significant increases in the intensity, frequency, and duration of blooms, as well as the spatial distribution of medusae, especially after 1993. While this species may be confined near river systems due to intolerance of high salinities, it has been found in more than one river in the San Francisco Estuary and has the potential to expand its range by transport of sessile polyps (Rees and Gershwin 2000). Initial invasion may have been by a solitary polyp, as all early collections of medusae were male. The inability for these medusae to reproduce sexually appears inconsequential due to the prolific asexual reproduction by polyps (Mills and Sommer 1995). Interestingly, a few female medusae were found in the Napa River in 1998 (Rees and Gershwin 2000).

*Blackfordia virginica* was first collected in the San Francisco Estuary in 1970, with the discovery of polyps densely covering living, invasive barnacles in 1997 (Mills and Rees 2000). Collections in 1993 included both male and female medusae (Mills and Sommer 1995). Larger females were found to be producing eggs, and size distributions suggested hydroids were continuously budding medusae throughout the summer. This species has also been found in one other location in the California Current LME. First observed in Coos Bay, Oregon in 1998, thousands were seen in 1999 (Mills and Rees 2000). Unidentified species of *Moerisia* have also been found in the San Francisco Estuary since at least 1993 (Mills and Rees 2000). While the presence of this species was more sporadic, it does seem to have impressive reproductive capacity through asexual budding of polyps. In laboratory culture, budding polyps grew to dense colonies within months (Rees and Gershwin 2000). Another culture grew to over 200 individuals from a solitary polyp (originally misidentified) and its budded offspring (Mills and Sommer 1995).

Wintzer *et al.* (2011) placed plastic settling plates in the San Francisco Estuary and quickly found polyps of two of the aforementioned invaders (*B. virginica* and *Moerisia* sp.). Settling rates were estimated in the hundreds of thousands of hydranths•day<sup>-1</sup>•m<sup>-2</sup>, although the polyps may suffer from predation and competition and by other organisms soon after settlement. The polyps also appeared to show a preference for the underside of plates with a horizontal orientation, again suggesting that artificial substrates may contribute to increasing jellyfish populations by providing additional habitat for polyps (Purcell *et al.* 2007; Hoover and Purcell 2009; Duarte *et al.* in review).

Evidence suggests that a number of cryptic species have also invaded San Francisco Bay. Greenberg *et al.* (1996) note that *Aurelia* sp. have been blooming annually in Foster City lagoon since they were first noticed in 1988. Based on morphological and allozyme evidence, the authors conclude that the *Aurelia* sp. found in Foster City are an isolated population of an introduced species, possibly originating from Japan. The hydrozoan *Cladonema* sp. may have also been introduced from East Asia. Specimens were not directly collected from the field; however, medusae from two different aquaria in 1979 and 1981 lead Rees (1982) to conclude that a nonindigenous species of *Cladonema* may have invaded the Bay area.

Another invasive hydrozoan was noted in nearby Bodega Harbor in the late 1990s. A hydroid of *Amphinema* sp. was collected from floats in the harbor and was cultured to produce medusae which were raised to maturity (Rees 2000). This species was not detected during numerous intensive surveys of the area between 1971 and 1980 (Rees 1975, 2000).

*Phyllorhiza punctata* also appears to be a successful invader in this LME. Collected in Mission Bay in 1981, this species now seems to be established in San Diego Bay (Larson and Arneson 1990; Graham and Bayha 2007).

#### *LME #4 – Gulf of California*

Knowledge of jellyfish in this LME is sparse; however, a fishery for the cannonball jellyfish *Stomolophus meleagris* has developed here over the last decade, as fishers sought additional income due to lower revenues from the shrimp and squid fisheries (Ocampo *et al.* 2010). This fishery may harvest anywhere from 1,000 to 15,000 tonnes of jellyfish each year in the state of Sonora (Ocampo *et al.* 2010). Despite this, populations of *S. meleagris* around Sonora appear to have increased in recent years (L. Ocampo, CIBNOR, pers. comm., Sept. 2010).

#### *LME #5 – Gulf of Mexico*

Data from the United States National Marine Fisheries Service (NMFS) Southeast Area Monitoring and Assessment Program (SEAMAP) were analysed by Graham (2001). The data contained biannual (spring and summer) shrimp and groundfish trawl surveys, divided into ten statistical regions in the northern Gulf of Mexico. In total, over 10,000 individual trawls were included in the analysis. Two species of scyphomedusae were presented in the study, both of which are abundant and widely distributed in the region. *Chrysaora quinquecirrha* typically peak in the summer months, whereas *Aurelia aurita* peak in the fall. Thus, the biannual seasonal trawl data are well suited for analysing the abundance of these two species. Numerical trawl data were normalized, allowing comparison between years as a standardized catch. As jellyfish were not the target species, and bottom-trawls do not sample the entire water column evenly, the data provide an index of relative abundance rather than estimates for absolute biomass. Data for *C. quinquecirrha* and *A. aurita* spanned 11 and 13 years respectively.

Interannual variations in regional densities up to an order of magnitude occurred for both species, and were frequent for *A. aurita*. Statistically significant long-term increases were found for 2 of the 10 regions for *C. quinquecirrha*; however, additional regions showed dramatic cycling between presence and absence. Shifts in distribution for this species were also significant in some areas, with a trend toward offshore waters in 4 of the 10 regions. While there was no significant temporal correlation between hypoxia and *C. quinquecirrha* populations in the two regions of numerical increase, there was substantial spatial overlap.

Long-term increases in *A. aurita* were more widespread, occurring in 6 of the 10 regions. Several neighbouring regions showed increases up to an order of magnitude through the 1990s. Distributional shifts offshore were less widespread, occurring in 3 of 10 regions. However, this dataset was visited more recently and updated through 2006, and abundance of *A. aurita* has returned to pre-increase levels comparable to the 1980s (W.M. Graham, DISL, pers. comm., May 2010). Therefore, this chronicle was classified as stable/variable (*Abundance Trend* = 0). Although the details were not available at the time of writing, data since 2007 are again showing signs of increasing abundances (K. Robinson, DISL, pers. comm., Feb. 2011).

There is anecdotal evidence to suggest that populations of *Cassiopea* spp. have increased in areas with intensive coastal development in this LME. Fitt and Costley (1998) note that while there has been little monitoring of populations over time, “many canals and near-shore areas in the Florida Keys have become filled with adult medusae during the past ten years where apparently few if any existed before.” Anecdotal reports indicate the continued spread of this epibenthic jellyfish in developed areas of the Keys, with distributions showing high spatial variability (L. Chiaverano, DISL, pers. comm., Nov. 2010). It now appears there are at least 3 different species of *Cassiopea* in the Florida Keys, with considerable morphological variation among locations (Chiaverano *et al.* 2010). Abundance of *Cassiopea* spp. may have also increased in a coastal lagoon in Cancun, Mexico that is highly impacted from coastal development (Arai 2001 and references therein).

Florida’s Gulf Coast has also been witness to unusually large blooms of *Pelagia noctiluca* over the last several years (Alvarez 2011; Kuo 2011; Taylor 2011). Although this species is more common in the eastern Atlantic and Mediterranean Sea, it is unclear if the recent blooms in the Gulf of Mexico are a new phenomenon, as there were also blooms of this species in the Gulf of Mexico in the late 1990s (Raines 2011).

Another unusual jellyfish event took place in this LME in 2000. Williams *et al.* (2001) report a “population explosion” of *Drymonema* sp. from Louisiana to Florida that persisted for several months. This jellyfish had not been noted previously in the Gulf of Mexico and the authors consider it an “invader” of tropical origin. However, the taxonomy of this group has recently been investigated and these specimens are now described as belonging to the species *D. larsoni*, which is distributed in the Caribbean (Bayha and Dawson 2010). As such, its presence in the Gulf of Mexico likely represents a range expansion or shift, rather than a true invasion. In addition, these jellies are known to disappear for decades before blooming again (Bayha and Dawson 2010), so they may have historically escaped detection in many locations. While specimens have been observed in the Gulf of Mexico almost annually since 2000, there were none seen in 2010, despite considerable effort (K. Bayha, DISL, pers. comm., Nov. 2010). Therefore, this species has been excluded from the analysis until a more complete understanding of its population dynamics can be developed.

#### Invasive Species in LME #5 – Gulf of Mexico

Graham *et al.* (2003) report an invasion of a large population of *Phyllorhiza punctata* in 2000 along the northern Gulf of Mexico. Sampling of the population included 13 small-boat trips, six aerial surveys, and one large vessel survey which examined an aggregation in Lake Borgne, spanning 150 km<sup>2</sup>. Estimated abundance for this aggregation alone was over 5 million medusae weighing nearly 35,000 tonnes. In total, an estimated 10 million large medusae occupied the Mississippi Sound region in 2000 (Bolton and Graham 2004). While 2000 marked this spectacular bloom, confirmed reports indicate that this species may have been present since 1993 (Graham *et al.* 2003). This species has subsequently been observed in Louisiana in several years since 2000, including 2001 (Graham *et al.* 2003), 2004 (Johnson *et al.* 2005), and 2007 (Britt 2007), as well as 2006 in Texas (Barord *et al.* 2007). These repeat observations suggest

additional invasions or a newly established population of *P. punctata* in the Gulf of Mexico. Interestingly, the invaders possessed no photosymbiotic zooxanthellae and had a bleached appearance, unlike their native counterparts in the tropical western Pacific. Despite the lack of photosynthetic symbionts, *P. punctata* collected in the northern Gulf were considerably larger than described populations from other parts of the world. This adaptation is especially concerning, as it suggests that this species can move between vastly different productivity regimes (Graham *et al.* 2003). In addition, medusae analysed for sex were all male, suggesting the initial bloom may be the result of an invasion by a solitary individual. This is potentially an example of how invasive jellyfish can thrive in a new environment from the introduction of a single polyp or cyst.

### *LME #6 – Southeast U.S. Continental Shelf*

Numbers of the cubomedusae *Carybdea marsupialis* have apparently “skyrocketed” in North Carolina waters over the past few years (Anonymous 2009a). This is potentially the same species that has been blooming in increasing numbers and areas along the Florida coast over the last decade (Anonymous 1998, 2010f). Another box jellyfish, *Tripedalia cystophora*, has also apparently been increasing in abundance in Florida mangroves near Boca Raton since 2009 (Anonymous 2012). Other species, such as sea nettles of the genus *Chrysaora*, may also be blooming unusually in North Carolina (James 2010) and Florida (Asuaje 2010). However, the identity of the species in question has not been confirmed (P. Anderson, WLMB, pers. comm., Dec. 2010). These blooms illustrate how species identification is often problematic in the popular media. For example, a bloom responsible for over 2,000 stings in Florida’s Volusia County over the 2011 Independence Day holiday weekend were often reported as moon jellyfish (*Aurelia* sp.) (e.g., Anonymous 2011d). However, photographs and other media reports identify them as sea nettles (*Chrysaora* sp.) (e.g., Burbank 2011).

Interestingly, there was an unusually large bloom of *Pelagia noctiluca* along central Florida’s Brevard County in 2011, which stung over 1800 people around the Memorial Day holiday (Alvarez 2011; Kuo 2011). This species is rarely found in the coastal waters of the eastern U.S.A., but may have been transported there from the Gulf of Mexico (Taylor 2011).

The cannonball jellyfish, *Stomolophus meleagris*, has been identified as a major component of overall biomass in this LME and is the target of a developing fishery. Starting in 2001, specimens of *S. meleagris* have been recorded separately from other species by the SEAMAP South Atlantic Coastal Survey, which consists of over 100 tows per season from North Carolina to Florida (SCDNR 2005). As the entire survey area is sampled only once per season, aggregations of *S. meleagris* can obviously escape detection due to their patchy variability over time. However, the consistent sampling methods and the wide spatial coverage of the surveys provide a useful index of relative abundance. Hendrix and Boylan (2010) and Petersen (2011) present annual density measurements of *S. meleagris* for 2001-2010, which are high at the beginning and end of the decade, but depressed through the middle years (*Abundance Trend* = 0). The data for 2011 had not been published at the time of writing. However, abundances were reportedly some of the highest on record, at times clogging the sampling nets (Petersen 2011). As mentioned, this species is the target of a developing fishery, with harvests over the past 10 years averaging a modest 300 tonnes (FAO 2011).

There is interesting evidence to suggest that populations of *Cassiopea* spp. have increased in this LME, which also points to anthropogenic impacts as the cause. Stoner *et al.* (2011) compared populations of *Cassiopea* spp. at sites adjacent to areas of dense human population with those of uninhabited sites on Abaco Island, Bahamas. Although the analysis does not contain a time series of abundance data, it is some of the most convincing evidence to date that the populations of a species of jellyfish are directly affected by anthropogenic impacts. The results showed a significant increase in both abundance and individual

size for *Cassiopea* spp. that were adjacent to areas populated by humans. There was also a significant correlation with total phosphorus in the water, suggesting that the mechanism involved may include increased nutrient input from anthropogenic sources supporting symbiotic zooxanthellae found in these jellyfish (Stoner *et al.* 2011).

#### Invasive Species in LME #6 – Southeast U.S. Continental Shelf

The invasive scyphozoan *Phyllorhiza punctata* has been reported in more than one location in this LME. Graham *et al.* (2003) note this species was first detected in Florida's Indian River Lagoon in 2001. It was detected in the same location again in 2002 and 2009, as well as several other locations in Florida (Anonymous 2009c; Waymer 2009). This species has also been reported as far north as North Carolina (Britt 2007).

The hydrozoan *Turritopsis dohrnii* has been present in Fort Pierce, Florida, since at least 2006 (Miglietta and Lessios 2009). This invasion is not noted as a separate chronicle as it overlaps with the chronicle used for *P. punctata*. However, the presence of this species is noteworthy, as *Turritopsis* spp. have become increasingly invasive around the globe. This is possibly due to their unique ability to reverse their life cycle through the process of transdifferentiation, potentially increasing the chances of being transported through ballast water (Miglietta *et al.* 2007; Miglietta and Lessios 2009). There is also reportedly an established population of the invasive *Blackfordia virginica* in South Carolina (USGS 2011).

Another hydrozoan, *Phialella falklandica*, may also be invasive in this LME. Kramp (1970a) notes that this jellyfish was collected in the late 1960s near the Bahamas. Previously, this species was only known to occur in New Zealand and South America. However, the author only describes the new distribution as “interesting”, and also notes that species may have been collected nearby in Florida in the late 19<sup>th</sup> century. The invasiveness and establishment of this jellyfish remains unclear in this LME, and therefore it has been excluded from the analysis.

#### LME #7 – Northeast U.S. Continental Shelf

Link and Ford (2006) analysed stomach content data of the spiny dogfish (*Squalus acanthias*) from the Northeast Fisheries Science Center (NEFSC) bottom trawl survey program. Standardized sampling methods in 1981 allowed the comparison of over 40,000 spiny dogfish stomachs from a wide range of locations within the Northeast U.S. Continental Shelf LME. At least 1000 stomachs were analysed throughout each year. Stomach contents were examined immediately after the catch was sorted on deck, eliminating concerns surrounding preservation and rapid digestion. As *S. acanthias* do not appear to masticate ctenophores, but rather ingest them whole, these prey items are readily identifiable in the stomach contents. While Ctenophora prey items were not identified to species, they are assumed to be any combination of *Mnemiopsis leidyi*, *Pleurobrachia pileus*, or *Bolinopsis infundibulum*.

There was a significant increase by a factor of 2 to 8 in the frequency of occurrence of ctenophores over the study period. This increase was also widespread, showing expansion both northward and southward in the LME. There was no significant trend over the study period for either percent composition or gross consumption of ctenophores in the stomach contents. Consistent with the knowledge that spiny dogfish are omnivores and opportunistic feeders, this suggests that feeding on ctenophores is a routine, non-selective process that is primarily dependent on encounter probability. Therefore, examining frequency of occurrence in stomach contents should provide a good indicator for the relative abundance of ctenophores (Link 2004; Link and Ford 2006). This long-term and widespread dataset is a unique and important component of knowledge regarding jellyfish populations. It provides an extremely strong indication that

ctenophore populations have increased in this LME. As will be discussed, this finding is supported by other studies in bays located in the region.

Chesapeake Bay is the largest estuary in the United States. It is home to the sea nettle *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*, both of which can form large populations in the summer. Cargo and King (1990) present an index of relative abundance derived from daily summer sight counts of *C. quinquecirrha*. The 26-year dataset (1960-1986) shows dramatic interannual variation with count densities varying from 0 to 320 m<sup>-2</sup>. There was no obvious long-term trend over the study. Purcell and Decker (2005) present densities for the same species as well as *M. leidyi* from 1987-1990 and 1995-2000. During the study period, either the scyphomedusan (*C. quinquecirrha*) or the ctenophore (*M. leidyi*) dominated the bay. Of the 10 years with data, *C. quinquecirrha* dominated half of the time (1987-1990, 1995) and *M. leidyi* dominated the other half (1996-2000). As ctenophore densities showed a significant increase during the second half of the study period, and since ctenophore densities were typically one to four orders of magnitude higher than medusae densities, it can be said that jellyfish biomass increased over the course of the study.

Up the coast from Chesapeake Bay is Narragansett Bay, where there is further evidence that ctenophore populations are increasing. Sullivan *et al.* (2001) present data from a 1999 study on *M. leidyi* abundance, combined with 14 years of data from both published and unpublished reports, dating back to 1950. Comparison with these historical accounts showed that peak densities of *M. leidyi* greater than 1 cm in length were 2-3 times higher in 1999 than in the early 1970s. In addition, dates of first appearance and peak blooms had shifted earlier by an alarming two months. It appears that these changes in phenology can be attributed to climatic warming, especially in the shallow embayments of Narragansett Bay (Costello *et al.* 2006). Recent data show more variability in this *M. leidyi* population, with high abundances of individuals (>1 cm) until 2005, when abundances appeared to decline precipitously (Rynearson 2010). The year 2007 had a summer with virtually no individuals, potentially due to predation by *Beroe* spp. the previous fall (Rynearson 2010). Abundances appear to have remained relatively low since 2005, with the exception of a large spike of specimens less than 1 cm in size in 2008, which reached a peak density of over 877 individuals per m<sup>3</sup>. Despite the apparent decline since 2005, this chronicle was still classified as an increase (*Abundance Trend* = 1) due to the increases sustained through the 1980s, 1990s, and early 2000s, as well as the dramatic shift to peak abundances occurring earlier in the year. However, to account for the recent decline, the *Reliability Score* was reduced to *Low*.

Although it was not included as a separate chronicle, there is evidence to suggest an increase in the population of *M. leidyi* in the estuaries of Long Island, New York. McNamara *et al.* (2010) note that ctenophore abundances measured in 2006 in Great South Bay and Peconic Bay were two to five times higher than in the 1970s and 1980s. In addition, peak abundances occurred an astounding two months earlier than in the prior studies. In contrast with these findings, Nuttall *et al.* (2011) compiled ecological data for Great South Bay and note a decline in ctenophore biomass of about 50% from the 1980s to the 2000s. It remains unclear why the information from these two studies is in disagreement. Interestingly, it appears there was an even more dramatic decline in ctenophore biomass in Great South Bay from the 1880s to the 1930s (Nuttall *et al.* 2011).

Barnegat Bay, New Jersey has been highly impacted by development and pollution. Sea nettle jellyfish (*Chrysaora* sp.) were “unheard of” prior to 2000 (Dutzik and O'Malley 2010), but they have become increasingly problematic in recent years, stinging swimmers and causing beach closures (APP 2010; Campbell 2010). Other reports suggest these jellyfish were present in the Bay more than a century ago, but echo the rapid increase over the past decade (*e.g.*, Nee 2011). Recent government bills and plans have been approved in an attempt to mitigate the perceived causes, including limiting the amount of nutrients flowing into the bay, upgrading storm-water basins, and closing the Oyster Creek Nuclear Generating

Station 10 years ahead of schedule (Parry 2010). There have also been suggestions that the sea nettles are proliferating due to increased anthropogenic habitat for polyps (Nee 2011). Regardless of the causes, the sea nettle infestation in Barnegat Bay continues, with 2011 being one of the worst years on record (Moore 2011; Nee 2011).

Several sources also point to an increase in *Cyanea capillata* around New York State in recent years (*e.g.*, Gaskell 2008; Parry 2008; Grossman 2010), including unprecedented observations during winter months (Beeler 2011). While some of the reported locations are within 200 km of Barnegat Bay, the trend appears to extend further. In addition, this increase is a different species and occurs on a different timescale, and was therefore recorded as a separate chronicle, albeit with lower confidence (*Confidence Index = Low*).

Large blooms of *Aurelia* sp. have also been reported further north, such as in Boston Harbor (Ryan 2007; O'Neil 2011). While these events were not included as a separate chronicle, there are indications that the frequency and intensity of these blooms may be increasing, and that the size of individual medusae may also be increasing (R. Dicker, UMB, pers. comm., Feb. 2011).

One station from the Atlantic Zooplankton Monitoring Program (AZMP) is in this LME. The AZMP was implemented in 1998 with the aim of increasing the capacity to understand, describe, and forecast the state of the marine ecosystem, as well as to quantify changes (Harrison *et al.* 2009). The Prince-5 station, located near the mouth of the Bay of Fundy, was sampled on at least a monthly basis. Unfortunately, data on jellyfish abundance are only presented pooled with appendicularians, so the *Reliability Score* was reduced to *Low*. Despite this, there appears to be no obvious trend in the jelly+appendicularia group relative to other zooplankton groups from 1999 to 2008 (Harrison *et al.* 2009). The only anomaly is a large “pulse of jellies and appendicularia” observed in the summer of 2004 (Harrison *et al.* 2005).

#### Invasive Species in LME #7 – Northeast U.S. Continental Shelf

Several species of invasive hydromedusae have also been reported from Chesapeake Bay. *Maeotias marginata* was collected in 1968 (Calder and Burrell 1969), and again in 1993 (USGS 2011). Additional invasive hydromedusae from Chesapeake Bay include *Blackfordia virginica* (Mills and Sommer 1995) and *Moerisia lyonsi* (Purcell *et al.* 1999; Ruiz *et al.* 2000).

#### *LME #8 – Scotian Shelf*

Data from this LME are exclusively from Canada's Department of Fisheries and Oceans zooplankton surveys. Numerous transect lines are investigated twice a year in this LME as part of the Atlantic Zooplankton Monitoring Program (see Fig. 1 in Harvey and Devine 2009). Most transects show high interannual variability between 2001 and 2009, and while some stations appear to show modest increases in recent years (*e.g.*, TASO transect in fall), there is no consistent trend across space or time (M. Harvey, DFO, pers. comm., Aug. 2010). As such, this chronicle was classified as stable/variable (*Abundance Trend* = 0). A separate, fixed station known as Halifax-2 is also in this LME, and has been monitored for even longer. As jellyfish abundance is only presented pooled with appendicularians, this chronicle is assigned a *Reliability Score = Low*. Nonetheless, this station shows no obvious trend over the course of the dataset (see Fig. 27 in Harrison *et al.* 2009). A notable spike in abundance was observed in 2005, where total zooplankton was higher than other years, apparently due to jellyfish and/or appendicularians.

Annual zooplankton surveys are also conducted in the Gulf of St. Lawrence, with numerous transects in and around the estuary (see Fig. 14 in Harvey and Devine 2009). Average abundances and biomass for data collected from 1995 to 2008 are relatively stable, with the obvious exception of a large peak of *Aglantha digitale* in 2004 (see Fig. 16 in Harvey and Devine 2009). Average biomass is larger after 2004

than it was in the preceding years; however, the overall trend is not significant. The year 2003 also marks a change in sampling methods from collection in September to October-November. Thus, the time-periods are not directly comparable, and within each time-period, abundances are relatively stable. Therefore, this chronicle is classified as stable/variable (*Abundance Trend* = 0).

### *LME #9 – Newfoundland-Labrador Shelf*

Jellyfish are not the focus of any studies in this region. However, the Atlantic Zooplankton Monitoring Program (AZMP) of Fisheries and Oceans Canada provides some useful data on jellyfish populations. As part of the AZMP, four large transects are monitored in this LME – three off of Newfoundland (Southeast Grand Banks, Flemish Cap, and Bonavista) and one off of Labrador (Seal Island) (see Fig. 1 in DFO 2008). These transects are investigated between one and three times per year, and collectively provide good temporal and spatial coverage of this LME. Pepin *et al.* (2009) present seasonally-adjusted relative abundance data for *Aglantha digitale* and the much less abundant *Pelagia noctiluca* for the period 1999-2008. Data for both species from all transects show no obvious trends over the time period. Interestingly, the Seal Island and Southeast Grand Banks transects show a spikes of *A. digitale* in 2004; however, these peaks are not evident in data from the other transects. While *A. digitale* can be abundant at times, and *Aurelia* spp. occasionally form large blooms, jellyfish abundance in this LME is generally assumed to be insignificant compared to other taxa, and no long-term trends are evident (P. Pepin, DFO, pers. comm., Dec. 2009).

### *LME #10 – Insular Pacific-Hawaiian*

There is considerable evidence to suggest that the box jellyfish *Carybdea alata* has increased in Hawaiian waters. Although this species has been present since at least the late 19<sup>th</sup> century, abundances around the main Hawaiian Islands increased dramatically in the late 1980s (Thomas *et al.* 2001). Since 1994, box jellyfish have been sighted every year on Oahu (Crow *et al.* 2010), and are now a major concern for tourism at many Hawaiian beaches due to an irritating sting. Interestingly, large influxes of these jellies tend to show a strong correlation with the lunar cycle, peaking 9 or 10 days after the full moon, making management of stings possible (Thomas *et al.* 2001).

#### Invasive Species in LME #10 – Insular Pacific-Hawaiian

At least two species of *Cassiopea* have invaded Hawaii (Holland *et al.* 2004) and these jellies are now found throughout the main Hawaiian Islands (Eldredge and Smith 2001). Members of this unique genus of scyphomedusa typically rest with the dorsal side of their bell on the ocean floor with oral arms and tentacles pointing upward, giving them the common name of the ‘upside-down jellyfish’. Mucous containing nematocysts may be released from the jellyfish to help ensnare zooplankton prey. Medusae will swim if disturbed and may release mucous during avoidance (Daoust 2009). In conjunction with their semi-sessile lifestyle, *Cassiopea* host photosymbiotic zooxanthellae and are therefore generally restricted to shallow environments. *Cassiopea* spp. are thought to have spread to Hawaii via ships, first to Pearl Harbour in the 1940s, and then to Honolulu Harbour by 1950 (Devaney and Eldredge 1977). An invasion prior to 1950 would normally be excluded from this analysis (see Materials and Methods); however, the continued spread of these jellies and possible subsequent invasions after 1950 permit inclusion. Polyps of this species have been observed on discarded plastic in Hawaii, and in some rare cases, the medusae can actually be hermaphroditic (Hofmann and Hadfield 2002). Molecular analysis of *Cassiopea* samples from Oahu showed two distinct lineages, geographically separated on the windward and leeward shores of the island (Holland *et al.* 2004). These divergent lineages are thought to represent two distinct invasions, one suspected from the Indo-Pacific region and the other from the Red Sea or western Atlantic Ocean. While



*Cassiopea* can clearly colonize new nearshore areas, it is not a strong natural disperser (Holland *et al.* 2004) and removal of this species has been successful at other locations in Hawaii (Hofmann and Hadfield 2002; Kelsey 2009). Thus, management of these species may be possible.

The combination of molecular analysis and ocean circulation modelling has identified an invasive species of *Aurelia* in Hawaii, hereafter referred to as *Aurelia* sp. 4. Dawson *et al.* (2005) note that *Aurelia* sp. 4, which is endemic to Borneo and Palau, occurs in Hawaii. However, a current model reveals “there is no available ocean pathway that naturally connects these zones of occurrence...” In addition, the genus *Aurelia* was not reported from Hawaii prior to the 1950s, despite surveys of jellyfish starting in the 1900s. Therefore, the authors conclude that the occurrence of *Aurelia* sp. 4 in Hawaii “is most likely due to anthropogenic translocation”.

The scyphomedusa *Anomalorhiza shawi* also appears to be invasive in Hawaii. Cooke (1984) notes that this jellyfish, which is endemic to the Philippines, “was not seen before 1983” in Hawaii. Specimens of this jellyfish were collected in 1983 and 1984 in Kaneohe Bay, and despite infrequent observations since, the observation of an adult specimen in the same location in 2001 suggests an established, reproducing population (Lum 2001).

The highly invasive *Phyllorhiza punctata* also appears to be established in Hawaiian waters. However, in their study of Juvenile Attraction Devices (JADs) on carangid fish, Clarke and Aeby (1998) note the disappearance of this jellyfish from Kaneohe Bay, Oahu. The primary author notes that *Phyllorhiza punctata* formed high densities several times during the period 1968-1970, which was followed by a sudden disappearance in the early 1970s. Despite this disappearance, *P. punctata* is present in several other locations on Oahu (Eldredge and Smith 2001). However, it is likely that invasion occurred prior to 1950 (Eldredge and Smith 2001), and therefore this jellyfish has been excluded from the analysis. Numerous species of cryptogenic hydrozoa have also been reported from Kaneohe Bay (Coles *et al.* 2002).

### *LME #11 – Pacific Central-American Coastal*

Information on jellyfish from this LME is sparse, especially in English. Aside from a study linking hydromedusa blooms to upwelling events (Miglietta *et al.* 2008), the only reported change for a native species concerns the rhizostome *Stomolophus meleagris* (cannonball jellyfish). Ocaña-Luna and Gómez-Aguirre (1999) report that this jelly has colonized and thrives in a pair of coastal lagoons in Mexico. The authors suggest that *S. meleagris* occurs at lower abundances in lagoons to the north due to a strong oscillation of the water temperatures. However, they suggest that in Oaxaca’s Lagunas Superior and Inferior, reduced runoff due to irrigation has reduced temperature fluctuations, thereby allowing the cannonball population to thrive. As there are no recent data on this population, a *Time Score of Low* was used.

#### Invasive Species in LME #11 – Pacific Central-American Coastal

There are several reports of invasive jellyfish in this LME, all concerning small hydrozoans (*Invasive Reliability Score = Low*). *Blackfordia virginica* is reported to have invaded the lagoons of Chantuto-Pensacola, Chiapas in the 1990s (Álvarez-Silva 1999; Álvarez-Silva *et al.* 2003). The invasive *Turritopsis dohrnii* has also been reported from Panama Bay since at least 2006 (Miglietta and Lessios 2009). As mentioned, this tiny jellyfish has successfully invaded a number of locations around the globe, possibly facilitated by the unique ability to reverse its life cycle through the process of transdifferentiation (Miglietta *et al.* 2007; Miglietta and Lessios 2009). Several other small hydromedusae were recently reported from this LME for the first time, including *Amphinema dinema*, *Sarsia cocometra*, and *Clytia mccradyi* (Segura-Puertas *et al.* 2010). These jellies occur at such low abundances relative to others that

they likely make no detectable contribution to the gelatinous biomass at present, and were therefore not included in the analysis. However, these species may become more abundant in this LME in the future, as *C. mccradyi* is the most abundant jellyfish in some coastal systems of the Caribbean (Segura-Puertas *et al.* 2010 and references therein).

### *LME #12 – Caribbean Sea*

There is very little information on jellyfish populations in the Caribbean. Williams *et al.* (2001) report an unprecedented “population explosion” of *Drymonema* sp. around all coasts of Puerto Rico throughout the summer and fall of 1999. Previously, this jellyfish was only observed around Puerto Rico in small numbers in the 1970s. Unfortunately, it is unclear if the blooms experienced in 1999 have repeated in the last decade, and therefore this event was not included in the analysis. In addition, jellies from this genus are known to disappear for decades at a time before blooming again (Williams *et al.* 2001 and references therein; Bayha and Dawson 2010). As species of *Drymonema* can prey on other jellyfish, larger populations of jellyfish at lower trophic levels will be required to sustain it. Therefore, sustained blooms of this species may indicate large blooms of other jellyfish species. In addition, *Drymonema* may be important in regulating these blooms (Williams *et al.* 2001). Recent investigations of this genus have resulted in improved taxonomy, with the description of a new family (Drymonematidae) and new species descriptions (Bayha and Dawson 2010). Such investigations greatly improve the knowledge of this group of enigmatic jellies, and should help with understanding of their population dynamics in the future.

Williams *et al.* (2001) also report on other jellyfish blooms in the Caribbean. Annual blooms of *Aurelia aurita* are noted around Puerto Rico; however, there is no information to suggest if these blooms are either changing or stable. A “population explosion” of unidentified jellyfish is also reported from the region around Bocas del Toro in Panama, indicating such outbreaks have occurred several times in this region since 1997. While it is unclear if these events occurred previous to 1997, a local marine expert notes there have been no major changes in jellyfish abundance in this region over the last 10 years (G. Jacome, STRI, pers. comm., Jan. 2011).

Measurements of the gelatinous community in Lime Cay, Jamaica were reported from 1985/1986 by Clarke (1988) and then again from 1992/1993 by Persad *et al.* (2003). Abundance, biomass, and production were recorded for a number of hydromedusae and ctenophores, although larger scyphomedusae were present but not sampled. Despite the large fluctuations in samples within both studies, overall abundance and biomass measurements were remarkably similar between the two, suggesting the gelatinous community in Lime Cay may be relatively stable (Persad *et al.* 2003). Interestingly, there was a dramatic spatial decline in abundance of the hydromedusae population from the harbour to Lime Cay, while this was not the case with ctenophores. This suggests that the nearshore habitat of the harbour may be important for jellyfish with a meroplanktonic life cycle (Persad *et al.* 2003).

### Invasive Species in LME #12 – Caribbean Sea

The invasive *Phyllorhiza punctata* was first reported from Jamaica in the 1960s (Vanucci 1964)<sup>3</sup>. Cutress (1973) also noted that this species occurs in Jamaica, but a specific location was not reported. A healthy specimen of this species was observed and photographed off the cliffs of Negril, Jamaica in October 2010 (pers. obs.). This species is also reported from Laguna Joyunda, Puerto Rico; however, it likely invaded this location prior to 1950 (Graham and Bayha 2007), and therefore only the Jamaican location was included in the analysis.

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<sup>3</sup> This is cited in Kramp (1970b) as *Mastigias albipunctatus*, which was later attributed to *Phyllorhiza punctata* in most places around the world (K. Bayha, DISL, pers. comm., Dec. 2010).

The globally invasive *Turritopsis dohrnii* has also been reported in this LME from at least two locations Panama: Galeta and Bocas del Toro (Miglietta and Lessios 2009). As discussed, this jellyfish has the unique ability to reverse its life cycle through transdifferentiation, potentially increasing the probability that it will be successfully transported through ballast water (Miglietta *et al.* 2007; Miglietta and Lessios 2009). Despite the ability of *T. dohrnii* to occur in high abundance, it is relatively small in size and unlikely to contribute significantly to the gelatinous biomass (*Invasive Reliability Score = Low*).

### *LME #13 – Humboldt Current*

While jellyfish populations in the majority of this large LME remain understudied, there is one excellent dataset of jellyfish abundance, once again from fisheries surveys. A 37-year record of the large scyphozoan *Chrysaora plocamia* from the coast of Peru was presented by Quiñones *et al.* (2010b). This valuable time series is the result of extensive sampling performed at least twice per year along the coastline from 4° S to below 18°S. The population of jellyfish showed high variability throughout the dataset, and there was a strong correlation with the Peruvian Oscillation Index (POI). As the POI is the best representation of ENSO pulses along the Peruvian coast (Quiñones *et al.* 2010a), jellyfish abundance appears highly influenced by climatic oscillations in this LME, which is also one of the most heavily fished ecosystems in the world due to the massive catches of Peruvian anchoveta (*Engraulis ringens*). Despite the dramatic variation in jellyfish abundance, a linear regression of the dataset reveals a significant negative trend, albeit with a poor fit ( $R^2 = 0.12$ ,  $p = 0.04$ ), and has therefore been classified as a decrease (*Abundance Trend* = -1).

Interestingly, abundance of *C. plocamia* may also influence populations and behaviour of the endangered green turtle *Chelonia mydas*. A time-series of landings of *C. mydas* showed a tight correlation with ENSO events, and large populations of these turtles were observed feeding extensively on abundant jellyfish in Peruvian waters during the 1987 El Niño event (Quiñones *et al.* 2010a).

There have been several other studies of jellyfish in this region (*e.g.*, Pagès and Orejas 1999; Pagès *et al.* 2001; Galea 2007; Palma *et al.* 2007), but they lack a temporal component. Palma *et al.* (2011) note an increase in abundance for numerous jellyfish species from 2004-2006 in the Chiloé Interior Sea of Chile. However, it is unclear if these increases are sustained. The authors also document several species new to Chilean waters. Unfortunately, the scarcity of records in the region prevents recognition of non-indigenous species.

Jellyfish have also interfered with aquaculture operations in Chile, with high mortality of farmed salmon in 2002 (Palma *et al.* 2007) and again in 2009/2010 (H. Mianzan, INIDEP, pers. comm., Jan. 2010). Recent initiatives to catalogue the jellyfish of South America should help to improve the knowledge of jellyfish dynamics in this LME (Oliveira *et al.* 2010).

### Invasive Species in LME #13 – Humboldt Current

A species of the genus *Aurelia* was detected in the South East Pacific for the first time in 2005. Information presented by Häussermann *et al.* (2009) from the Chilean fjord region describes observations of several medusae and numerous scyphozoan polyps. Morphological and molecular evidence indicate the medusae and polyps are *Aurelia aurita*, which the authors infer to be invasive. This species likely arrived via offloaded ballast water, but surprisingly, this jellyfish has not been observed in major ports nearby.

The hydromedusa *Heterotiara minor* was also recently identified in Chilean waters for the first time (Palma *et al.* 2007). However, it is unclear if this species is invasive.

### *LME #14 – Patagonian Shelf*

Data from over 1,000 plankton samples from the Buenos Aires coast were analysed by Genzano *et al.* (2008). Spanning 13 years, the dataset revealed a large bloom of the tiny hydromedusan *Obelia longissima* in 2003. *Obelia* was found at very low densities between 1993 and 2002, never surpassing five individuals per m<sup>3</sup>. In October of 2003, a bloom of this species increased the frequency of occurrence to more than four times previously recorded levels, and densities increased more than two orders of magnitude. Interestingly, this bloom was followed by large shoreline accumulations of the hydroid phase of the same species a few months later. Medusae abundance declined in the following years (2004-2006). However, it remained higher than in years preceding the bloom. A linear regression of the mean densities over time recorded in this study does not result in a significant relationship. Nonetheless, a linear regression applied to the frequency of occurrence does yield a significant trend over time, suggesting that although the densities encountered may not be increasing significantly, this jellyfish is definitely being encountered more often in the latter part of the dataset. Thus, it can be concluded that *Obelia* has increased over the course of the study.

Recent initiatives to catalogue the diversity of jellyfish around South America will further the understanding of jellyfish dynamics in this LME (Oliveira *et al.* 2010). In addition, the abundant scyphomedusan *Lychnorhiza lucerna* is now being considered for commercial exploitation in this region (Schiariti 2008).

#### Invasive Species in LME #14 – Patagonian Shelf

The highly invasive hydrozoan *Blackfordia virginica* was detected in the Río de la Plata estuary for the first time in 2000. Genzano *et al.* (2006) report no detection of this species from 1983 to 1999; however, in 2000 it was found in abundance with thousands of medusae per sample. Specimens of both sex and different size classes suggest local reproduction and an established population. This species was found again in the same estuary in 2005 and 2006, also at very high abundances.

### *LME #15 – South Brazil Shelf*

Historical knowledge of jellyfish from Brazil is poor. However, recent surveys are rapidly cataloguing the diversity of species (*e.g.*, Cornelius and Silveira 1997; Silveira and Cornelius 2000; Nogueira and Haddad 2006; Nogueira *et al.* 2010; Oliveira *et al.* 2010). Unfortunately, the lack of baseline data in this LME makes identifying abundance trends difficult. Jellyfish researchers in the area suggest that Brazil is at least 100 years behind Europe in understanding local jellyfish populations (Marques *et al.* 2003). Nonetheless, there are some indications that native jellyfish populations may be stable in this LME, thanks to a study that interviewed local fishermen. Nagata *et al.* (2009) interviewed 48 fishers from Paraná and Santa Catarina states who regularly use trawl nets to target shrimp. As half of the fishermen interviewed had more than 30 years of experience, a *Time Score* of *Very high* was used. Although the communities that the interviewees called home are not more than 200 km apart, the fishermen are assumed to fish in a large region, and thus a *Space Score* of *Medium* was used. Interviewed between 2003 and 2007, the fishers were asked about the nuisance of jellyfish to their trawl fishing activities. The majority of interviewees regarded jellyfish as a nuisance to their fishing activities and more than 70% claimed economic losses caused by jellyfish interference. Although all respondents reported interannual fluctuations of jellyfish abundance, “they did not report any recent frequency increase in massive occurrences of medusae.” Interestingly, one species which is blamed for major interference with trawling activities, *Lychnorhiza lucerna*, may soon be the target of an experimental fishery in nearby Argentina (Schiariti 2008).

An unusual number of *Aurelia* sp. was detected off of the coast near the Paraná/Santa Catarina state border in 2005 (M. Nogueira, UFP, pers. comm., Sept. 2010). This came as a surprise both to scientists and local fishermen, as this species had not been documented in high abundance in the region before. However, large aggregations have not been reported since, and thus this unique event has not been included in the analysis.

#### Invasive Species in LME #15 – South Brazil Shelf

While the invasive *Phyllorhiza punctata* has been noted in this LME on more than one occasion, it seems to disappear after several years of detection, at least at the medusa stage. The possibility remains that polyp colonies have successfully established in this LME. However, the sudden disappearance of medusae after several consecutive years of presence, as well as the long time frame between new detection events, suggests multiple invasions. The first Brazilian specimens were recorded in the 1950s around Rio de Janeiro, São Paulo State, and Paraná State (Kramp 1970b; Moreira 1961 in Haddad and Nogueira 2006). Briefly very abundant, this population disappeared a few years later and medusae were not seen again in this region until 2001, when they began to be reported annually (Haddad and Nogueira 2006). Abundant until 2005, this population then began to decline and no medusae have been detected since 2007 (M. Nogueira, UFP, pers. comm., Sept. 2010). While these fluctuations are categorized as stable/variable (*Abundance Trend* = 0) for the purposes of this analysis, the probability of subsequent invasions remains high due to the history of invasions in the region, high shipping traffic, and the presence of this species in the nearby East Brazil Shelf LME. In fact, Haddad and Nogueira (2006) suggest that *P. punctata* is likely occurring along the entire coast of Brazil, but scattered records make the distribution uncertain. Interestingly, recent molecular evidence suggests that the invasive populations found in Brazil may be a separate species from other invasive *Phyllorhiza* populations, and that populations in Brazil may have originated in Indonesia (Bayha *et al.* 2010).

Medusae of both *Moerisia inkermanica* and *Blackfordia virginica* were collected in the Paranaguá Bay system in 2004 and 2005 (Nogueira and de Oliveira 2006). Due to a lack of previous samples, the authors consider these species cryptogenic. However, it is likely they are invasive given that they are native to the Black Sea, are well-known invaders, and the area is subject to high port traffic (Nogueira and de Oliveira 2006). *B. virginica* was collected in this area again in 2007 and 2008, as well as a number of other estuaries along the coast, including the Cananéia complex, Guaratuba Bay, and Babitonga Bay (Bardi and Marques 2009b). While it is unclear if this species persists in all of these locations, individuals of both sexes and a variety of size classes have been collected in Paranaguá Bay and Babitonga Bay, suggesting established populations. The discovery of medusae in these new locations provides additional support for invasions, as this species was not detected in earlier extensive plankton studies of southern Brazil (Bardi and Marques 2009b and references therein). Combined with the fact that it is now found only in estuaries with high shipping traffic, it is considered invasive.

#### *LME #16 – East Brazil Shelf*

As mentioned, knowledge of jellyfish in Brazil is poor, and is estimated to be at least 100 years behind jellyfish knowledge in Europe (Marques *et al.* 2003). While recent surveys are cataloguing the diversity of jellyfish in this LME (e.g., Morandini *et al.* 2006; Oliveira *et al.* 2010), there are no sources of data to identify trends in native jellyfish populations.

#### Invasive Species in LME #16 – East Brazil Shelf

The invasive *Phyllorhiza punctata* is reported from two disparate locations in this LME. The first population, in Todos os Santos Bay in Bahia State, was reported as early as 1991 and appears to be

established (Silveira and Cornelius 2000). Medusae have also been seen further north in Fortaleza, Ceará State, apparently since 2003 (Haddad and Nogueira 2006). It is unclear if these populations have disappeared like those further south in Brazil (see LME #15 – South Brazil Shelf), but as they represent separate populations, they are assumed to be established. As stated, it is possible that *P. punctata* is occurring along the entire Brazilian coast (Haddad and Nogueira 2006).

The invasive hydromedusan *Blackfordia virginica* was also reported in this LME prior to 1963 (Paranaguá 1963 in Moore 1987). However, it remains unclear if it is established.

### *LME #18 – West Greenland Shelf*

Pedersen and Smidt (2000) present the results of oceanographic surveys conducted off of southwestern Greenland by the Greenland (Danish) Fisheries Research Institute from 1950 to 1984. The only jellyfish reported was the hydromedusa *Aglantha digitale* (assumed dominant), for which a “red type” and “white type” were enumerated. An index of abundance for *A. digitale* is presented from 1956 to 1982 for section S3 (southernmost section). While there were variations in abundance across sections, the trend observed for section S3 is assumed to apply to the entire study area. Over the course of the study, *A. digitale* shows a decreasing trend through the 1960s and an increasing trend thereafter. Although this increasing trend continues through the 1970s and into the 1980s, abundance levels did not return to levels seen in the 1960s by the end of the study period. Therefore, the overall trend is classified as a significant decrease (*Abundance Trend* = -1). Without recent data, it is unknown whether the increasing trend has continued in recent decades and if this population has recovered to historic levels. This LME has experienced major regime shifts in recent decades, driven by interactions between climate and anthropogenic influences (Buch *et al.* 2004). As such, it is likely that jellyfish populations in this region have also experienced significant changes. Due to the low spatial resolution of the data presented, the lack of data from the past three decades, and the likelihood of recent changes, the solitary chronicle in this LME is classified with high uncertainty (*Reliability Score* = Low).

### *LME #21 – Norwegian Sea*

The mesopelagic *Periphylla periphylla* appears to have increased in several Norwegian fjords, where it now occurs in very high abundances. After Lurefjorden (see LME #22 – North Sea) became dominated by *Periphylla* in the 1970s (Fosså 1992), it was followed by Halsafjorden in the 1980s (Sørnes *et al.* 2007). *Periphylla* are normally deep-ocean jellyfish with an entirely holopelagic lifestyle (Jarms *et al.* 1999), and their success in Norwegian fjords is likely due to a combination of retention and light attenuation (Sørnes *et al.* 2007). Sills of the fjord basins, as well as vertical migration, facilitate retention of the medusae. As light has lethal effects on *Periphylla* (Jarms *et al.* 2002), sufficient optical depths must be achievable for these jellyfish to survive. The precipitous increase of this species in Norwegian fjords may be due to decreasing light levels mediated by climatic changes and cultural eutrophication in the North and Baltic Seas (Eiane *et al.* 1999; Sørnes *et al.* 2007). Populations of this species continue to be discovered in fjords where it was not previously observed (Hosia 2007). This species of jellyfish, as well as others, are now being considering for exploitation as commercial food fisheries in Norway (Wang 2007).

There is circumstantial evidence that siphonophores may also be increasing in the Norwegian Sea (Båmstedt *et al.* 1998; Fosså *et al.* 2003; Hosia 2007). However, the scope of the events is unclear and will be discussed as part of the North Sea LME.

### Invasive Species in LME #21 – Norwegian Sea

The invasive ctenophore *Mnemiopsis leidyi* was recently documented in this LME. Underwater photographs from 2008 confirmed the identity of *M. leidyi* in Trondheimsfjorden, which is at 64 °N (A. Hosia, IMR, pers. comm., Oct. 2010). As such, it appears that the range of this highly invasive jellyfish continues to expand.

### *LME #22 – North Sea*

The Continuous Plankton Recorder (CPR) survey is one of the most temporally and spatially extensive plankton datasets in the world. Recorders are towed behind ships of opportunity at a depth of approximately 10 m (see Batten *et al.* 2003). Although the entrance aperture for sampling is only 1.27 cm<sup>2</sup>, the survey records samples of cnidarian tissue and nematocysts. While this device is clearly not designed to sample jellyfish, the consistent sampling methods over time and space allow for an index of presence of Cnidaria sampled. In the North Sea, the most common species sampled is assumed to be the hydromedusan *Aglantha digitale* (Attrill and Edwards 2008). Licandro *et al.* (2010) analysed CPR data from the North Sea from 1958-2007 and found an increase in frequency of Cnidaria since the early 1980s. This is consistent with another analysis of this dataset over similar scales (Attrill *et al.* 2007; Attrill and Edwards 2008). While CPR data likely do not provide a true index of relative abundance, and despite concerns surrounding collection and analysis methods (Haddock 2008), it is assumed that the increase in the frequency of occurrence of Cnidaria sampled represents an increase in the integrated gelatinous biomass, at least for the species sampled.

An extensive survey of jellyfish abundance in the North Sea comes from yet another fisheries dataset. Hay *et al.* (1990) present data on scyphomedusae bycatch collected during the ICES International o-group Gadoid Surveys in June and July from 1971-1986. Trawls were fished for one hour using a standard depth profile of 20 minutes near the sea bottom, 20 minutes at the thermocline or in mid-water, and 20 minutes near the surface (5-10 m). While this method underestimates total jellyfish biomass, the consistent methods used throughout the study allow for comparison and an index of relative abundance. In total, over 2000 trawls were made, catching more than 430,000 jellyfish. While much of the northern area of the North Sea was sampled extensively, four sub-areas were established based on consistent sampling and occurrence of dominant jellyfish species. Populations of jellyfish showed high variability in all of the sub-areas over the time-series, with no significant linear temporal trends (Lynam *et al.* 2004). While the findings from this dataset do not necessarily agree with the CPR data discussed above, the surveys are thought to sample different gelatinous communities (Haddock 2008; Lynam *et al.* 2010). The trawl dataset was also analysed by Lynam *et al.* (2004, 2005; 2010), who demonstrated that jellyfish abundance was significantly correlated with several climate indices including the North Atlantic Oscillation Index (NOAI), as well other hydrographic measurements. These results suggest that the dominant jellyfish species in the North Sea may be highly influenced by climatic changes.

Jellyfish populations appear to be changing in the Dutch Wadden Sea. Catch data from a fish fyke off Texel Island in the Netherlands have been collected on a daily basis (except during winter and mid-summer) for 50 years by the Royal Netherlands Institute for Sea Research (NIOZ). The fyke works much like a set net, and although it was designed for monitoring fish populations, jellyfish are also counted. Findings from the analysis on jellyfish have not yet been published, but van Walraven (2010) presented some preliminary results. While there has been no consistent trend in abundance for all jellyfish, the ctenophore *Pleurobrachia pileus* appeared with greater frequency in recent decades. The most dramatic finding from the dataset is revealed when jellyfish phenology is examined. Numerous scyphomedusae, including *Aurelia aurita*, *Chrysaora hysoscella*, *Cyanea capillata*, and *Cyanea lamarcki* have all shown a dramatic shift in the time of first appearance in latter decades. In most cases, these shifts are on the order

of weeks or even months. Such remarkable changes in phenology may be due to warmer water temperatures, which have increased significantly in the Wadden Sea in recent decades (Martens and van Beusekom 2008). *Rhizostoma pulmo* did not show the same trend, and actually declined in abundance over the course of the study, but this could be because it is predominantly a summer species. The last two years of data show extreme variability, with 2009 exhibiting low densities for most native species and a precipitous spike in the population of the invasive ctenophore *Mnemiopsis leidyi*. After a very cold winter, 2010 resulted in fewer *M. leidyi* and a return to higher abundances for most native species.

As discussed for the Norwegian Sea LME, populations of the holoplanktonic *Periphylla periphylla* appear to have increased in several Norwegian fjords. This species has been reported from Lurefjorden in varying amounts since at least the 1940s, but 1973 marked a “population explosion” that was a nuisance to fishers (Fosså 1992). Since then, the problem has become increasingly worse (Fosså 1992), and recent measurements show even higher abundances of *Periphylla* in this fjord (Youngbluth and Båmstedt 2001; Sørnes *et al.* 2007). As mentioned, *Periphylla* is normally a mesopelagic species. Its success in Norwegian fjords is likely due to a combination of retention and light attenuation in the fjord basins (Sørnes *et al.* 2007). Climatic changes and cultural eutrophication in the Baltic and North Seas may have increased light attenuation in these fjords in recent decades, facilitating the increase of this unique and fascinating jellyfish (Eiane *et al.* 1999; Sørnes *et al.* 2007). In addition, *Periphylla* populations have recently been discovered in several fjords where it was not observed previously (Hosia 2007). Norway is now considering a commercial harvest of this jellyfish, as well as other species (Wang 2007).

There is circumstantial evidence to suggest that siphonophores may be increasing in the northern part of this LME. Although the evidence did not meet the qualifications to be included as a chronicle in the analysis, the trend is worthy of discussion. Båmstedt *et al.* (1998) note a mass occurrence of *Apolemia uvaria* in Norwegian waters in 1997, which caused high mortality to fish in aquaculture operations. While fishers report that the high abundance of siphonophores is not a new phenomenon, confusion with salps may have occurred (Båmstedt *et al.* 1998). More impacts on farmed salmon due to this species were reported in 2001 (Fosså *et al.* 2003). A similar event involving *Muggiaea atlantica* occurred in 2002, the first time a mass occurrence has been described from Norway (Fosså *et al.* 2003). Reports of stings came from swimmers in Denmark and Norway, and more than 1,000 tonnes of farmed salmon died as a result of lesions and suffocation (Fosså *et al.* 2003). While it is unclear if these events involving siphonophores are indications of increased populations, it seems likely that more southerly species will continue to appear as waters warm and currents are affected (Hosia 2007).

There is also evidence to suggest that jellyfish have increased in Limfjorden, a highly eutrophicated system in Denmark that connects the North Sea with the Kattegat. Riisgård *et al.* (2012) tell a compelling story that begins with increasing nutrient input through the 1960s and 1970s, due primarily to runoff from agricultural activities. This caused increased eutrophication in Limfjorden, which now suffers from annual summer hypoxia that can cover up to 40% of the bottom. These events result in the release of toxic hydrogen sulphide from the sediments and mass mortality of zoobenthos, including dense mussel beds and demersal fish. The dramatic reduction in demersal fish through the 1980s was associated with a concurrent increase in jellyfish, primarily the scyphomedusan *Aurelia aurita*. Predation by these jellies on zooplankton likely reduces grazing on phytoplankton, contributing to a positive feedback loop whereby eutrophication is exacerbated (Møller and Riisgård 2007a). Large blooms of jellies interfere with fisheries research trawls in Skive Fjord, a section of Limfjorden. Hoffmann (2005) has calculated the percentage of trawls that are not completed due to overloading of the fishing gear by jellyfish. This ‘Hoffmann -index’ (Møller and Riisgård 2007a) helps to demonstrate the large interannual variability of medusae populations, as they can be virtually absent in some years, whereas in other years they can interfere with more than half of the research trawls conducted. While the narrative presented by Riisgård *et al.* (2012) contains convincing evidence for an increase of the jellyfish population in this region, spectacular blooms



and interference with fishing are not a new phenomenon in Limfjorden. Poulsen *et al.* (2007) note that jellyfish frequently disrupted fishing for eel (*Anguilla anguilla*) in the 1800s. In 1827, “jellyfish took up so much space that the seines could not be drawn through the water,” and jellyfish were frequently reported to obstruct fishing in the 1840s. The authors suggest that the high abundances of jellyfish in the mid-1840s may have been due to the breaching of the isthmus at Agger in 1825, which resulted in a new connection between Limfjord and the North Sea, dramatically altering the species composition of the ecosystem. The fact that these historical events involving jellyfish are not mentioned by Riisgård *et al.* (2012) highlights an important issue concerning recent proliferations of jellyfish, *i.e.*, that a historical context may be lacking. As such, notable blooms in the present or recent past may therefore not necessarily be “new” events, but rather a consequence of ‘shifting baselines’ (Pauly 1995; Condon *et al.* 2012). While the present analysis attempts to examine changes in jellyfish abundance in the last 60 years, such changes are only part of longer-scale population dynamics, especially as there is a reporting bias from recent decades. As such, it is important that as much historical information as possible is gleaned from a variety of sources so that current observations can be viewed in a historical context. In addition, we must strive to collect as much detailed information as possible on jellyfish populations today, so that we can understand changes in the future.

In Limfjorden, changes in the jellyfish populations continue, perhaps partly controlled by hydrodynamics. In 2004 and 2005, intrusions of large volumes of high-salinity waters from the North Sea coincided with an absence of *Aurelia* and high abundances of the hydromedusan *Aequorea vitrina*, a jelly that had not previously been recorded in Limfjorden (Møller and Riisgård 2007b; Riisgård *et al.* 2012). Limfjorden has also recently been invaded by the prolific ctenophore *Mnemiopsis leidyi* (see below).

The Helgoland Roads dataset is unique in that it represents a long time-series from a single offshore station that actively samples gelatinous zooplankton, typically three times per week (Greve *et al.* 2004). Analyses of interannual changes in mean annual abundance and phenology were presented by Greve *et al.* (1996) covering the period from 1974–1994. The hydrozoans *Aglantha digitale* and *Obelia* spp. both showed no obvious trend. Further information was presented for the ctenophore *Pleurobrachia pileus* by Greve *et al.* (2004), and additional details on the seasonality of *P. pileus* and *Beroe gracilis* can be found in Schlüter *et al.* (2010). *P. pileus* and *B. gracilis* both showed dramatic phenological changes, including a shift to permanent earlier appearances starting in 1987–1989 of 4–10 weeks, and expansions of peak abundance into spring and summer. While this may indicate an increase in integrated jellyfish biomass, more recent abundances of *P. pileus* are still well below the peak abundance recorded in 1984. Information is also presented for *Muggiaea atlantica*, which did not appear in the zooplankton until 1989, when it was observed in extraordinary abundance in the German Bight (Greve 1994). *M. atlantica* has been part of the local fauna since then, but only sporadically and never in abundances comparable to those in 1989 (Greve *et al.* 2004). This detailed, long-term dataset highlights the challenges of identifying trends in jellyfish populations. Despite the phenological changes observed in *P. pileus* and *B. gracilis*, as well as the recent occurrences of *M. atlantica*, this dataset is conservatively classified as variable (*Abundance Trend* = 0), due to the aforementioned dynamics of *P. pileus*. However, due to the possible increase of the other two species, the *Reliability Score* of this chronicle is reduced to *Low*. A more robust statistical analysis including all jellyfish in this valuable dataset is required before definitive conclusions can be drawn regarding a change in gelatinous biomass.

One of the few observed declines in a species of jellyfish occurs in this LME. Attrill and Thomas (1996) report on jellyfish recorded from samples taken at the West Thurrock Power Station in the Thames Estuary. Samples were taken every two weeks between 1977 and 1992, until the power station was closed in 1993. The ctenophore *Pleurobrachia pileus* was recorded consistently in summer over the course of the study, often occurring in blooms so dense as to rupture sampling nets. Despite the high seasonality and some interannual variability, *P. pileus* showed no obvious trend over the period sampled. In contrast,

large blooms of *Aurelia aurita* were observed in the first half of the dataset, but abundances were dramatically reduced after 1984, with many years showing a virtual absence of this species. While this rapid decline of a conspicuous scyphozoan is alarming, the lack of data after 1992 makes it unclear if this decrease persists or not. The decline may also simply represent a change in the hydrodynamics of the estuary, as *A. aurita* typically peak later in the season at this location compared to nearby areas, which could reflect a period required for medusae to move up the estuary (Attrill and Thomas 1996).

Although it was not included as a separate chronicle because the details were not available at the time of writing, there is an interesting dataset from this LME that will hopefully be available soon. Daily visual counts of *Aurelia* spp. and *Cyanea* spp. have been made from a quay in Arenal, Norway from 1992 to the present. The data show high variability, thus making analysis difficult. However, there appears to be a small decrease in *Aurelia* spp., with no change for *Cyanea* spp. (T. Falkenhaus, IMR, pers. comm., March 2011).

#### Invasive Species in LME #22 – North Sea

The highly invasive ctenophore *Mnemiopsis leidyi* appears to have successfully invaded the North Sea and is rapidly expanding its range. This species was first observed in 2005 in southeast Norway (Oliveira 2007) and western Denmark (Tendal *et al.* 2007), and then in several locations in 2006, including the Netherlands (Faasse and Bayha 2006), Sweden (Hansson 2006), Helgoland (Boersma *et al.* 2007), and many additional locations in Danish waters (Tendal *et al.* 2007). It has also since been observed in western Norway (Hosia 2007). While 2005 marked the first confirmed observation, it is likely that *M. leidyi* has been present in the North Sea for much longer (Faasse and Bayha 2006; Hansson 2006; Boersma *et al.* 2007) and it continues to be detected (Selander *et al.* 2010). In 2007, Denmark's Limfjorden was witness to populations of *M. leidyi* with densities exceeding 800 individuals  $\text{m}^{-3}$  and biovolumes up to 300  $\text{mL} \cdot \text{m}^{-3}$ , eclipsing the peak biovolumes from the Black Sea (Riisgård *et al.* 2007).

#### *LME #23 – Baltic Sea*

Barz and Hirche (2005) report on scyphomedusae abundance and biomass in the Bornholm Basin and compare their measurements to those published from earlier years. An examination of abundance in the month of August allows comparison of data back to 1994, as well as inclusion of additional data from 2003 reported by Barz *et al.* (2006). Thus, four separate abundance measurements over a 10-year span can be examined for *Aurelia aurita* and the less abundant *Cyanea capillata*. Such a comparison reveals a stable/variable trend for these species, with abundances in 1998 and 2002 being roughly double what they were in 1994 and 2003. The different patterns observed in 2002 and 2003 highlight the large potential for interannual variability in this system (Barz and Hirche 2005; Barz *et al.* 2006). In addition, the possible absence of ephyrae combined with the late arrival of medusae point to advection as the controlling factor for medusae in the central Baltic – a hypothesis supported by circulation models (Barz *et al.* 2006).

Schneider and Behrends (1994) similarly report interannual variation for *A. aurita* in Kiel Bight. Median abundance and biomass was measured and compared with earlier studies, allowing comparisons from 1978-1993. Both abundance and biomass varied by an order of magnitude, sometimes between consecutive years. More recent data on jellyfish populations would allow further comparison and would be useful for fisheries managers, as *A. aurita* appear to be a major predator in this region, potentially exerting top-down control on larval herring (Möller 1984), as well as copepods and other ichthyoplankton (Möller 1979; Behrends and Schneider 1995). In years of high *A. aurita* abundance, intense predation may result trophic cascades (Schneider and Behrends 1998).

### Invasive Species in LME #23 – Baltic Sea

Several species of invasive jellyfish have been reported from the Baltic Sea. The highly invasive ctenophore *Mnemiopsis leidyi* was first observed in this LME in the Kiel Bight in 2006, where it increased to very high abundances (Javidpour *et al.* 2006). The range of *M. leidyi* appeared to spread further in 2007, when it was detected in several additional locations (Kube *et al.* 2007; Tendal *et al.* 2007) including the Bornholm Basin (Haslob *et al.* 2007). While the population in the Bornholm Basin is likely not self-sustaining, average autumn abundance increased from 2007 to 2009 (Schaber *et al.* 2011). There are also reports that *M. leidyi* has spread further into the central and northern Baltic (*e.g.*, Lehtiniemi *et al.* 2007). However, there is some doubt as to whether the species detected is truly *M. leidyi*, as no molecular evidence has confirmed its presence in more northerly locations (Gorokhova *et al.* 2009; Gorokhova and Lehtiniemi 2010). Therefore, a *Space Score* = *Medium* has been conservatively assigned to this chronicle.

The species that was potentially misidentified as *M. leidyi* in the northern and central Baltic is more likely *Mertensia ovum*. Gorokhova *et al.* (2009) confirmed the presence of this species from various samples taken from numerous locations in the northern half of the Baltic Sea, based on molecular evidence. This jellyfish is known to have a broad distribution at high latitudes, but had not previously been reported from the Baltic. As such, this jellyfish is assumed invasive; however, a *Reliability Score* = *Low* was used to reflect the uncertainty concerning the invasion (Anonymous 2009b).

The invasive hydromedusan *Maeotias marginata* was first detected in the Väinameri Archipelago of the northern Baltic Sea near Estonia in 1999, with ballast water suggested as a potential vector (Väinölä and Oulasvirta 2001). Medusae were not observed in 2000, but sampling from 2002-2005 did reveal at least two individuals in 2002 and 2003 (Ojaveer and Kotta 2006). While this chronicle is scored with *Confidence Index* = *Low* due to the confirmation of only a few individuals, the presence of this species cannot be ignored as it has been shown to occur at high abundances in other non-indigenous locales (Mills and Sommer 1995).

The hydromedusan *Gonionemus vertens* is also likely invasive in the Baltic. However, this species was detected there well before 1950 (Leppäkoski *et al.* 2002) and was therefore not included in the analysis.

### *LME #24 – Celtic-Biscay Shelf*

While the Continuous Plankton Recorder (CPR) is certainly not designed to sample jellyfish, it can be useful for identifying trends in the frequency of occurrence (see LME #22 – North Sea for further discussion). Licandro *et al.* (2010) analysed CPR data for presence of cnidarian tissue and nematocysts in an area spanning this entire LME. Data were divided into two periods, 1958-2001 and 2002-2007. Mean spatial distributions were calculated for each period, along with the associated anomaly. Waters in this LME showed an increase in the frequency of Cnidaria in the latter period (*i.e.*, since 2002). While this trend was evident throughout the LME, the region of greatest increase was located off southwest Ireland (see Fig. 2a in Licandro *et al.* 2010). Genetic analysis of Cnidaria samples from 2007 and 2008 revealed the dominant species was *Pelagia noctiluca* (Baxter *et al.* 2010; Licandro *et al.* 2010), while four species of siphonophore were also identified. *P. noctiluca* lacks a polyp stage and has a wide distribution across ocean basins (Arai 1997; Purcell 2005). This species was also involved in a major fish kill at an aquaculture operation in 2007, resulting in the death of more than 250,000 fish and losses in the millions of dollars (Anonymous 2007b; Doyle *et al.* 2008).

Lynam *et al.* (2011) analysed annual spring survey data for juvenile gadid fish in the Irish Sea from 1994 to 2009. Double-oblique tows were conducted and jellyfish were separated from the catch and weighed. Ctenophores were also separated from the catch; however, no data are presented on their abundance or

biomass. Since 2007, jellyfish catch has been separated by species and has been dominated by *Aurelia aurita*, *Cyanea capillata*, and *Cyanea lamarckii*. Several other species were also detected at low abundances. Analysis revealed an increasing linear trend in annual catch weights of jellyfish ( $R^2 = 0.26$ ,  $n = 16$ ,  $p = 0.03$ ). Frequency of occurrence data from the CPR survey in the same region showed a significant positive correlation to jellyfish catch weights, lending strength to the validity of both datasets. The authors conclude that “in the Irish Sea, an increase in jellyfish abundance was evident”. Recent anecdotal reports indicate that the populations of *Cyanea* spp. have remained high in 2010 and 2011 around Ireland (Gittens 2011).

Lilley *et al.* (2009) report on abundance of the conspicuous *Rhizostoma octopus* over three years (2003–2005) from aerial surveys of two “hotspots” in the Irish Sea. A third hotspot had only two years of data, but showed a similar trend. All stations showed high average abundances ( $>25$  jellyfish·m<sup>-2</sup>) during 2003, followed by much lower abundances in 2004 and 2005 (2 stations only). While this could be evidence of a decline in jellyfish biomass over the short 3-year timespan, the authors also compiled historical reports of *Rhizostoma* spp. in European waters. The authors note that the reports appear to suggest an increased frequency of large blooms in the late 20<sup>th</sup> century. However, the sporadic nature of the reports casts some doubt on this conclusion, and it was therefore not included as a separate chronicle in the analysis. Recently, there have been reports of large blooms of *R. octopus* and other jellyfish in the Irish Sea (Anonymous 2011f, 2011h), including blooms that extend into cooler seasons than usual (Murphy 2011).

The Plymouth Marine Laboratory has been collecting weekly data on zooplankton abundance at a coastal station known as “L4” since 1998. Located in the Western English Channel, the L4 station is sampled using vertical net hauls from the sea floor (~55 m) to the surface. The 20-year time-series reveals a significant decline in average abundance for hydromedusae (WCO 2011). However, if siphonophores are also included in the analysis, there is no significant trend. Therefore, this chronicle is classified as stable/variable (*Abundance Trend* = 0).

There is also knowledge of jellyfish populations in Southampton Water (C. Lucas, NOC, pers. comm., Jan. 2011), an estuary in southern England. Abundances of *Aurelia* sp. were relatively high in the 1980s and appeared to decline in the 1990s. No *Aurelia* medusae were spotted in 2006 and 2007; however, in recent years the population appears to have returned to high abundances. In addition, ctenophores of the genus *Pleurobrachia* have been observed in high abundances in recent years, and appear to be in the water column for longer periods. While the sampling for jellies in this region has not been consistent over the years, the recent observations of high abundances of medusae and ctenophores suggest populations may have increased in this location. *Aurelia* polyps were also discovered on mussel shells attached to the underside of floating pontoons in the estuary in 2009 (Duarte *et al.* in review). As such, this chronicle has been classified as an increase (*Abundance Trend* = 1), albeit with the highest level of uncertainty (*Confidence Index* = Low).

#### Invasive Species in LME #24 – Celtic-Biscay Shelf

While not included as a separate chronicle in this LME, several species of invasive hydrozoans have been reported from the Loire Estuary in France, including *Maethias inexpectata*, *Nemopsis bachei*, and the Ponto-Caspian invader *Blackfordia virginica* (Denayer 1973). It remains unclear to what extent these invaders have established in this LME.

#### *LME #25 – Iberian Coastal*

The Instituto Español de Oceanografía (I.E.O.) has been monitoring plankton communities and other variables at numerous stations along the north and northwest coasts of Spain for over a decade (Valdés *et*

*al.* 2007). Stations *Vigo* and *Coruna* report on siphonophores and salps, as does *Santander*, with the addition of medusae. While the sampling gear used in the surveys is not designed for jellyfish and therefore must be interpreted with caution (A. Bode, IEO, pers. comm., June 2010), consistent methods allow for comparison of relative abundance. All stations show high variability in the density of these groups from the mid-1990s into the mid-2000s (IEO 2010). Peak years for salps and siphonophores are obvious, but show no significant trends over the time period (*Abundance Trend* = 0).

#### Invasive Species in LME #25 – Iberian Coastal

Medusae of the globally invasive *Blackfordia virginica* were found in high densities in the Guadiana Estuary in 2008 (Chícharo *et al.* 2009). Comprehensive surveys of this estuary from 1999 to 2003 did not detect this species, suggesting a recent invasion. While it may be too early to indicate that this species has successfully established itself here, specimens have been found of both sexes over a wide range of size classes. Combined with the high abundances observed, this would suggest local reproduction (Chícharo *et al.* 2009). This species was also detected nearby in the Mira Estuary in 1984 (Moore 1987); however, it is unclear if that population has persisted.

#### *LME #26 – Mediterranean Sea*

Jellyfish population changes are perhaps better documented in the Mediterranean than anywhere else, thanks primarily to a combination of long-term datasets and high public interest due to tourism impacts. By far the most notorious jellyfish in the Mediterranean is the mauve stinger, *Pelagia noctiluca*. This scyphomedusan lacks a polyp phase, *i.e.*, it has a holoplanktonic lifestyle that does not restrict it to coastal waters. Nonetheless, blooms of this jellyfish are often found near shorelines, inflicting painful but non-fatal stings to tens of thousands of seabathers each year (Purcell *et al.* 2007; Anonymous 2010h). The population dynamics of this species can be depicted as “presence-absence” (UNEP 1984, 1991), whereby blooms occur for several consecutive years followed by periods lacking major outbreak events. A long-term dataset constructed by Goy *et al.* (1989) from various sources has records of *P. noctiluca* dating back to the 18<sup>th</sup> century, indicating bloom years and non-bloom years. Although some observations were made from single locations (such as the extensive records from the Station Zoologique de Villefranche-sur-Mer, France), most rigorously described blooms indicate a trend that appears to cover the entire western basin of the Mediterranean (Goy *et al.* 1989). The analysis from 1875-1986 indicated that episodes of bloom years showed a significant period of about 12 years. However, blooms of *P. noctiluca* began to deviate from this pattern in the late 1990s, and persistent blooms have since occurred in the western Mediterranean quasi-annually (Anonymous 2008b, 2010c; Daly Yahia *et al.* 2010). Although the number of several species of jellyfish observed along Spain’s Catalan coast do not show an obvious trend over the last decade (Atienza *et al.* 2010), there are reportedly increases of *P. noctiluca* in recent years further to the west along Costa Blanca (Anonymous 2010h).

When other gelatinous groups are considered – such as hydromedusae, siphonophores, and ctenophores – the patterns of jellyfish abundance in the western Mediterranean become increasingly complex. Abundance of the small, holoplanktonic hydromedusae *Liriope tetraphylla* showed considerable seasonal, interannual, and decadal variation from 1966-1993 at Villefranche-sur-Mer, but there was no overall increasing or decreasing trend apparent in the dataset (see Fig. 2 in Buecher *et al.* 1997). Interestingly, the abundance of *L. tetraphylla* appeared to correspond negatively to that of *P. noctiluca*, with the strongest years for *L. tetraphylla* occurring during periods when *P. noctiluca* was absent (Buecher *et al.* 1997). It remains unclear whether this correlation is due to competition, predation, or environmental conditions (Legović 1987; Buecher *et al.* 1997). García-Comas *et al.* (2011) analysed the seasonality and abundance of numerous zooplankton groups at Villefranche-sur-Mer using ZooScan technology, which facilitated the processing of large samples. Data from 1974 to 2003 were included, and

gelatinous zooplankton were divided into carnivorous medusae and siphonophores. Both of these groups showed relatively low abundances through the 1970s along with increases through the 1980s. These results are consistent with those of Molinero *et al.* (2005; 2008a; 2008b), who examined only selected species of jellyfish. However, the increases observed in the early 1990s were not observed in the analysis of the entire jellyfish community. Rather, the medusae and siphonophore populations continued a near-decadal cycle by exhibiting relatively low abundance through the 1990s, followed by returns to higher abundances in the last few years of the dataset (see Figs. 3 and 4 in García-Comas *et al.* 2011). In addition, the ctenophore *Pleurobrachia rhodopsis* appeared to decrease in the late 1980s (Molinero *et al.* 2008a), and salps showed periodic blooms but no consistent trends (Licandro *et al.* 2001). This dataset highlights some of the differences between examining individual species versus considering entire community groups, such as jellyfish and zooplankton. As stated by García-Comas *et al.* (2011), "...the analysis of broad groups [...] does not substitute but efficiently complements the species level approach..."

The population of jellyfish appears to have increased in Mar Menor, a Spanish coastal lagoon. This hypersaline lagoon is relatively shallow (~3.5 m average depth) and is separated from the Mediterranean by a sandy barrier with several inlets. Traditionally, this lagoon was a singular ecosystem that supported important artisanal fisheries, as well as a small population of *Aurelia* spp. (Pagès 2001). However, the lagoon has been subject to major environmental changes due to anthropogenic disturbances, starting in the 1970s, which have dramatically changed the ecosystem. The disturbances began with the enlargement of several inlets to facilitate the passage of recreational boats, and have continued to include the construction of new harbours, dredging and dumping of sand for artificial beaches, mining operations, changes in runoff, increased eutrophication, and intensive coastal development (Pérez-Ruzafa *et al.* 1991; Pagès 2001). In the mid-1980s, two new scyphozoans (*Cotylorhiza tuberculata* and *Rhizostoma pulmo*) were recorded in the lagoon and began forming large blooms in the mid-1990s (Pérez-Ruzafa *et al.* 2002). These large blooms have been problematic for the tourist industry ever since and there are now efforts to capture and remove thousands of tonnes of jellyfish from this lagoon (Pagès 2001; Conesa and Jiménez-Cárceles 2007; Prieto *et al.* 2010). Nonetheless, it appears that both of these species have completed their life cycle in Mar Menor (Fuentes *et al.* 2011) and continue to thrive there. Curiously, *R. pulmo* directly consumes diatoms in Mar Menor, and may benefit from increased production due to eutrophication (Pérez-Ruzafa *et al.* 2002; Lilley *et al.* 2009). Polyps of *Aurelia* spp. and *C. tuberculata* have been reported from this lagoon attached to artificial dock structures and marine debris (Duarte *et al.* in review). As polyps of *C. tuberculata* appear highly influenced by temperature, it is suspected that blooms of this jellyfish will be increasingly recurrent in Mar Menor under global warming scenarios (Prieto *et al.* 2010).

The recent changes in *Pelagia noctiluca* populations in the western basin are not consistent with the rest of the Mediterranean, but rather demonstrate different dynamics in recent decades. Blooms in the Aegean Sea appear to be maintaining the aforementioned 12-year periodicity (Daly Yahia *et al.* 2010). However, there are indications that blooms of *Chrysaora hysoscella* are larger in this region in recent years (Öztürk and İşinibilir 2010). In the Adriatic Sea, *P. noctiluca* was relatively rare until 1977, when it began blooming frequently (Zavodnik 1987). Blooms continued for about 10 years, until 1987, when *P. noctiluca* blooms in the Adriatic appeared to subside and virtually disappear for more than a decade. However, in 2004, blooms began in this region again (Daly Yahia *et al.* 2010) and continued until 2007 (Kogovšek *et al.* 2010).

In addition to the periodic appearances of *P. noctiluca*, the Adriatic Sea shows other signs of increasing jellyfish populations. Kogovšek *et al.* (2010) performed a wavelet analysis of jellyfish blooms in the Adriatic over the last 200 years, and found that blooms have been occurring more frequently in recent decades. Several scyphozoans were included in the analysis, with *Aurelia* spp. being the most frequently reported. Species of this genus showed periodic blooms throughout the dataset, but the frequency of these

events increased during the 1990s. While increased observations of this species may be partially due to improved sampling techniques, major blooms of *Aurelia* appear to be on the rise in the Adriatic, and have occurred annually since 2004. *Rhizostoma pulmo* also showed similar dynamics, with an increased recurrence of blooms over the last two decades. However, the abundance of this species appears to have decreased since 2006. Potentially playing a role in the increase of *Aurelia* medusae, polyps have been discovered on anthropogenic habitat in this region. Scyphopolyps were reported in Koper Harbor, Gulf of Trieste, on the undersides of oyster shells attached to piers (Duarte *et al.* in review). Di Camillo *et al.* (2010) also recorded scyphopolyps on underside portions of an iron shipwreck near Ancona, Italy, but did not find polyps in the proximate natural environment, which includes rocky cliffs. Polyps on the wreck were monitored at densities up to 45 polyps·cm<sup>-2</sup> and the authors estimate 780,000 to 2,600,000 ephyrae could be released per m<sup>2</sup>.

Information presented by Malej (2001) also appears to confirm a possible increase in “irregular events” involving jellyfish in the Northern Adriatic. With the exceptions of *P. noctiluca* (discussed above) and *Cotylorhiza tuberculata*, numerous species of jellyfish appeared to show an increase in the frequency of blooms through the 1970s, 1980s, and/or 1990s. These included *Aurelia* spp., *Aequorea forskalea*, *Chrysaora hysoscella*, *Rhizostoma pulmo*, and Ctenophora. Despite the apparent increase in large scyphomedusae in the Northern Adriatic, Benović *et al.* (1987; 2000) discuss a decline in the hydromedusan community. The authors point to increased hypoxic and anoxic events due to anthropogenic disturbance as a cause for decreased abundance and species diversity, primarily for meroplanktonic species. While it is presumed that the overall biomass of jellyfish in this system has increased (see above), the decline in hydrozoan biodiversity highlights the fact that different groups of jellyfish will respond differently to anthropogenic impacts, and some groups may be affected negatively (Purcell *et al.* 1999).

There have been many reports of jellyfish around Malta in recent years, thanks primarily to a recent citizen science campaign entitled “Spot the Jellyfish” (see [www.ioikids.net/jellyfish](http://www.ioikids.net/jellyfish)). Not surprisingly, this program has revealed large variations in abundance, with sizeable blooms reported in 2009 and fewer sightings in 2010 (Anonymous 2010e) and 2011 (Anonymous 2011g). As problems with jellyfish have been reported from Malta every decade since the 1950s (Deidun 2011), trends in jellyfish populations in Maltese waters remain unclear.

#### Invasive Species in LME #26 – Mediterranean Sea

Numerous species of invasive jellyfish appear to be thriving in the Mediterranean Sea. The highly invasive ctenophore *Mnemiopsis leidyi* was first recorded in the Mediterranean in the 1990s in the Aegean Sea near Greece (Shiganova *et al.* 2001; Shiganova *et al.* 2004b) and Turkey (Kideys and Niermann 1994), as well as in the eastern Mediterranean near Syria (Shiganova 1997), and in the Marmara Sea (Isinibilir *et al.* 2004), where a number of jellyfish species appear to have been introduced (Isinibilir *et al.* 2010). *M. leidyi* was subsequently discovered in the northern Adriatic in 2005 (Shiganova and Malej 2009) and in Spain in 2008 (Fuentes *et al.* 2010). Then, in 2009, large blooms of this invader spanned many disparate locations in the Mediterranean, including Israel (Galil *et al.* 2009a), Italy (Boero *et al.* 2009), and Spain (Fuentes *et al.* 2010). The species identity of *M. leidyi* from the Mediterranean has been confirmed using molecular techniques, and given the widespread occurrence of simultaneous blooms, it is likely that this species has been well distributed and established in the Mediterranean for some time (Fuentes *et al.* 2010). Although the abundances of many other jellyfish were unusually low during the 2009 blooms of *M. leidyi* (Fuentes *et al.* 2010), the large aggregations of *M. leidyi* suggest that the gelatinous biomass in the Mediterranean may be increasing due to this infamous invader.

Interestingly, the reliable predator of *M. leidy* – *Beroe ovata* – has also been found in the Mediterranean; initially in 2004 in the Aegean Sea (Shiganova *et al.* 2007), then in 2005 in the Adriatic (Shiganova and Malej 2009), and in 2011 off the coast of Israel (Galil *et al.* 2011). Currently, it remains unclear to what extent *B. ovata* is established in the Mediterranean, and whether it has significantly reduced the abundance of *M. leidy*, as is the case for the Black Sea (see LME #62).

The conspicuous scyphomedusan *Rhopilema nomadica* first appeared along the coast of Israel in 1977 (Galil *et al.* 1990; Galil 2000) and blooms have continued to increase there ever since (Lotan *et al.* 1992; 1994; Marshall 2010; Waldoks 2010). This species appears to have extended its range to Lebanon and Syria (Lotan *et al.* 1994), as well as Egypt, Turkey (Kideys and Gücü 1995), Greece (Siokou-Frangou *et al.* 2006), and on two occasions, even Malta (Anonymous 2011i). Massive blooms of *R. nomadica* have occurred annually along the SE Levantine coast since the 1980s, directly interfering with numerous industries including fishing, power generation, desalination, shipping, aquaculture, and tourism, resulting in significant economic losses (Lotan *et al.* 1992; Galil *et al.* 2010; Öztürk and İşinibilir 2010). Notably, the success of this invasive species may partly be at the expense of the native scyphozoan *Rhizostoma pulmo*, which has exhibited a decline in abundance in this region (Galil 2000). However, it is unlikely that the decline of *R. pulmo* is comparable to the dramatic increase in *R. nomadica*, as the former was not frequently reported to form large blooms in the Mediterranean on a historical basis (Lilley *et al.* 2009). It should also be noted that blooms of the indigenous *R. pulmo* are still reported from other areas of the Mediterranean, including Mar Menor (see above), as well as near Tuscany and Barcelona (Lilley *et al.* 2009).

The invasive *Phyllorhiza punctata* also appears to have established a growing population in the Mediterranean. A solitary specimen was observed in Mediterranean waters in 1965 (Galil *et al.* 1990), but there have been reports of individual medusae and large blooms from the coast of Israel since 2005 (Galil *et al.* 2009b). A reproducing population of this invader also exists in a bay on a Greek island in the Ionian Sea, where it has occurred for roughly a decade (Abed-Navandi and Kikinger 2007). In 2009, a single *P. punctata* specimen was also observed near Sardinia, Italy (Boero *et al.* 2009), and in 2010 a bloom of this species forced the closure of six different beaches in Spain's Costa Brava, after more than 100 swimmers were stung (Anonymous 2011a).

*Cassiopea andromeda* is also suspected to be invasive in the eastern Mediterranean, having been detected in the Aegean Sea and in the waters near Israel (Spanier 1989 and references therein) and Lebanon (Galil *et al.* 1990 and references therein). However, there is at least one report of *Cassiopea* spp. in the eastern Mediterranean before 1950 (see Galil *et al.* 1990), so these invasions may have occurred prior to their reporting and are therefore not included as a separate chronicle. Regardless, it appears the range expansion of *Cassiopea* spp. will continue, with recent sightings from Turkey (Çevik *et al.* 2006; Özgür and Öztürk 2008) and Malta (Schembri *et al.* 2010). Another species in this genus – *C. polypoides* – was reported from the coast of Lebanon in 1987 (Lakkis 1991), but it remains unclear to what extent this invader is established.

The cubomedusan *Carybdea marsupialis* also appears to have invaded the Mediterranean Sea. While this species may have been observed in the Adriatic in 1878 (Claus 1878), it was not reported again until 1985 (Boero and Minelli 1986), after which it became increasingly widespread (Di Camillo *et al.* 2006). This jellyfish “is now an obnoxious stinger” in the Mediterranean (CIESM 2008) and has recently been reported from Italy and Spain (Bordet *et al.* 2011), as well as France (Cuneo 2009) and Malta (Schembri 2010; Anonymous 2011b).

Though not included as a separate chronicle in the analysis, hydrozoans of the genus *Clytia* also appear to be invasive in the Mediterranean. *C. linearis* was first reported from the Suez Canal in 1938 and then in



the Mediterranean in the 1950s (Boero *et al.* 2005). The hydroid of this species is now one of the most abundant and widespread in the Mediterranean (Bouillon *et al.* 2004). *C. hummelincki* was first reported from the Ionian coast of Italy in 1996 (Boero *et al.* 1997), and colonial hydroids of this species have since been widely recorded in the northern Mediterranean, including the Adriatic Sea, Sardinia, and Majorca (Gravili *et al.* 2008). Despite these reports, the spread of these highly successful invaders continues largely unnoticed due to a lack of specialists (Boero *et al.* 2005; Gravili *et al.* 2008).

New invasions of jellyfish continue to be documented in the Mediterranean Sea in recent years. A new genus was described for *Marivagia stellata*, which was first found in Israel in 2006, and several recent detections suggest an established population (Galil *et al.* 2010). In 2010, the first sighting of the large scyphomedusan *Catostylus tagi*, which is normally restricted to Atlantic waters, was reported from the Sicily Channel in Italy (Nastasi 2010). In addition, the Indo-Pacific hydromedusan *Aequorea globosa* was observed in Iskenderun Bay, Turkey continuously through 2011, suggesting an established population (Turan *et al.* 2011).

### *LME #28 – Guinea Current*

No time-series data on jellyfish populations were available for the Guinea Current. However, there are anecdotal reports suggesting jellyfish have been increasing in the region (B. Asiedu, U. Ghana, pers. comm., Jan. 2010), and that fishers have been catching more jellyfish in their nets over the last decade (F.K.E. Nunoo, U. Ghana, pers. comm., Feb. 2010).

### *LME #29 – Benguela Current*

The Benguela Current LME is arguably the most productive upwelling system in the world (Carr 2001), along with the Humboldt Current LME. The high variability associated with this ecosystem can result in similar variability in the gelatinous community (Gibbons and Buecher 2001). There is evidence to suggest that the Benguela Current LME has experienced a large increase in jellyfish over the last half-century, but a lack of baseline data inhibits drawing definitive conclusions. This historical data deficiency has led some scientists to question the perceived increase of jellies in this LME (*e.g.*, Mills 2001). However, the circumstantial evidence supporting a large increase in jellyfish appears to outweigh a lack of evidence to the contrary.

The most convincing indication of an increase is the absence of large jellyfish from the reports of comprehensive surveys conducted in the 1950s and 1960s (Hart and Currie 1960; Fearon *et al.* 1992 and references therein). While it is true that jellyfish have historically been ignored, avoided, and discarded from plankton studies (Pugh 1989; Mills 2001; Hay 2006), these early surveys from the Benguela ecosystem documented small jellyfish, including hydromedusae and ctenophores. Thus, it seems highly unlikely that conspicuous jellyfish would have been omitted from the reports, especially if they had occurred at high levels of abundance. Today, two large jellyfish are present in this ecosystem at very high abundances. *Chrysaora hysoscella* and *Aequorea forskalea* now dominate the gelatinous biomass of the Namibian coast (Fearon *et al.* 1992), and it has been suggested that the gelatinous biomass now eclipses that of fish in this ecosystem (Lynam *et al.* 2006).

More evidence that jellyfish have increased in this region comes from reports of interference with fisheries. Venter (1988) notes that jellyfish have become an “increasingly irritating nuisance” for fishers since the 1970s. An increase of jellyfish in this region now appears to be accepted by most scientists (*e.g.*, Brierley *et al.* 2001; Sparks *et al.* 2001; Bakun and Weeks 2006; Utne-Palm *et al.* 2010). However, it is curious that this shift was not discussed in papers that examined the ecosystem through the 1980s (*e.g.*,

Gibbons *et al.* 1992; Shannon *et al.* 1992). Nonetheless, the evidence in this LME suggests an increase in jellyfish biomass with little evidence to the contrary, and it appears the increase continued in the 1990s (Heymans *et al.* 2004).

Formal studies to identify changes in jellyfish populations in this LME are rare, likely due to a lack of funding (Sparks *et al.* 2001). Buecher and Gibbons (2000) document a decline in jellyfish species diversity through the 1990s in St. Helena Bay. However, there is no indication of how this trend affected the overall gelatinous biomass and it was therefore excluded from the analysis. There have also been suggestions of an increase in box jellyfish off Namibia (Hartman 2011), but the details are unclear. Recent interest in cataloguing the gelatinous zooplankton of this region (*e.g.*, Pagès *et al.* 1992; Gibbons and Thibault-Botha 2002; Gibbons *et al.* 2010) will help to identify future changes.

### *LME #30 – Agulhas Current*

While there are no scientific data from this LME that examine jellyfish populations over time, limited anecdotal evidence suggests that populations are stable. The inshore waters of KwaZulu-Natal are periodically witness to large blooms of conspicuous medusae every three to five years. However, there are no indications that these blooms have become larger or more frequent in at least the past 35 years (R. van der Elst, ORI, pers. comm., Jan. 2010).

An informal survey of delegates was conducted at the Marine Biodiversity workshop of the South West Indian Ocean Fisheries Project (SWIOFP) held in Mauritius (van der Elst 2010). Respondents were asked about jellyfish “outbreaks” in their region, and were notified of the survey in advance so they could deliberate with colleagues at their institutes. While there were reports of periodic blooms, representatives from Mozambique, Comoros, and Madagascar all reported that there have been no noticeable recent changes in jellyfish populations.

#### Invasive Species in LME #30 – Agulhas Current

Although it was not included as a separate chronicle, a single specimen of the invasive hydromedusan *Blackfordia virginica* was observed in this LME in 1990 (Buecher *et al.* 2005). While it remains unclear if this species is established in the Agulhas Current, it appears that the global spread of this Ponto-Caspian invader continues.

Interestingly, the aforementioned informal survey conducted at the Marine Biodiversity Workshop of SWIOFP identified a large bloom of jellyfish in Mauritius in October 2009 that had not been seen previously. A photograph of these jellies revealed that they were mostly likely a species of *Cassiopea*, marking yet another possible invasion for this synanthropic jellyfish. This bloom was not included in the analysis, as Mauritius is not part of any LME.

### *LME #31 – Somali Coastal Current*

As with the neighbouring Agulhas Current LME, there are no scientific data on jellyfish from eastern Africa. However, anecdotal data suggest jellyfish populations may be stable. As mentioned, an informal survey to identify trends in jellyfish abundance was conducted at the Marine Biodiversity workshop of the South West Indian Ocean Fisheries Project (SWIOFP) held in Mauritius (van der Elst 2010). While there were reports of periodic blooms, representatives from Tanzania and Kenya both reported that there have been no noticeable, recent changes in jellyfish populations.

### *LME #32 – Arabian Sea*

Interviews with 90 fishers were conducted by Ganapathiraju Pramod in September 2008 in four Indian states within this LME (Pramod 2010). Small-scale fishers and mechanized trawler operators were asked about interannual and decadal changes in jellyfish populations. In three of the states (Gujarat, Maharashtra, and Karnataka) the majority of interviewees responded that jellyfish populations were stable (G. Pramod, UBC, pers. comm., Sept. 2010). In the state of Kerala, the majority of interviewees indicated that jellyfish had increased, as more jellyfish were being caught in fishing nets as bycatch and more jellyfish were washing up on shore, as well as over longer distances (G. Pramod, UBC, pers. comm., Sept. 2010). Other evidence also supports an increase in some regions of India, with fishers from the west coast reporting losses due to interference with jellyfish (B. Ingole, NIO, pers. comm., Oct. 2010), and more jellies washing up on beaches (Anonymous 2010b). The results of the interviews by G. Pramod were included in the analysis for this LME as two separate chronicles, each with a differing *Abundance Trend* and *Space Score*.

In 2002, a massive bloom of the scyphomedusan *Crambionella orsini* occurred throughout the Persian Gulf and the Gulf of Oman. This bloom interfered with fisheries and clogged intake pipes of desalination plants and power stations. It also resulted in a massive flux of organic matter to the sea bed as the medusae died, exceeding the average annual flux of organic carbon by more than an order of magnitude (Billett *et al.* 2006). Dryanabard and Dawson (2008) discuss data from demersal trawls that have been conducted since 1998 along the coast of Iran. They note that *C. orsini* typically occurs at very low abundances in these trawls. With the obvious exception of 2002, there have been no recent blooms of this species (Billett *et al.* 2006; Dryanabard and Dawson 2008). In addition, it would appear that while blooms of this species are not annual, they have been occurring for at least half a century. Erdman (1950) reports a bloom of jellyfish in the Persian Gulf containing “more individual jellyfish [...] than one could possibly count.” His description of the jellyfish in question fits well with *C. orsini*. As there are no indications that *C. orsini* is blooming with increased frequency in recent years or decades, this chronicle is classified as variable (*Abundance Trend* = 0).

Additional anecdotal reports from the Persian Gulf suggest that jellyfish populations are increasing. Erftemeiger and Langenberg (2010) state that “outbursts of large numbers of jellyfish are observed in what appears to be increasing quantities throughout the Gulf.” They suggest an increase over the last 7-10 years, and point to evidence from Internet blogs, sting reports, clogged intake pipes, and interference with fisheries. While the evidence supporting an increase is circumstantial, it is substantial, and there are certainly reports of complaints by both sport fishers (Picow 2010) and commercial fishers (Al-Rubiay *et al.* 2009), who may even haul jellyfish to shore and dump them on beaches (Nazzal 2006). There is also a report of a new species occurring in Dubai, but it may have been a singular event due to a hurricane (Bardsley and Landaïs 2007). The species in question was reported as belonging to the genus *Aurelia*, but the photographs and content of the article suggest otherwise.

While the majority of evidence seems to support an increase of jellyfish in the Gulf (Erftemeiger and Langenberg 2010), catches of jellyfish in Bahrain tell a different story. Established in 2003, the jellyfish fishery in Bahrain annually harvests hundreds of tonnes of jellyfish for export to Asia (Erftemeiger and Langenberg 2010). However, catch rates in 2007 were so low that the processor estimated they had fallen by 90% (Mohammed 2008). The decline was blamed on jellyfish moving further offshore, due to land reclamation and the large amount of sediment used. Therefore, this decline is excluded due to the fact that it is a suspected spatial relocation (see Materials and Methods), as well as the potential effects of jellyfish harvesting. In fact, there are suggestions that overfishing of jellyfish has reduced jellyfish populations around Karachi, Pakistan over the last 5 years (Roghay 2011).

Although not included as a separate chronicle, it appears that select species of hydrozoans may suffer from cultural eutrophication in an estuary within this LME. Santhakumari *et al.* (1997; 1999) document a gradient of declining hydromedusan species diversity at progressively interior stations in Bombay Harbour. While this may simply be due to the presence of holoplanktonic species at the outer stations, it may also be due to the sensitive nature of some hydrozoan species to cultural eutrophication, as has been observed in other systems (*e.g.*, see LME #26 – Mediterranean Sea). Although abundance of particular hydrozoan species may still be high in polluted environments (Santhakumari *et al.* 1999), these studies highlight the fact that not all groups of jellyfish will respond to changes and stressors in the same way. It should also be noted that the hydromedusan *Blackfordia virginica* was reported as one of the dominant species in this system. As this jellyfish is thought to be a Ponto-Caspian invader, it is likely invasive to this region as well. However, the fact that it has historically been identified as being “common in backwaters and swamps of [the] west coast of India” (Santhakumari *et al.* 1999 and references therein) makes the timing of invasion(s) unclear.

### *LME #34 – Bay of Bengal*

Anecdotal data from this LME show conflicting reports of both stable and increasing jellyfish populations. Interviews with over 100 fishers were conducted by Ganapathiraju Pramod in September 2008 in 5 Indian states within this LME (Pramod 2010). Small-scale fishers and mechanized trawler operators were asked about interannual and decadal changes jellyfish populations. In three of the states (Tamil Nadu, Andhra Pradesh, Andaman and Nicobar Islands) the majority of interviewees responded that jellyfish populations were stable (G. Pramod, UBC, pers. comm., Oct. 2010). In the states of Orissa and West Bengal, the majority of interviewees indicated that jellyfish had increased, as more jellyfish were being caught in fishing nets as bycatch and more jellyfish were washing up on shore (G. Pramod, UBC, pers. comm., Oct. 2010). Orissa has always experienced jellyfish blooms, but reports indicate that these blooms have been increasing in both abundance and frequency – from every 3-4 years previously to almost annually now (G. Pramod, UBC, pers. comm., Oct. 2010). The results of these interviews are included in the analysis for this LME as two separate chronicles, each with a differing *Abundance Trend* and *Space Score*.

Other anecdotal evidence points to an increase of jellyfish on the east coast of India, but the timescale is unclear as increases have been reported in each of the past several decades. Marine scientists point to an increase of numerous jellyfish in recent years, especially tropical species including *Limnognathia* spp., *Crambionella* spp., and *Dactylometra quinquecirrha* (B. Ingole, NIO, pers. comm., Oct. 2010). Jellyfish are also reportedly being caught by fishers in increasing numbers (B. Ingole, NIO, pers. comm., Oct. 2010). James *et al.* (1985) present catch rates of jellyfish for a 5-year period (1981-1985) and state that their “analysis clearly shows that the medusae of *Crambionella stuhlmanni* are becoming more abundant year after year.” However, the authors also note that “swarms of jellyfish are a common sight off Madras” and a linear regression performed over the short time-series does not reveal a significant increase. Interference with power plants in this region was also reported in the 1980s and 1990s, due primarily to *D. quinquecirrha* and *Crambionella* spp. (Rajagopal *et al.* 1989; Masilamoni *et al.* 2000). Reports of interference and high jellyfish abundance from earlier decades cast some doubt on more recent perceptions of increases, and the possibility of the shifting baselines syndrome exists (Pauly 1995), especially due to the pulsed nature of jellyfish populations (Condon *et al.* 2012). Nonetheless, the opinion of contemporary marine scientists should not be ignored, as they are often aware of the shifting baselines syndrome. In addition, marine scientists are keenly tuned to changes in the oceanic environment and they are often the best source of information in the absence of scientific data. Thus, the opinions of Dr. Baban Ingole were included in the analysis with an associated *Confidence Index = Medium-low*.

Scattered reports of jellyfish fisheries from the east coast of India confuse the issue further. Jellyfish harvesting has existed in India for some time. However, the scale of this harvesting is unclear, as catches are not reported to the Food and Agriculture Organization of the United Nations (FAO). Harvesting of jellyfish along India's east coast likely began in the 1980s, mainly for the purpose of exporting *Crambionella stuhlmanni* (Kuthalingam *et al.* 1989). The jellyfish fishery in India is still small compared to other Asian countries. However, India reportedly had a very large catch of *C. stuhlmanni* in 2003 (CMFRI 2009), when there was also an apparent expansion to the fishery, as well as harvesting of *Lobonema smithii* (Murugan and Durgekar 2008). This expansion is said to be due to dwindling catches of more valuable fish species, and provides an example of fishing down the food web (Pauly *et al.* 1998; Murugan and Durgekar 2008). The rapid expansion is also said to have caused major conflict as merchants and fishers scrambled to compete in the fishery, and concerns over pollution from jellyfish processing huts exacerbated the problem (Magesh and Coulthard 2004). The 2004 tsunami reportedly caused severe damage to jellyfish fishery infrastructure in India (CMFRI 2009), and this, in combination with declining catch rates, instigated a scaling back of the jellyfish fishery in Tamil Nadu in 2005 (Manickaraja and Balasubramanian 2006). It appears the fishery has expanded eastward in recent years, with catches reported from Andhra Pradesh (CMFRI 2009). In addition, there are complaints that overharvesting of jellyfish off the state of Orissa has resulted in a decline, a concern due to the perceived importance of jellyfish in the diet of Olive Ridley sea turtles (*Lepidochelys olivacea*) (Anonymous 2007a, 2008a). While there appear to be no empirical data to back up this claim, catches of jellyfish in Orissa may be much larger than in other parts of India (G. Pramod, UBC, pers. comm., Oct. 2010). While the reported decline of jellyfish due to overharvesting in Orissa conflicts with the results of the aforementioned interviews by G. Pramod, it was included in the appropriate phase of the analysis (see Effects of Jellyfish Overexploitation).

Government officials in Malaysia are becoming increasingly concerned with high numbers of jellyfish in Penang waters, along with the associated effects on tourism (Kwang and Yahya 2010). Evidence of trends in jellyfish populations in this region are rare; however, recent reports of unusual blooms in both Malaysia (*e.g.*, Lau 2010) and Thailand (*e.g.*, Morison 2009) suggest that jellyfish may be increasing in this region. As well, there appears to be a general consensus from interviews with locals that there are more intense and frequent blooms in recent years along the western coast of the Malay Peninsula (M.R.B. Idid, IBS, Jan. 2011), and recent blooms near the Straits of Malacca are surprising fishers and causing them problems (Anonymous 2011c).

Populations of jellyfish studied at Penang National Park appear stable, but data are only available for the past several years (S.Y. Kwang, CMCS, pers. comm., Jan. 2010). Adding to the inconsistent trends in this region, there are also reports of declines in harvested jellyfish species. In 2005, Malaysian jellyfish harvesters reported a "dramatic drop in catch in recent years, believed to be due to increasing pollution" (Heng 2005). Not surprisingly, FAO statistics add further confusion, as there was a decline in the Malaysian harvest at this time, but Thailand recorded massive harvests in 2005 and 2006, before dropping to zero again in 2008 (FAO 2011). Interestingly, possible declines of harvested jellyfish species were reported in the Andaman Sea as far back as the 1970s (Soonthonvipat 1976), while FAO has no record of catches in this area before 1978 (FAO 2011).

Recent stings and tourist deaths due to box jellies in this area have also received media attention (*e.g.*, Wipatayotin 2008), and there are some suggestions that these events are due to recent range expansions (*e.g.*, Morison 2008) or increases in abundance (Anonymous 2010a). However, it is more likely that these species of jellies have long been present in the region (Phattrasaya and Morison 2008; Fenner *et al.* 2010), and recent attention is more likely due to increased media exposure (Lippmann *et al.* 2011). In addition, the anecdotal evidence suggesting increases appears to refer more to the Gulf of Thailand

(Suntrarachun *et al.* 2001). Therefore, these events have been excluded from this LME but are discussed below.

### *LME #35 – Gulf of Thailand*

As mentioned, the Gulf of Thailand has recently received media attention for increased sightings of box jellyfish, along with the severe and sometimes fatal stings of these venomous jellies (Fenner and Lippmann 2009). While these reports are outside the previously known distribution for many of these species (*e.g.*, de Pender *et al.* 2006) and may indicate a range expansion of box jellyfish, anecdotal reports suggest an increase in abundance and species diversity (Suntrarachun *et al.* 2001). However, it may be the case that these jellies have occurred in this region for a long time (Fenner *et al.* 2010). Serious and fatal stings due to jellyfish have historically occurred in Thailand, with the vast majority of cases likely going unreported (Fenner and Lippmann 2009). The apparent recent increase in reports is potentially linked to the attention by foreign media due to cases involving tourists, as well as the viral nature of the Internet (Fenner and Lippmann 2009). While this suggests anecdotal reports of increases should be questioned, they should also not be ignored. Therefore, the reports suggesting increases of jellies in this region are included, albeit with the highest degree of uncertainty (*Confidence Index = Low*).

### *LME #36 – South China Sea*

One of the most interesting and convincing examples that aquaculture operations can lead to increased jellyfish populations comes from this LME. Lo *et al.* (2008) report on an “experiment” in Tapong Bay, a tropical lagoon in Taiwan. For decades, this bay has been used extensively for aquaculture, primarily oyster raft and fish pen operations. As a result, the bay became highly eutrophic due to increased nutrient input and reduced water circulation. In addition, Tapong Bay was subject to frequent blooms of *Aurelia aurita*. In 2002, the aquaculture rafts and pens were completely removed from the bay, which resulted in the complete disappearance of jellyfish thereafter. This remarkable correlation suggests that the aquaculture operations were wholly responsible for the abundance of jellyfish in the bay, and the study of variables both before and after the removal of the structures permits exploration of the mechanisms involved. As the rafts and pens likely provided ideal habitat for jellyfish polyps, their removal as substrate is likely the main cause for the absence of jellyfish. The authors also note significant increases in water clarity and circulation after removal, suggesting that the hydrodynamic effects of the rafts may have also influenced the proliferation of jellyfish. Copepod abundance increased sixfold after removal, suggesting that predation by fish and jellies, as well as competition from oysters, may have controlled copepod populations. The fact that jellyfish were absent even with this increased food source further supports the hypothesis that the aquaculture operations were responsible for influencing jellyfish populations. With such a tight correlation between jellyfish abundance and aquaculture production, it seems unlikely that jellyfish were present in this bay prior to any aquaculture operations. As such, this chronicle is scored as stable/variable (*Abundance Trend = 0*), rather than a decrease. This *in situ* experiment provides convincing support for the hypothesis that increased aquaculture production around the globe may contribute to increased jellyfish populations (Purcell *et al.* 2007; Lo *et al.* 2008; Duarte *et al.* in review).

The massive power outage that affected much of the Philippines in December 1999 was apparently attributed to jellyfish clogging the intake screen of a coastal power plant (Anonymous 1999). While this event would not normally be included as evidence of an increase (see Data Selection), a report of the incident was accompanied by anecdotal evidence that the jellyfish population in Lingayen Gulf had dramatically increased due to overfishing (Anonymous 1999). As this claim was from an unidentified environmental group, and since there are no recent reports on increased jellyfish populations from the region, it was included in the analysis with high uncertainty (*Confidence Index = Low*).

In Malampaya Sound, Philippines, *Lobonema* spp. are harvested and processed for export to Korea and Japan. In this region, more than 10% of the population may directly benefit from the jellyfish fishery. Evidence suggests that intensive harvesting has contributed to a decrease in jellyfish populations in this region, at least for targeted species (PCAMRD 2008).

### *LME #40 – Northeast Australian Shelf*

Quantitative information on jellyfish populations is lacking in this LME; however, investigations of stings by cubomedusae provide some insight into changes. While a change in the frequency of sting events does not warrant inclusion in the analysis (see Data Selection), there is evidence of both temporal and spatial increases of the stinger season in this LME. Box jellyfish expert Dr. Jamie Seymour has commented on the dramatic change in the length of the season for Irukandji syndrome, suggesting that it has increased by 3–4 months over the last several decades in Queensland, possibly due to warmer water temperatures (Anonymous 2010d). Analysis of data from nearby Darwin Harbour (located in the neighbouring Northern Australia Shelf LME) revealed a strong correlation between the number of *Chironex fleckeri* stings and the average daily minimum SST (Jacups 2010). With predicted warming, the length of the stinger season is likely to increase in this and neighbouring LMEs (Jacups 2010). Spatial distributions have also reportedly increased, with increasing cubomedusae reports from further south in Queensland over the last 5 years (Donaghey 2009). Changes in the seasonal and distributional patterns of cubomedusae in this LME are echoed by other experts who suggest the dynamics in recent years are exceptionally unusual (Smail 2010). While these trends are especially concerning from a public health perspective and may be indicative of ecosystem changes, the contribution of cubomedusae to overall jellyfish biomass in this LME is uncertain (*Reliability Score = Low*).

### *LME #41 – East Central Australian Shelf*

Though not included in the analysis as a separate chronicle, the spatial expansion of cubomedusae noted in the Northeast Australian Shelf LME may also be extending into this LME. Recent reports of box jellyfish as far south as Coffs Harbor have been called “very strange” by experts, but a lack of funding has so far prevented formal study (Anonymous 2011e).

Surveys conducted in this LME by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in conjunction with the University of New South Wales revealed a large increase in the salp *Thalia democratica* in the waters off Sydney in 2008, with abundances more than an order of magnitude higher than surveys dating back 70 years (Strong 2008; Henschke 2009). However, measurements from 2009 indicate that abundances have returned to levels closer to those measured from the 1940s, and the recent data do not support a significant increase over historical values (K. Pitt, GU, pers. comm., May 2010). Rather, the high biomass measured in 2008 was associated with a very large cold core eddy, and salp abundances outside of such formations are expected to be much lower (J. Everett, UNSW, pers. comm., Feb. 2011).

Presence of the conspicuous scyphomedusan *Catostylus mosaicus* has been monitored in a large region around Moreton Bay since 2002 as part of the Ecosystem Health Monitoring Program (EHMP). Over the course of the dataset, *C. mosaicus* showed a low presence for three years, increased presence over the next three years, followed by a subsequent return to low abundances in recent years (K. Pitt, GU, pers. comm., May 2010).

There is also evidence that some jellyfish populations in this LME have been eradicated due to collection for science. The upside-down jellyfish *Cassiopea* used to be present in Myora Drain, an artificial tidal

channel. However, numerous collections in 2007 (*e.g.*, Bouchet 2007; Templeman and Kingsford 2010) led to the complete eradication of this species in this location, with no specimens present since 2007 (K. Pitt, GU, pers. comm., May 2010). A similar story seems to have played out in the nearby tidal lagoon known as Pelican Waters, where further collection for science (*e.g.*, Mortillaro *et al.* 2009) has eradicated the population (K. Pitt, GU, pers. comm., May 2010). These collections highlight the fact that discrete populations of jellyfish may be vulnerable to overharvesting, and intentional removal of *Cassiopea* spp. can be a successful management strategy for this synanthropic jellyfish (also see LME #10 – Insular Pacific-Hawaiian).

### *LME #42 – Southeast Australian Shelf*

The conspicuous scyphomedusan *Catostylus mosaicus* has been monitored in Port Phillip Bay for nearly two decades. Port Phillip Bay is a large, nearly-enclosed embayment important for recreational and industrial uses, as well as fishery resources (DPI 2010). Annual trawl surveys reveal pulses of *C. mosaicus* in 1995, 1997, 2004, 2008 and 2009, with lower abundances or near absence in other years (Coleman 2004; K. Pitt, GU, pers. comm., May 2010). While there is no significant trend over the course of the dataset, it will be interesting to see if the high abundances seen in the last two years continue. A developmental fishery has recently been established for *C. mosaicus* in Port Phillip Bay (Coleman 2004; DPI 2006); however, annual catches remain small or nil.

Wilcox *et al.* (2008) studied polyps of *Aurelia* on anthropogenic structures in Tasmania. The polyps were monitored starting in 2002 at two nearby sites – the underside of a cement breakwater in Hobart and the underside of a floating marina in Kettering. The proportion of polyps strobilating showed large variation between sites and years. While there is no evidence to suggest that *Aurelia* medusae populations have increased in this area, large blooms have caused significant interference and economic losses to aquaculture operations (Wilcox *et al.* 2008). In addition, *Aurelia* medusae in this region form intense blooms in some years but not others (Wilcox *et al.* 2008; Naidoo 2009), and therefore increases in favourable polyp habitat due to anthropogenic structures may facilitate persistence and growth of medusae populations (Duarte *et al.* in review).

### Invasive Species in LME #42 – Southeast Australian Shelf

Several species of hydromedusae or their associated hydroids have been reported from Port Phillip Bay. While many detections occurred prior to 1950, new species continued to be reported in the 1970s and 1980s including *Turritopsis nutricula*, *Bougainvillea muscus (ramose)*, *Clytia hemisphaerica*, and *Obelia dichotoma (australis)* (Hewitt *et al.* 2004). While most of these hydromedusae have a cosmopolitan distribution and are cryptogenic, they are included here as some of these species are highly invasive (*e.g.*, *Turritopsis* spp.) and the detailed historical monitoring of Port Phillip Bay suggests they are new additions to the ecosystem.

### *LME #47 – East China Sea*

The East China Sea is one of only two LMEs with the maximum possible *Jellyfish Index* (also see LME #62 – Black Sea), and evidence suggests that several species are increasing over a large spatial scale (Cheng *et al.* 2004). Due to these changes, recent initiatives have been announced that allocate millions of dollars to study jellyfish dynamics in this region (Stone 2010; Sun *et al.* 2011). Yan *et al.* (2004) state that fisheries surveys from 1990-2003 show an increase in jellyfish biomass in recent years compared with the 1990s for a region extending from 28°30' N to 34° N and from the coast to 127° E. The trend applies to



both *Nemopilema nomurai*<sup>4</sup> and *Cyanea* spp., and appears to be correlated with declines in fish stocks (Yan *et al.* 2004; Ding and Cheng 2005). Causal links are speculative, but it appears there may be a positive feedback loop with increasing jellyfish and declining fish, possibly triggered by overfishing (Hong *et al.* 2008). The increase in *N. nomurai* is also being observed in the northern part of this LME near Korea, with dramatic increases since 2003 (Ding and Cheng 2005; Yoon *et al.* 2008; Rahn 2009). Recent evidence from DNA analyses suggests that the population of *N. nomurai* in the East China Sea is distinct from the population in the Yellow Sea (Hanzawa *et al.* 2010).

Increasing jellyfish blooms have also been reported from the Yangtze Estuary. Xian *et al.* (2005) note that *Rhopilema esculentum* used to be common in this region, but overharvesting of this species has resulted in a gradual replacement by *Cyanea* spp. since 1997. Then, in 2004, *Sanderia malayensis*, which was previously only recorded in the South China Sea, began blooming in the estuary. *S. malayensis* dominated the jellyfish catch, and the authors point to possible links with declining fisheries catches. Although *R. esculentum* has most certainly declined in this region, it has been harvested there for decades or possibly even centuries. Therefore, it is unlikely that the biomass of this targeted species has declined as precipitously as the increases in the other species, especially given the fact that recent blooms of *S. malayensis* may completely cover the surface in parts of the estuary (Xian *et al.* 2005). Interestingly, *S. malayensis* began blooming only one year after the Three Gorges Dam filled the first one-third of its storage capacity, which resulted in a dramatic reduction of river flow to the Yangtze estuary and the East China Sea. Within months, ecological changes were observed in the microbial food web (Jiao *et al.* 2007) and more profound changes are forecast (Wu *et al.* 2004).

Eutrophication has also been blamed for increases of jellyfish in this region, and countermeasures such as erosion prevention, wetland conservation, and seaweed planting have all been proposed in an attempt to prevent increased jellyfish blooms (Guan *et al.* 2007). In addition, anthropogenic habitat for polyps has been documented in this LME. Miyake *et al.* (1997) found polyps on the undersurface of floating polystyrene piers in an engineered canal in Kagoshima Bay, Japan. These polyps were observed again several years later, and it is assumed that they persist in this location. Notably, polyps were also observed attached to a discarded cellophane cigarette package (Miyake *et al.* 2002).

#### Invasive Species in LME #47 – East China Sea

Evidence suggests that *Aurelia* populations have been spreading throughout this part of the world. There is no record of these jellyfish in Korean waters prior to 2000, but since then, at least two dense blooms have occurred. Ki *et al.* (2008) found that *Aurelia* medusae from Korea have the same genotype as those from California, and only slightly different than specimens from Japan. With such a broad distribution and the inability to attribute this distribution to natural dispersion patterns, it appears that *Aurelia* sp. 1 is invasively spreading due to anthropogenic translocation (Dawson *et al.* 2005; Ki *et al.* 2008).

#### *LME #48 – Yellow Sea*

Jellyfish dynamics in the Yellow Sea are very similar those in the East China Sea, and several species appear to be increasing throughout this LME (Cheng *et al.* 2004). The giant jellyfish, *Nemopilema nomurai*, has been blooming more frequently in the Yellow Sea near Korea (Yoon *et al.* 2008), in Jiaozhou Bay, China (Sun *et al.* 2010), and in the Bohai Sea (Dong *et al.* 2010). *N. nomurai* tend to drift over a large region of this LME, as well as into and out of other LMEs, so reports from different areas

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<sup>4</sup> Reports of *Stomolophus meleagris* from Chinese literature are assumed to be *Nemopilema nomurai* (Omori and Kitamura 2004).

could represent the same populations. However, recent genetic analysis suggests that populations of *N. nomurai* in the Yellow Sea are distinct from those in the East China Sea (Hanzawa *et al.* 2010).

Problems with jellyfish along the south coast of Korea have prompted officials to release filefish (Monacanthidae) at beaches in Busan (Jun-shik 2009). Filefish, which are also targeted by the Korean fishery, are predators of jellyfish and it was hoped that releasing hundreds of thousands these fish at beaches would result in fewer jellyfish. While there was indeed a reduction of stings along Busan beaches in 2007 and 2008 (Jun-shik 2009), jellyfish along the south coast of Korea continue to be a problem (Rahn 2009). As mentioned for the East China Sea LME, other countermeasures have also been proposed to combat eutrophication, including erosion prevention, wetland conservation, and seaweed planting (Guan *et al.* 2007).

Also similar to the East China Sea LME, *Rhopilema esculentum* appears to have declined in the region, while *Cyanea nozakii* has increased. Dong *et al.* (2006) note increases in *C. nozakii* in the Yellow Sea and the Bohai Sea, which appear to have been more of a problem since at least 1997 (Zhong *et al.* 2004). Interference with fishing activities has been reported, including broken nets and shortened seasons (Dong *et al.* 2006). Blooms of *C. nozakii* have also been blamed for the reduced harvest of *R. esculentum*, such as the dramatically low catch in Liaodong Bay in 2004, which represented an 80% decline and a loss of US\$70 million (Ge and He 2004; Zhang *et al.* 2005). This is despite attempts to restock waters with *R. esculentum* by means of hatcheries, whereby hundreds of millions of juvenile medusae are released in the spring with the hopes of harvesting them in the fall (Dong *et al.* 2009). While such hatchery methods achieved economic success in the 1990s through the release of billions of young medusae (You *et al.* 2007), it remains unclear if these programs continue to be successful, and efforts appear to be shifting towards pond culturing of jellyfish (You *et al.* 2007). In an attempt to adapt to the decline in *R. esculentum* and the shift in species composition, *C. nozakii* has been successfully processed into food since the 1980s. However, the poor quality of the product has resulted in values only one hundredth of those for *R. esculentum* (Lu *et al.* 2003; Zhong *et al.* 2004). Unfortunately for jellyfish fishers in the region, the story with attempts to process and sell *Nemopilema nomurai* is all too similar (Dong *et al.* 2010).

#### Invasive Species in LME #48 – Yellow Sea

Populations of *Aurelia* spp. appear to be increasing in parts of this LME. Interference with fishing and cooling water intakes are reported in numerous locations in the Yellow and Bohai Seas (Ki *et al.* 2008; Dong *et al.* 2010). These reports are not necessarily indications of increasing abundance (see Data Selection), but *Aurelia* populations appear to be invasive in at least Korean waters, where no records are found prior to 2000 (Ki *et al.* 2008). The species in Incheon has the same genotype as other parts of the world, a fact that cannot be explained by natural oceanic dispersal (Dawson *et al.* 2005; Ki *et al.* 2008). Han and Uye (2010) also note that chronic blooming of *Aurelia* populations is now common in eutrophic bays and inlets in Korea, such as Shihwa Lake. This artificial lake is a failed experiment that now contains hypoxic sea water (Han and Park 1999). This suggests that other factors, such as cultural eutrophication, may assist in the establishment of invasive species (Occhipinti-Ambrogi and Savini 2003).

#### *LME #49 – Kuroshio Current*

While there is evidence for a decline of one species of jellyfish in this LME, the majority of species showing changes in abundance appear to be increasing. The most obvious example concerns the giant jellyfish, *Nemopilema nomurai*. Records of this jellyfish blooming extend back to the early part of the century, and “bloom years” are clearly distinct from “non-bloom years”. Historically, this species would bloom every 35-40 years, with blooms occurring in 1920, 1958, and 1995 (Uye 2008). However, these

blooms have become increasingly frequent, occurring in 2002, 2003, 2005, 2006, 2007, and 2009 (S. Uye, HU, pers. comm., May 2010). While 2010 and 2011 were not bloom years (Uye 2011), 2009 was perhaps the largest bloom of this species ever witnessed (S. Uye, HU, pers. comm., May 2010). These jellyfish appear to originate along the coasts of China and Korea, and then drift into the Sea of Japan LME (Uye 2008; Hanzawa *et al.* 2010; Uye 2010; Uye *et al.* 2010). In the fall, many medusae are then carried through the Tsugaru Strait into this LME, where they can interfere with fisheries in a variety of ways, causing substantial economic losses (Kawahara *et al.* 2006).

Jellyfish also appear to be increasing in and around the Seto Inland Sea. Uye and Ueta (2004) surveyed over one thousand fishers, each with at least 20 years of experience. 65% of the respondents indicated that populations of *Aurelia* had increased in the last 20 years. While 65% is not overwhelming support for an increase, the authors note that in widespread areas of the Inland Sea “an elongation of the period of occurrence of medusae is obvious.” Other sources of information also point to increased jellyfish populations in the area. Monthly reports of fishing and oceanographic conditions in the Seto Inland Sea indicate an increase in jellyfish in the late 1990s (Nagai 2003). In addition, polyps of this species have been observed on the underside of floating docks and on pier pilings in the region, suggesting increased anthropogenic habitat (Miyake *et al.* 2002; Duarte *et al.* in review). Eutrophication, increased polyp habitat, overfishing, and combinations thereof have all been suggested as mechanisms for increased jellyfish populations in this region (Shoji *et al.* 2010; Uye 2010). Supporting evidence for increased *Aurelia* populations is also found from studies along western Shikoku, near the entrance to the Seto Inland Sea. An unusually large aggregation was observed in 2000, likely caused by a rapid intrusion of offshore waters (Uye *et al.* 2003; Takahashi *et al.* 2010). The cause of this bloom might suggest that jellyfish populations in other years were not necessarily smaller, but rather more sparsely distributed. However, indications are that while populations have been variable over the last 7-8 years, there was an apparent increase in the late 1990s, prior to which no medusa aggregations were found, despite frequent field surveys (S. Uye, HU, pers. comm., Oct. 2010). Starting in 1998, wet weights of jellyfish (predominantly *Aurelia* spp.) were recorded daily from the screens of the Ikata Nuclear Power Station near Seto, and were analysed by Kaneda *et al.* (2007). The 7-year dataset reveals interannual variations, but no obvious trend (see Fig. 2 in Kaneda *et al.* 2007). The lack of an increase in this dataset is in contrast with the majority of the anecdotal data from the Seto Inland Sea (see above). However, most of the increases were reported to occur in the 1990s, with variable or stable populations thereafter. Therefore, the temporal scale of the data from the Ikata Power Station may not extend back far enough to capture the increase. As discussed above, there are numerous anecdotal sources suggesting an increase in the jellyfish population of the Seto Inland Sea in recent decades. While the dataset from the Ikata Nuclear Power Station does not add to this evidence, it also does not preclude an increase in the 1990s. Therefore, the chronicle for the Seto Inland Sea is included as an increase (*Abundance Trend* = 1), with the *Reliability Score* reduced to *Low*.

Numerous jellyfish species appear to have increased in the highly eutrophic bays of coastal Japan, including Tokyo Bay and Mikawa Bay. The most conspicuous is *Aurelia*, which used to be found only in low abundances throughout most of the 20<sup>th</sup> century (Nomura and Ishimaru 1998). However, with increased eutrophication through the 1960s, a shift in zooplankton coincided with increasingly larger *Aurelia* blooms in Tokyo Bay (Omori *et al.* 1995; Nomura and Ishimaru 1998; Ishii 2001) and Mikawa Bay (Toyokawa *et al.* 2011). These blooms have been interfering with human activities for decades, such as blocking seawater intakes at coastal power stations (Kuwabara *et al.* 1969; Toyokawa *et al.* 2000). *Aurelia* polyps have been observed to colonize artificial substrates in both locations (Watanabe and Ishii 2001; Toyokawa *et al.* 2011), and they appear to benefit from the hypoxic conditions as they can out-compete other sessile organisms for habitat due to a tolerance for low oxygen (Ishii *et al.* 2008).

The populations of other jellyfish species in Tokyo Bay, such as the ctenophore *Bolinopsis Mikado*, appear to have increased through the 1980s (Nomura and Ishimaru 1998), while the 1990s showed high variability (Kasuya *et al.* 2000; Kinoshita *et al.* 2006). Species composition has also changed over the past several decades, including new appearances of jellies such as *Beroe cucumis* (Nomura and Ishimaru 1998; Arai 2001).

While increasing jellyfish populations appear to be common in this LME, it is not the case with all species. The hydromedusan *Spirocodon saltatrix* appears to have decreased throughout much of its range in coastal Japan (Mills 2001). Ironically, some of the factors that have been blamed for increased populations of jellyfish in this region, such as eutrophication and coastal development, may be responsible for the decline of *S. saltatrix* (Mills 2001; S. Uye, HU, pers. comm., Oct. 2010). The most dramatic decline of *S. saltatrix* populations took place in the Seto Inland Sea. There has been some recovery of this population, and the overall decline is assumed to be small relative to the increases of other jellyfish in this region. Decreases of this species have also been noted in other locations, such as the Misaka Marine Biological Station, where harvesting for research has likely contributed to its decline (C. Mills, WU, pers. comm., Oct. 2010). While this species has most certainly been negatively impacted, the extent of the decline is unclear, and therefore a *Spatial Score = Low* has been used. While *S. saltatrix* may be abundant at times, it is not considered a dominant species. In addition, the few areas where decreases have been documented also show dramatic increases in other species, and therefore a *Reliability Score = Low* was used.

#### Invasive Species in LME #49 – Kuroshio Current

As mentioned, hydromedusae belonging to the genus *Turritopsis* have a unique ability to reverse their life cycle through transdifferentiation. During this process, starving or damaged medusae revert to a benthic cyst. These cysts can subsequently produce a new polyp colony that is capable of releasing new medusae. This remarkable ability has led to these jellyfish being acclaimed as the world's only "immortal" organism (*e.g.*, Than 2009), and it may increase the probability of *Turritopsis* spp. being transported to new locations through ballast water (Miglietta *et al.* 2007; Miglietta and Lessios 2009). At least one species, *T. dohrnii*, appears to be invasive in Okinawa Island and possesses a revealing Mediterranean haplotype (Miglietta *et al.* 2007). While blooms of this species may occur at high abundance, the medusae are relatively small and may not contribute significantly to the gelatinous biomass (*Invasive Reliability Score = Low*).

#### *LME #50 – Sea of Japan*

As with neighbouring LMEs, the Sea of Japan has suffered from recent increases of the giant jellyfish, *Nemopilema nomurai*. Large blooms of this species have increased dramatically in the last decade, causing interference with fisheries and millions of dollars in economic losses (Kawahara *et al.* 2006). The medusae appear to originate from coastal Korea and China, and are then transported through the Tsushima Strait into this LME, where they spend much of the summer (Uye 2008, 2010; Uye *et al.* 2010). While the medusae from these blooms do not appear to originate in this LME, they may have the potential to colonize it (Kawahara *et al.* 2006).

Blooms of edible jellyfish belonging to the genus *Rhopilema* were historically rare in the Russian Far East waters. However, since 2000, there have been blooms of these jellyfish almost annually (A. Zavolokin, TINRO, pers. comm., Dec. 2011). The apparent spatial expansion of these blooms has been blamed on warm currents from China, and a fishery is currently being developed in order to process the edible jellyfish for export to Asia (Domnitskaya 2011).

Anthropogenic substrate for *Aurelia* polyps has also been identified in this LME. Matsumura *et al.* (2005) observed large and dense polyp colonies in three harbours in Wakasa Bay. As with other documented anthropogenic habitat, the colonies were found on the shadowed undersurfaces of quays and pontoons. While there are no direct data that suggest *Aurelia* medusae have increased in this LME, there have been problems with medusae at a nearby power plant. Molecular evidence suggests that the medusae invading this plant originated from polyps on the anthropogenic structures in Wakasa Bay (Matsumura *et al.* 2005).

### *LME #51 – Oyashio Current*

Knowledge of jellyfish in this region comes from recent publications concerning a Russian dataset that spans three LMEs. This extensive dataset, yet another of fisheries origin, is based on trawls and zooplankton surveys conducted by the Pacific Fisheries Research Center (TINRO) between 1984 and 2009. Zavolokin (2011) reports on data from epipelagic trawl surveys conducted between 1991-2009. Biomass and abundance information is reported for numerous large jellyfish, with over 95% of the biomass representing contributions from scyphomedusae in the genera *Chrysaora*, *Cyanea*, *Phacellophora*, and *Aurelia*, as well as hydromedusae from the genus *Aequorea*. Surveys in this LME appear to show a drop in jellyfish biomass in the last decade compared to estimates in the 1990s, but the author suggests this may be due to a change in sampling times (from late summer to early summer). As such, the data are only comparable from 2004-2009. Analysis over those five years shows variable jellyfish biomass with no significant change (*Abundance Trend* = 0).

Over 9,000 plankton samples were also taken during more than 100 surveys. Volkov (2008) summarizes the zooplankton characteristics from this dataset, and reports biomass trends grouped by time periods and regions. Although the boundary of the “Northwestern Pacific” reported by the author differs somewhat from the boundary separating this LME from the West Bering Sea LME, the Oyashio Current LME is within the region classified as the Northwestern Pacific. The trends show a separation between what the author labels “biotopes” – “Outer shelf” waters, where jellyfish populations appear to be reasonably stable, and the “Deepwater area”, where jellyfish appear to be increasing. However, due to the inconsistency of the methods used in the analysis of the plankton samples, the published results must be interpreted with caution. In the 1980s and 1990s, jellies were apparently considered “undesirable bycatch” and only the small hydromedusan *Aglantha digitale* was enumerated separately (A. Zavolokin, TINRO, pers. comm., Dec. 2011). The data appear to reflect this inconsistency (which is unfortunately not mentioned by the author of the publication), as the values reported for *A. digitale* and those reported for all ‘Coelenterata’ are relatively congruent in the early part of the dataset and begin to diverge with time. As such, only the values for *A. digitale* can be considered to represent consistent (*i.e.*, comparable) data. In both biotopes, there appears to be a decline in *A. digitale*. In the “Outer shelf”, biomass values since 1999 are less than half of those for the 1980s and 1990s. In the “Deepwater area”, there is a sharp decline in *A. digitale* biomass in the early 1990s, followed by a slight recovery in 1999. Despite this variability, values from the 1980s are clearly higher than those reported thereafter, and thus the biomass of *A. digitale* is considered to have declined in this region (*Abundance Trend* = -1). This chronicle is assigned a *Reliability Score* = Low due to the fact that there are clearly other species of significant biomass within this LME that cannot be included due to the inconsistent methodologies discussed above.

### *LME #52 – Sea of Okhotsk*

The aforementioned Russian datasets also cover this entire LME. Zavolokin (2011) reports on epipelagic jellyfish biomass for a number of large scyphomedusae in the Sea of Okhotsk from 1994-2009, including *Chrysaora* and *Cyanea*. While there are several gaps in the dataset, the relative biomass shows no

significant trend. Other analyses of jellyfish data from the Sea of Okhotsk appear to show declines in jellyfish biomass from the 1990s into the 2000s (Il'inskii and Zavolokin 2007; Zavolokin 2010). However, these declines are not evident in the data presented covering a longer timespan (*i.e.*, Zavolokin 2011). As such, this chronicle is categorized as variable (*Abundance Trend* = 0). In addition to the epipelagic surveys, data for large mesopelagic jellyfish are also reported for the period 1992-2005 by Zavolokin (2010). Despite high biomass of scyphozoans in 2005, the data do not show a significant trend.

Based on the data presented by Volkov (2008), it would appear there has been a large increase in 'Coelenterata' in recent years. However, as discussed with the Oyashio Current LME, only the hydromedusan *Aglantha digitale* will be considered due to inconsistent treatment of other jelly species. Data from "Inner shelf" waters indicate a steady increase in *A. digitale* biomass over the course of the study. However, this increase is not represented in "Outer shelf" or "Deepwater area" waters, where *A. digitale* biomass appears variable. As such, the records from this survey have been divided into two chronicles in this LME, each with a differing *Abundance Trend* and *Space Score*. As discussed, chronicles resulting from this dataset are classified with *Reliability Score* = Low.

There is also evidence to suggest that blooms of the giant jellyfish, *Nemopilema nomurai*, are appearing in this LME. According to a report by the Japanese Fisheries Service Center, these jellies have been observed in the Sea of Okhotsk along the coast of Hokkaido (Anonymous 2009d), but their abundance and distribution in this LME remains unclear.

### *LME #53 – West Bering Sea*

As with the Oyashio Current and Sea of Okhotsk LMEs, the Russian dataset based on Pacific Fisheries Research Center (TINRO-Center) trawl surveys reveals insight into temporal changes in jellyfish biomass in this LME. Zavolokin (2011) illustrates a declining trend (*Abundance Trend* = -1) in overall relative biomass for numerous large scyphomedusae and hydromedusae in the northwestern Bering Sea, especially *Chrysaora melanaster*. In the southwestern Bering Sea, the trend is much more variable (*Abundance Trend* = 0). As the data in these two regions also cover different timescales, they are included as two separate chronicles. In addition to the large scyphozoans, the hydromedusan *Aequorea forskalea* also appears to be an abundant component of the jellyfish in this region, comprising the majority of the gelatinous biomass in some years (Zavolokin *et al.* 2008; Zavolokin 2011).

As discussed, changes reported by Volkov (2008) in "Coelenterata" cannot be included due to the inconsistency in dealing with small hydromedusae species (A. Zavolokin, TINRO, pers. comm., Dec. 2011). Nonetheless, increases in *Aglantha digitale* populations are revealed in all regions reported in this LME, with much larger biomass in 1997-2006 compared to 1984-1996.

### *LME #60 – Faroe Plateau*

Continuous Plankton Recorder (CPR) data spanning this LME were presented by Licandro *et al.* (2010). While CPR surveys are clearly not designed to sample jellyfish, they can provide an index of occurrence for the species sampled (see LME #22 – North Sea). CPR data reveal an increase in the jellyfish anomaly from 1958-2007 in roughly one half of this LME (the northeast), while the southwest section shows a decline. Therefore, this dataset was classified as variable (*Abundance Trend* = 0).

### *LME #61 – Antarctic*

Jellyfish are a major component of the plankton in this LME, which can include large salp blooms and several abundant ctenophores and medusae (Pagès *et al.* 1996). Like many populations, jellyfish in this LME show high interannual variability, with populations changing from high abundance to near absence in consecutive years (Larson and Harbison 1990; Pagès *et al.* 1996). In the Antarctic, there is a negative correlation between salps and krill, whereby one group or the other tends to dominate in a particular year. This relationship appears to be mediated by sea ice, as ice algae provide food for krill in winter, hence promoting larval recruitment. In contrast, salps occupy open waters with lower primary production, and therefore sea ice extent may dictate whether krill or salps dominate (Loeb *et al.* 1997; Moline *et al.* 2004). Salp populations monitored at Elephant Island over the past several decades appear to be highly variable, with alternating regimes of salp and krill dominance (Lee *et al.* 2010). A similar trend was evident for Prydz Bay through the 1980s (Perissinotto and Pakhomov 1998). While these examples would lead one to conclude that salp populations do not show significant changes, analysis at a larger scale suggests otherwise. Atkinson *et al.* (2004) compiled data for krill and salp populations extending back to the 1920s, covering an extensive area of this LME. Abundance data from 1976-2003 were compared with that from 1926-1939, revealing a significant decline in krill and a concurrent increase in salps. This pattern was evident for several disparate locations around the Antarctic continent. While data prior to 1950 were generally not included in this analysis (see Materials and Methods), an exception was made in this case due to the extensive temporal and spatial coverage of the database, which comprises nearly 12,000 net hauls. In addition, the significant decline in krill shown from 1976 to 2003 may indicate a similar trend for salps over the same time period due to the inverse correlation discussed above. If warming trends continue in this LME, salp populations may continue to increase (Loeb *et al.* 1997; Moline *et al.* 2004).

### *LME #62 – Black Sea*

The Black Sea has a unique and fascinating history of changing jellyfish populations, linked primarily to a number of anthropogenic impacts including eutrophication, overfishing, and species invasions (see below). The history of this ecosystem must also be viewed in light of climatic conditions, which likely played a significant role in driving the observed ecological changes (Niermann 2004).

The scyphomedusan *Aurelia aurita* is suspected to be invasive here (Dawson *et al.* 2005); however, the timeline concerning this invasion is unclear. As *Aurelia* has been present here since at least the 1950s, it was therefore classified as a native species for the purposes of this analysis. Abundances of *Aurelia* were relatively low in the 1950s and 1960s, with a total biomass somewhere between 1 million tonnes (Niermann 2004) and 30 million tonnes (Bat *et al.* 2009 and references therein). Abundances of *Aurelia* increased dramatically through the 1970s and 1980s due to eutrophication and other anthropogenic stressors (Niermann 2004), ultimately reaching a peak biomass on the order of 400-600 million tonnes (Gomoiu 1981; Flint *et al.* 1989). The invasion of the ctenophore *Mnemiopsis leidyi* in 1988 (see below) resulted in a significant reduction of *Aurelia* thereafter (Shushkina and Vinogradov 1991), possibly due to the fact that *Aurelia* populations are constrained by a sessile polyp phase requiring suitable substrate within the oxygenated zone, whereas ctenophores release gametes directly into the water column (Gücü 2002; Niermann 2004). The population of *Aurelia* in the Black Sea now appears to be on the order of 100 million tonnes (Mutlu *et al.* 1994; Bat *et al.* 2009). As this is still much higher than the biomass reported from the 1950s and 1960s, *Aurelia* is considered to have increased in this region over this time period (*Abundance Trend* = 1). While the fluctuations of *Aurelia* biomass tend to be negatively correlated with biomass of *M. leidyi*, it would appear that the overall gelatinous biomass of the Black Sea shelf has increased since the 1950s and 1960s due to the presence of both species (Kovalev and Piontkovski 1998; Oguz and Velikova 2010).

The ctenophore *Pleurobrachia pileus* also occurs in the Black Sea in high abundances. While no major population changes are suspected over the past several decades (Mutlu *et al.* 1994), there is a suggestion that the *P. pileus* population has been reduced since 1999 due to predation by the invasive ctenophore *Beroe ovata* (see below). However, this decline does not appear to be significant, as a lower biomass of *P. pileus* was also observed in the mid-1990s, prior to the invasion of *B. ovata* (Shiganova *et al.* 2004a), and *P. pileus* abundance continues to be high in the southern Black Sea (Mutlu 2009).

Interestingly, the scyphozoan *Rhizostoma pulmo* used to be one of the most common jellyfish in coastal areas of the southern Black Sea, but was not observed in 2006/2007 (Mutlu 2009). The sudden disappearance of this conspicuous species is noteworthy, especially if its absence continues. Nonetheless, the decline of *R. pulmo* is surely not sufficient to offset the increased biomass due to the other jellyfish in the Black Sea.

#### Invasive Species in LME #62 – Black Sea

The highly invasive ctenophore *Mnemiopsis leidyi* is native to the eastern U.S.A. and was accidentally introduced to the Black Sea in the 1980s, presumably via ballast water from cargo vessels (Shiganova 1998). *M. leidyi* was first detected in the inshore waters of Sudak Bay in 1982, and began to spread throughout the Black Sea in 1988 (Shiganova 1998 and references therein). The population of *M. leidyi* in the Black Sea quickly grew to astounding abundances in 1989 and 1990, subsequently declining thereafter. This pattern appears to have repeated, with additional peaks in the population occurring in the mid-1990s and early-2000s, both of which were followed by years of variable abundance (Shiganova 1998; Mutlu 2009).

In 1997, another invasive ctenophore – *Beroe ovata* – was detected in the Black Sea, also presumably due to ballast water from shipping (Finenko *et al.* 2001 and references therein). Ironically, this jellyfish preys almost exclusively on other ctenophores, and intentional introduction was being considered in the Black Sea as a possible means of controlling *M. leidyi* blooms (Shiganova and Malej 2009). *B. ovata* quickly established a large population, subsequently suppressing *M. leidyi* abundance (Shiganova *et al.* 2004a). Laboratory experiments suggest that *B. ovata* will regulate its own population size by adjusting reproduction to suit prey availability (Shiganova *et al.* 2004a), and indications are that it can control populations of *M. leidyi* effectively. While it appears that the populations of these invasive ctenophores have declined since their peaks in the 1990s, both species are considered successful invaders and appear established in the Black Sea (Mutlu 2009; Oguz and Velikova 2010).

#### *LME #63 – Hudson Bay*

Canada's Department of Fisheries and Oceans (DFO) has conducted annual surveys in Hudson Bay since 2003. Zooplankton data for summer (August or September) are collected from numerous stations along a large transect (~600 km) inside Hudson Bay, as well other transects in Foxe Basin and Hudson Strait. Dominant jellyfish are small hydromedusae, including *Aglantha digitale* and the less abundant *Aeginopsis laurentii*. Jellyfish abundance data for the period 2003-2006 show variability for Hudson Bay, with a notable peak of *A. digitale* in 2004 (M. Harvey, DFO, pers. comm., Aug. 2010). The other transects also show variability over several years of data. Interestingly, the peak of *A. digitale* is not evident in Foxe Basin, where jellyfish abundance was actually lower in 2004.



## CONCLUSIONS

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Jellyfish populations appear to be increasing in the majority of the world's coastal ecosystems and seas. While these increases are conspicuous in several locations, even basic knowledge of jellyfish populations in most regions is poor. While the increases were generally not due to invasive species of jellyfish, invasions were widespread, occurring in approximately half of the systems examined. In several regions, populations of invasive jellyfish appear to be thriving, and should serve as warnings for other ecosystems around the world. Many of the observed increases in jellyfish populations appear linked to human activities, but the mechanisms involved remain poorly understood. As jellyfish can have important and profound impacts on human activities and marine ecosystems, it is of paramount importance that we rapidly increase our understanding of these enigmatic creatures.

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## APPENDICES

## Appendix A – Jellyfish Chronicles

CI – Confidence Index; AT – Abundance Trend; TS – Time Score; SS – Space Score; RS – Reliability Score; **Invasive Species**; **Harvested Species**; **AT** – overharvesting

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
1	Very high	1	Very high	Very high	Very high	USA (Alaska)	Bering Sea	1975-2009	Primarily <i>Chrysaora melanaster</i>	(Brodeur <i>et al.</i> 2008a)	(Decker <i>et al.</i> 2009)
2	High	0	Very high	Medium	Very high	Canada & USA	Line P, Vancouver Island shelf, Hecate Strait, Salish Sea	1980s-2010	Numerous	(data provided by Galbraith 2010)	See discussion
2	Medium	1	Low	Medium	Very high	USA (Alaska)	Alaskan Peninsula	1973-1996	Scyphozoa	(Anderson and Piatt 1999)	
2	Medium-low	0	Low	Low	Very high	USA (Alaska)	Prince William Sound	1995-1999	<i>Aurelia labiata</i>	(Purcell <i>et al.</i> 2000)	(Purcell 2003)
3	High	1	Very high	Medium	Very high	USA	California coast (Southern Station)	1951-2006	Ctenophora, Hydromedusae, Salpida, Siphonophora	(CalCOFI 2010)	(Lavaniegos and Ohman 2003, 2007)
3	High	0	Very high	Medium	Very high	USA	California coast (Central Station)	1951-2006	Ctenophora, Hydromedusae, Salpida, Siphonophora	(CalCOFI 2010)	
3	Medium	1	High	Medium	Low	Mexico	Baja California	1998-2007	Numerous	(Lavaniegos 2009)	
3	High	0	Very high	Medium	High	USA	Oregon	1981; 2001/2002	<i>Chrysaora fuscescens</i>	(Suchman and Brodeur 2005)	(Shenker 1984)
3	Medium-high	1	Very high	Low	High	USA	San Francisco Bay	Since 1980s and 1990s	<b>Numerous Invasive spp.</b>	(Mills and Rees 2000; Rees and Gershwin 2000)	(Mills and Sommer 1995; Greenberg <i>et al.</i> 1996)
3	Medium	1	High	Low	Medium	USA	Coos Bay, Oregon	Since 1998/1989	<b>Blackfordia virginica</b>	(Mills and Rees 2000)	
3	Medium	1	Very high	Low	Medium	USA	Mission Bay & San Diego Bay	Since 1981	<b>Phyllorhiza punctata</b>	(Larson and Arneson 1990)	(Graham and Bayha 2007)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
4	Medium-low	1	Low	Low	High	Mexico	Sonora	Last several years	<i>Stomolophus meleagris</i>	(L. Ocampo, CIBNOR, pers. comm., Sept. 2010)	(Ocampo <i>et al.</i> 2010)
5	High	0	Very high	Medium	Very high	USA	Northern Gulf of Mexico	1985-2006	<i>Aurelia aurita</i> , <i>Chrysaora quinquecirrha</i>	(Graham 2001)	(W.M. Graham, DISL, pers. comm., May 2010)
5	Medium	1	High	Low	High	USA	Florida Keys	Since 1990s	<i>Cassiopea</i> spp.	(Fitt and Costley 1998)	(Chiaverano <i>et al.</i> 2010)
5	Medium-high	1	High	Medium	Medium	USA	Northern Gulf of Mexico	Since 2000 (possibly since 1993)	<i>Phyllorhiza punctata</i>	(Graham <i>et al.</i> 2003)	See Discussion
6	Medium	1	Medium	Medium	Medium	USA	North Carolina & Florida	Recent years and decade	<i>Carybdea marsupialis</i>	(Anonymous 2009a)	(Anonymous 1998, 2010f)
6	Low	1	Low	Low	Low	Bahamas	Abaco Island	2009 Site comparison	<i>Cassiopea</i> spp.	(Stoner <i>et al.</i> 2011)	
6	Medium	1	Medium	Medium	Medium	USA	North Carolina & Florida	Since 2001	<i>Phyllorhiza punctata</i> ( <i>Turritopsis dohrnii</i> & <i>Blackfordia virginica</i> also noted)	(Britt 2007; Waymer 2009)	(Miglietta and Lessios 2009; USGS 2011)
6	High	0	Medium	High	Very high	USA	North Carolina to Georgia	2001-2009	<i>Stomolophus meleagris</i>	(Hendrix and Boylan 2010)	(SCDNR 2005; Petersen 2011)
7	Very high	1	Very high	Very high	Very high	USA	Entire LME	1981-2000	Ctenophora	(Link and Ford 2006)	
7	Medium-high	1	High	Low	Very high	USA	Chesapeake Bay	1987-2000	<i>Mnemiopsis leidyi</i> & <i>Chrysaora quinquecirrha</i> ( <i>Blackfordia virginica</i> , <i>Maeotias marginata</i> , & <i>Moerisia lyonsi</i> also noted)	(Purcell and Decker 2005)	(Cargo and King 1990; Mills and Sommer 1995; Ruiz <i>et al.</i> 2000; USGS 2011)
7	Medium-low	1	Very high	Low	Low	USA	Narragansett Bay	1971-2009	<i>Mnemiopsis leidyi</i>	(Sullivan <i>et al.</i> 2001)	(Rynewson 2010)
7	Medium	1	High	Low	High	USA	Barnegat Bay	Since 2000	<i>Chrysaora</i> sp.	(Dutzik and O'Malley 2010)	(APP 2010; Campbell 2010)
7	Low	1	Low	Low	Low	USA	New York State	Since 2008	<i>Cyanea capillata</i>	(Grossman 2010)	(Gaskell 2008; Parry 2008)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
7	Medium-low	0	High	Low	Low	Canada	Prince-5 Fixed Station	1999-2008	Jelly + Appendicularia	(Harrison <i>et al.</i> 2009)	(Harrison <i>et al.</i> 2005)
8	High	0	Medium	High	Very high	Canada	Numerous transects	2001-2009	Numerous (primarily <i>Aglantha digitale</i> & <i>Diomphyes arctica</i> )	(M. Harvey, DFO, pers. comm., Aug. 2010)	(Harvey and Devine 2009)
8	Medium-high	0	High	Medium	High	Canada	Gulf of St. Lawrence	1995-2008	Primarily <i>Aglantha digitale</i>	(Harvey and Devine 2009)	
8	Medium-low	0	High	Low	Low	Canada	Halifax-2 fixed station	1999-2008	Jelly + Appendicularia	(Harrison <i>et al.</i> 2009)	
9	Very high	0	High	Very high	Very high	Canada	Wide-scale sampling	1999-2008	<i>Aglantha digitale</i> & <i>Pelagia noctiluca</i>	(Pepin <i>et al.</i> 2009)	(P. Pepin, DFO, pers. comm., Dec. 2009; DFO 2008)
10	High	1	Very high	Medium	High	USA	Main Hawaiian Islands	Since 1980s	<i>Carybdea alata</i>	(Thomas <i>et al.</i> 2001; Crow <i>et al.</i> 2010)	
10	Medium-high	1	Very high	Medium	Medium	USA	Main Hawaiian Island	Increased distribution since 1950s	<i>Cassiopea</i> spp.	(Devaney and Eldredge 1977; Eldredge and Smith 2001; Holland <i>et al.</i> 2004)	(Hofmann and Hadfield 2002; Daoust 2009; Kelsey 2009)
10	Medium	1	Very high	Low	Medium	USA	Oahu, Hawaii	Since 1953	<i>Aurelia</i> sp. 4	(Dawson <i>et al.</i> 2005)	
10	Medium-low	1	Very high	Low	Low	USA	Kaneohe Bay, Oahu, Hawaii	Since 1983	<i>Anomalorhiza shawi</i>	(Cooke 1984)	(Lum 2001)
11	Medium-low	1	Low	Low	High	Mexico	Lagunas Superior & Inferior, Oaxaca	Since at least 1988	<i>Stomolophus meleagris</i>	(Ocaña-Luna and Gómez-Aguirre 1999)	
11	Medium	1	Very high	Low	Low	Mexico	Lagoons of Chantutuo-Pensacola, Chiapas	Since at least 1997	<i>Blackfordia virginica</i>	(Álvarez-Silva 1999)	(Álvarez-Silva <i>et al.</i> 2003)
11	Low	1	Low	Low	Low	Panama	Panama Bay	Since at least 2006	<i>Turritopsis dohrnii</i>	(Miglietta and Lessios 2009)	
12	Medium-low	0	Low	Low	High	Jamaica	Lime Cay	1992/1993 & 1985/1986	Numerous	(Persad <i>et al.</i> 2003)	(Clarke 1988)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
12	Medium	0	High	Low	Medium	Panama	Bocas del Toro	Since 2000	Unknown	(G. Jacome, STRI, pers. comm., Jan. 2011)	(Williams <i>et al.</i> 2001)
12	Medium	1	Very high	Low	Medium	Jamaica	Negril	Since at least 1973	<i>Phyllorhiza punctata</i>	(Cutress 1973)	pers. obs.
12	Medium-low	1	Medium	Medium	Low	Panama	Galeta & Bocas del Toro	Since at least 2006	<i>Turritopsis dohrni</i>	(Miglietta and Lessios 2009)	
13	Very high	0	Very high	High	Very high	Peru	From Puerto Pizarro to beyond Mollendo	1972-2010	<i>Chrysaora plocamia</i>	(Quiñones <i>et al.</i> 2010b)	(Quiñones <i>et al.</i> 2010a)
13	Medium-low	1	Medium	Low	Medium	Chile	Chilean fjord region	Since at least 2005	<i>Aurelia aurita</i>	(Häussermann <i>et al.</i> 2009)	
14	High	1	High	Medium	Very high	Argentina & Uruguay	Buenos Aires coast	1993-2006	<i>Obelia longissima</i>	(Genzano <i>et al.</i> 2008)	
14	Medium	1	High	Low	Medium	Argentina	Río de la Plata	Since 2000	<i>Blackfordia virginica</i>	(Genzano <i>et al.</i> 2006)	
15	High	0	Very high	Medium	High	Brazil	States of Paraná & Santa Catarina	Interviews conducted 2003-2007	Numerous (esp. <i>Lychnorhiza lucerne</i> )	(Nagata <i>et al.</i> 2009)	
15	Medium-high	0	Very high	Medium	Medium	Brazil	States of São Paulo, Paraná, & Santa Catarina	History back to 1950s	<i>Phyllorhiza punctata</i>	(Haddad and Nogueira 2006)	(M. Nogueira, UFP, pers. comm., Sept. 2010)
15	Medium	1	Low	Medium	Medium	Brazil	Numerous locations	Since 2004 in Paranaguá Bay; Since 2007 in other locations	<i>Blackfordia virginica</i>	(Nogueira and de Oliveira 2006)	(Bardi and Marques 2009a)
16	Medium	1	Medium	Medium	Medium	Brazil	States of Bahia & Ceará	Since 2003 at latest	<i>Phyllorhiza punctata</i>	(Haddad and Nogueira 2006)	
18	Low	-1	Low	Medium	Low	Greenland (Denmark)	SW Greenland	1956-1982	<i>Aglantha digitale</i>	(Pedersen and Smidt 2000)	
21	Medium-high	1	Very high	Low	High	Norway	Halsafjorden	Since 1980s	<i>Periphylla periphylla</i>	(Sørnes <i>et al.</i> 2007)	
21	Low	1	Low	Low	Medium	Norway	Trondheimsfjorden	Since 2008	<i>Mnemiopsis leidyi</i>	(A. Hosia, IMR, pers. comm., Oct. 2010)	

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
22	Very high	1	Very high	Very high	High	Numerous	Entire LME	Since 1980s	Likely <i>Aglantha digitale</i>	(Attrill <i>et al.</i> 2007; Licandro <i>et al.</i> 2010)	(Attrill and Edwards 2008; Haddock 2008)
22	Medium-high	0	Low	High	Very high	Numerous	Wide-scale sampling in half of LME	1971-1986	Numerous	(Hay <i>et al.</i> 1990)	(Lynam <i>et al.</i> 2004, 2005)
22	Medium-high	1	Very high	Low	Very high	Netherlands	Texel Island	Recent decades	Numerous	(van Walraven <i>et al.</i> 2010)	
22	Medium-high	1	Very high	Low	High	Norway	Lurefjorden	Since 1970s	<i>Periphylla periphylla</i>	(Fosså 1992)	(Youngbluth and Båmstedt 2001; Sørnes <i>et al.</i> 2007)
22	Medium-high	1	Very high	Low	High	Denmark	Limfjorden	Since 1980s	<i>Aurelia aurita</i> (& others)	(Riisgård <i>et al.</i> 2012)	(Hoffmann 2005; Møller and Riisgård 2007a, 2007b)
22	Medium-low	0	Very high	Low	Low	Germany	Helgoland, German Bight	1975-1993; 1975-2002	Numerous	(Greve <i>et al.</i> 1996; Greve <i>et al.</i> 2004)	(Greve 1994; Schlüter <i>et al.</i> 2010)
22	Medium-low	-1	Low	Low	High	United Kingdom	Thames Estuary	Since 1985 (data 1977-1992)	<i>Aurelia aurita</i> ( <i>Pleurobrachia pileus</i> is variable)	(Attrill and Thomas 1996)	
22	Medium-high	1	Medium	High	Medium	Numerous	Numerous	Since at least 2005	<i>Mnemiopsis leidyi</i>	(Oliveira 2007; Tendal <i>et al.</i> 2007)	(Faasse and Bayha 2006; Hansson 2006; Boersma <i>et al.</i> 2007; Hosia 2007; Riisgård <i>et al.</i> 2007)
23	High	0	High	Medium	Very high	Sweden & Poland	Bornholm Basin	1994-2003	<i>Aurelia aurita</i> & <i>Cyanea capillata</i>	(Barz and Hirche 2005; Barz <i>et al.</i> 2006)	
23	Medium-low	0	Low	Low	Very high	Germany	Kiel Bight	1978-1993	<i>Aurelia aurita</i>	(Schneider and Behrends 1994)	(Möller 1979, 1984; Behrends and Schneider 1995; Schneider and Behrends 1998)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
23	Medium	1	Medium	Medium	Medium	Numerous	Southwestern Baltic	Since at least 2006	<i>Mnemiopsis leidyi</i>	(Javidpour <i>et al.</i> 2006; Haslob <i>et al.</i> 2007; Kube <i>et al.</i> 2007; Tendal <i>et al.</i> 2007)	(Gorokhova <i>et al.</i> 2009; Gorokhova and Lehtiniemi 2010)
23	Medium-low	1	Low	High	Low	Numerous	Northern and central Baltic	Since at least 2007	<i>Mertensia ovum</i>	(Gorokhova <i>et al.</i> 2009)	(Anonymous 2009b)
23	Low	1	Low	Low	Low	Estonia	Väinameri Archipelago	Since at least 1999	<i>Maeotias marginata</i>	(Väinölä and Oulasvirta 2001; Ojaveer and Kotta 2006)	
24	Very high	1	Very high	Very high	High	Numerous	Entire LME	1958-2007	Presumably <i>Pelagia noctiluca</i>	(Licandro <i>et al.</i> 2010)	(Baxter <i>et al.</i> 2010)
24	Medium-high	1	Very high	Low	Very high	Ireland	Irish Sea	1994-2009	Mainly <i>Aurelia aurita</i> & <i>Cyanea</i> spp.	(Lynam <i>et al.</i> 2011)	(Gittens 2011)
24	Medium-high	0	Very high	Low	Very high	United Kingdom	L4 station	1998-2007	Hydromedusae & siphonophores	(WCO 2011)	
24	Low	1	Low	Low	Low	United Kingdom	Southampton Water	Recent years	<i>Aurelia</i> sp. & <i>Pleurobrachia</i> sp.	(C. Lucas, NOC, pers. comm., Jan. 2011)	(Duarte <i>et al.</i> in review)
25	High	0	High	Medium	Very high	Spain	Vigo, Coruña, & Santander stations	Mid-1990s-mid-2000s	Salps & siphonophores	(IEO 2010)	(Valdés <i>et al.</i> 2007)
25	Low	1	Low	Low	Medium	Portugal / Spain	Guadiana Estuary	Since 2008	<i>Blackfordia virginica</i>	(Chícharo <i>et al.</i> 2009)	
26	Medium-high	0	Very high	Low	Very high	France	Villefranche-sur-Mer	1974-2003	Entire medusae & siphonophore communities	(García-Comas <i>et al.</i> 2011)	(Buecher <i>et al.</i> 1997; Licandro <i>et al.</i> 2001; Molinero <i>et al.</i> 2005; 2008a; 2008b)
26	High	1	Very high	High	High	Numerous	Western Mediterranean	Since 1990s (records back to 1800s)	<i>Pelagia noctiluca</i>	(Anonymous 2008b, 2010c; Daly Yahia <i>et al.</i> 2010)	(Goy <i>et al.</i> 1989; Molinero <i>et al.</i> 2005; 2008a; Anonymous 2010h; Licandro <i>et al.</i> 2010)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
26	Medium-high	1	Very high	Low	Very high	Spain	Mar Menor	Since 1990s	<i>Cotylorhiza tuberculata</i> & <i>Rhizostoma pulmo</i>	(Pagès 2001; Pérez-Ruzafa <i>et al.</i> 2002)	(Conesa and Jiménez-Cárceles 2007; Prieto <i>et al.</i> 2010; Fuentes <i>et al.</i> 2011; Duarte <i>et al.</i> in review)
26	Medium-high	1	Very high	Low	Very high	Slovenia, Italy, Croatia	Gulf of Trieste	Since 1960s (records back to 1800s)	<i>Aurelia</i> sp. & other scyphomedusae and ctenophores	(Kogovšek <i>et al.</i> 2010)	(Malej 2001; Di Camillo <i>et al.</i> 2010; Duarte <i>et al.</i> in review)
26	Medium-high	1	Low	Very high	High	Numerous	Numerous	Since 1990s; large blooms in 2009	<i>Mnemiopsis leidyi</i> & <i>Beroe ovata</i>	(Fuentes <i>et al.</i> 2010)	(Boero <i>et al.</i> 2009; Galil <i>et al.</i> 2009a; Galil <i>et al.</i> 2011)
26	High	1	Very high	Medium	High	Israel, Lebanon, Syria, Greece	Numerous	Since 1970s	<i>Rhopilema nomadica</i> , ( <i>Phyllorhiza punctata</i> , & <i>Marivagia stellata</i> also noted)	(Galil <i>et al.</i> 1990; Lotan <i>et al.</i> 1992; 1994)	(Galil <i>et al.</i> 2009b; 2010; Marshall 2010; Waldoks 2010)
26	Medium-low	1	Low	Medium	Medium	Greece, Spain	Numerous	Since early 2000s (Greece), 2010 (Spain)	<i>Phyllorhiza punctata</i>	(Abed-Navandi and Kikinger 2007)	(Anonymous 2011a)
26	Medium-low	1	Low	Medium	Medium	Italy, Spain, France, Malta	Numerous	Recent years	<i>Carybdea marsupialis</i>	(Di Camillo <i>et al.</i> 2006; CIESM 2008)	(Boero and Minelli 1986; Cuneo 2009; Schembri 2010; Bordehore <i>et al.</i> 2011)
26 28	Low Medium	1 1	Low High	Low Low	Low High	Italy Ghana	Sicily Channel	2010 2000s	<i>Catostylus tagi</i> Unknown	(Nastasi 2010) (B. Asiedu, U. Ghana, pers. comm., Jan. 2010)	(F.K.E. Nunoo, U. Ghana, pers. comm., Feb. 2010)
29	High	1	Very high	High	High	Namibia	Coastal and shelf waters	Since 1960s	<i>Chrysaora hysoscella</i> & <i>Aequorea forskalea</i>	(Lynam <i>et al.</i> 2006)	(Hart and Currie 1960; Fearon <i>et al.</i> 1992)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
29	High	1	Very high	Medium	High	Namibia	Coastal and shelf waters	Since 1970s	<i>Chrysaora hysoscella</i> & <i>Aequorea forskalea</i>	(Venter 1988)	
30	Medium-high	0	Very high	Low	High	South Africa	KwaZulu-Natal	1975-2010	Unclear	(R. van der Elst, ORI, pers. comm., Jan. 2010)	
30	Medium-high	0	Medium	Medium	High	Mozambique, Madagascar, Comoros		Unclear (assume min. 5 years)		(van der Elst 2010)	
31	Medium-high	0	Medium	Medium	High	Tanzania & Kenya		Unclear (assume min. 5 years)		(van der Elst 2010)	
32	High	0	Very high	High	High	India	States of Gujarat, Maharashtra, & Karnataka	Interviews conducted in 2008	Unclear	(G. Pramod, UBC, pers. comm., Sept. 2010)	(Pramod 2010)
32	Medium-high	1	Very high	Low	High	India	State of Kerala	Interviews conducted in 2008	Unclear	(G. Pramod, UBC, pers. comm., Sept. 2010)	(Anonymous 2010b; Pramod 2010)
32	Medium-high	0	Medium	High	High	Iran	Gulf of Oman	1998-2006	<i>Crambionella orsini</i>	(Daryanabard and Dawson 2008)	(Billett <i>et al.</i> 2006)
32	Medium	1	Medium	Low	High	Numerous	Persian Gulf	Last 7-10 years	Unclear	(Erftemeiger and Langenberg 2010)	Numerous (see Discussion)
32	Low	-1	Low	Low	Medium	Pakistan	Kerachi	Last 5 years	<i>Rhizostoma pulmo</i> and/or <i>Catostylus mosaicus</i> ?	(Roghay 2011)	
34	High	0	Very high	High	High	India	States of Tamil Nadu, Andhra Pradesh, Andaman & Nicobar Islands	Interviews conducted in 2008	Unclear	(G. Pramod, UBC, pers. comm., Sept. 2010)	(Pramod 2010)
34	High	1	Very high	Medium	High	India	States of Orissa & West Bengal	Interviews conducted in 2008	Unclear	(G. Pramod, UBC, pers. comm., Sept. 2010)	(Pramod 2010)



LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
34	Medium-low	1	Low	Low	High	India	Madras	Unclear (recent years or decades)	Numerous (incl. <i>Cambionella stuhlmanni</i> )	(B. Ingole, NIO, pers. comm., Oct. 2010)	(James <i>et al.</i> 1985; Rajagopal <i>et al.</i> 1989; Musilamoni <i>et al.</i> 2000)
34	Medium-low	-1	Low	Low	High	India	Orissa	Since 2007	Unknown	(Anonymous 2008a)	(Anonymous 2007a)
34	Medium	1	Low	Medium	High	Malaysia & Thailand	Langkawi, MY & Phuket, TH	2009 & 2010	Unknown; possibly <i>Cephea cephea</i> in Thailand	(M.R.B. Idid, IBS, Jan. 2011)	(Morison 2009; Kwang and Yahya 2010; Lau 2010)
34	Medium-low	-1	Very high	Low	Low	Thailand	Segenting	2005	<i>Catostylus mosaicus</i>	(Heng 2005)	
35	Low	1	Medium	Low	Low	Thailand	Gulf of Thailand beaches	Past decade	Unknown (likely cubomedusae)	(Suntrarachun <i>et al.</i> 2001)	(Anonymous 2010a)
36	Medium-high	0	Very high	Low	Very high	Taiwan	Tapong Bay	Since 2002	<i>Aurelia aurita</i>	(Lo <i>et al.</i> 2008)	
36	Low	1	Low	Low	Low	Philippines	Lingayen Gulf	December 1999	Unknown	(Anonymous 1999)	
36	Medium-low	-1	Low	Low	High	Philippines	Malampaya Sound	2008	<i>Lobonema</i> spp.	(PCAMRD 2008)	
40	Medium-low	1	Very high	Low	Low	Australia	Northern Queensland	Over last 30-40 years	Cubomedusae	(Anonymous 2010d)	(Smail 2010)
40	Medium-low	1	Medium	Medium	Low	Australia	Gold Coast	Last 5 years	Cubomedusae	(Donaghey 2009)	
41	Medium-high	0	Very high	Low	High	Australia	New South Wales	2008-2009 (& 1940s)	<i>Thalia democratica</i>	(K. Pitt, GU, pers. comm., May 2010)	(Strong 2008; Henschke 2009)
41	Medium-high	0	Medium	Medium	High	Australia	Around Moreton Bay	Since 2002	<i>Catostylus mosaicus</i>	(K. Pitt, GU, pers. comm., May 2010)	
41	Medium-low	-1	Low	Low	Very high	Australia	Myora Drain & Pelican Waters	Since 1997 (MD) & 1999 (PW)	<i>Cassiopea</i> sp.	(K. Pitt, GU, pers. comm., May 2010)	(Bouchet 2007; Mortillaro <i>et al.</i> 2009; Templeman and Kingsford 2010)
42	Medium-high	0	Very high	Low	Very high	Australia	Port Phillip Bay	1991-2009	<i>Catostylus mosaicus</i>	(K. Pitt, GU, pers. comm., May 2010)	(Coleman 2004; DPI 2006)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
42	Low	1	Medium	Low	Low	Australia	Tasmania	Since at least 2002	<i>Aurelia</i> sp. polyps	(Willcox <i>et al.</i> 2008)	(Naidoo 2009)
42	Medium-low	1	Very high	Low	Low	Australia	Port Phillip Bay	Since 1970s and 1980s	Numerous hydromedusae	(Hewitt <i>et al.</i> 2004)	
47	Very high	1	Very high	High	Very high	China	>Half of LME	1990-2003 (and after)	<i>Cyanea</i> spp. & <i>Nemopilema nomurai</i>	(Yan <i>et al.</i> 2004)	(Dong <i>et al.</i> 2010)
47	High	1	Very high	Medium	Very high	South Korea & China	Near Jeju Island	Since 2003	<i>Nemopilema nomurai</i>	(Yoon <i>et al.</i> 2008)	(Ding and Cheng 2005; Rahn 2009)
47	Medium-high	1	High	Low	Very high	China	Yangtze Estuary	Since at least 1997	Numerous	(Xian <i>et al.</i> 2005)	
47	Medium-low	1	Very high	Low	Low	Japan	Kagoshima Bay	Since at least 1993	<i>Aurelia aurita</i>	(Miyake <i>et al.</i> 1997)	(Miyake <i>et al.</i> 2002)
47	Medium	1	High	Low	High	Korea	Busan & Geoje-do	Since 2000	<i>Aurelia</i> sp. 1	(Ki <i>et al.</i> 2008)	
48	Very high	1	Very high	High	Very high	China & South Korea	Western Korea; Bohai Sea; Jiaozhou Bay	Since 2003	<i>Nemopilema nomurai</i>	(Yoon <i>et al.</i> 2008)	(Rahn 2009; Dong <i>et al.</i> 2010; Sun <i>et al.</i> 2010)
48	Medium-high	1	High	Medium	High	China	Yellow Sea & Bohai Sea	Since 1997	<i>Cyanea nozakii</i> (R. <i>esculentum</i> declined)	(Dong <i>et al.</i> 2006)	(Ge and He 2004; Dong <i>et al.</i> 2010)
48	Medium	1	High	Low	High	Korea	Incheon	Since 2000	<i>Aurelia</i> sp. 1	(Ki <i>et al.</i> 2008)	(Han and Uye 2010)
49	High	1	Very high	Medium	Very high	Japan	NE coast of Honshu	Since 2002 (records back to 1920s)	<i>Nemopilema nomurai</i>	(Uye 2008)	(Kawahara <i>et al.</i> 2006)
49	Medium	1	High	Medium	Low	Japan	Seto Inland Sea	Since 1990s	<i>Aurelia</i> sp.	(Uye and Ueta 2004)	(Nagai 2003; Uye <i>et al.</i> 2003; Kaneda <i>et al.</i> 2007; Takahashi <i>et al.</i> 2010)
49	High	1	Very high	Medium	High	Japan	Tokyo Bay & Mikawa Bay	Since 1960s and 1970s	<i>Aurelia</i> sp. & others	(Omori <i>et al.</i> 1995; Nomura and Ishimaru 1998; Toyokawa <i>et al.</i> 2011)	(Kasuya <i>et al.</i> 2000; Arai 2001; Kinoshita <i>et al.</i> 2006)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
49	Medium-low	-1	Very high	Low	Low	Japan	Unclear (see Discussion)	Since 1980s	<i>Spirocodon saltatrix</i>	(Mills 2001)	(C. Mills, UW, pers. comm., Oct. 2010; S. Uye, HU, pers. comm., Oct. 2010)
49	Low	1	Medium	Low	Low	Japan	Okinawa Island	Since at least 2003	<i>Turritopsis dohrni</i>	(Miglietta <i>et al.</i> 2007)	(Miglietta and Lessios 2009)
50	Very high	1	Very high	High	Very high	Japan	Entire west coast of Honshu	Since 2002 (records back to 1920s)	<i>Nemopilema nomurai</i>	(Kawahara <i>et al.</i> 2006; Uye 2008)	(Uye 2010; Uye <i>et al.</i> 2010)
50	Medium	1	High	Low	High	Russia	Near Vladivostok	Since 2000	<i>Rhopilema</i> spp.	(Domnitskaya 2011)	(A. Zavolokin, TINRO, pers. comm., Dec. 2011)
50	Low	1	Medium	Low	Low	Japan	Wakasa Bay	Since 2002	<i>Aurelia</i> sp. 1	(Matsumura <i>et al.</i> 2005)	
51	High	0	Medium	High	Very high	Russia	off Kuril Islands	2004-2009	Numerous	(Zavolokin 2011)	
51	Medium-high	-1	Very high	Very high	Low	Russia	Entire LME	1984-2006	<i>Aglantha digitale</i>	(Volkov 2008)	(A. Zavolokin, TINRO, pers. comm., Dec. 2011)
52	Very high	0	Very high	High	Very high	Russia	Northern Sea of Okhotsk	1994-2009	Numerous	(Zavolokin 2011)	(Il'inskii and Zavolokin 2007; Zavolokin 2010)
52	Medium	1	Very high	Medium	Low	Russia	'Inner shelf' waters	1984-2006	<i>Aglantha digitale</i>	(Volkov 2008)	(A. Zavolokin, TINRO, pers. comm., Dec. 2011)
52	Medium-high	0	Very high	High	Low	Russia	'Outer shelf' and 'Deepwater' areas	1984-2006	<i>Aglantha digitale</i>	(Volkov 2008)	(A. Zavolokin, TINRO, pers. comm., Dec. 2011)
52	Low	1	Low	Low	Medium	Japan	Northern coast of Hokkaido	2009	<i>Nemopilema nomurai</i>	(Anonymous 2009d)	
53	High	-1	High	Medium	Very high	Russia	Northwestern Bering Sea	2000-2009	Numerous	(Zavolokin 2011)	(Zavolokin <i>et al.</i> 2008)
53	High	0	Very high	Medium	Very high	Russia	Southwestern Bering Sea	1993-2009	Numerous	(Zavolokin 2011)	(Zavolokin <i>et al.</i> 2008)

LME ID	CI	AT	TS	SS	RS	Country	Location	Dates	Species	Main Reference(s)	Additional Reference(s)
53	Medium-high	1	Very high	High	Low	Russia	Russian EEZ	1984-2006	<i>Aglantha digitale</i>	(Volkov 2008)	
60	Very high	0	Very high	Very high	High	Numerous	Entire LME	1958-2007	Presumably <i>Aglantha digitale</i>	(Licandro <i>et al.</i> 2010)	
61	Very high	1	Very high	High	Very high	Antarctica	Several disparate locations	1926-2003	<i>Salpa thompsoni</i>	(Atkinson <i>et al.</i> 2004)	(Loeb <i>et al.</i> 1997; Perissinotto and Pakhomov 1998; Lee <i>et al.</i> 2010)
62	Very high	1	Very high	Very high	High	Numerous	Widespread sampling within LME	Since 1960s	<i>Aurelia aurita</i>	(Mutlu <i>et al.</i> 1994; Kovalev and Piontkovski 1998; Bat <i>et al.</i> 2009; Oguz and Velikova 2010)	(Gomoiu 1981; Flint <i>et al.</i> 1989; Shushkina and Vinogradov 1991; Niermann 2004)
62	Very high	1	Very high	Very high	Very high	Numerous	Widespread sampling within LME	Since 1988	<i>Mnemiopsis leidyi</i> & <i>Beroe ovata</i>	(Shiganova 1998)	(Finenko <i>et al.</i> 2001; Shiganova <i>et al.</i> 2004a)
63	Medium-high	0	Low	High	Very high	Canada	Large transect in Hudson Bay; also Foxe Basin & Hudson Strait	2003-2006	<i>Aglantha digitale</i> & <i>Aeginopsis laurentii</i>	(M. Harvey, DFO, pers. comm., Aug. 2010)	

*Appendix B – Belief Indexes*

LME ID	LME Name	Abundance Trend:	Belief Index					
			Native Species Only				Invasives Only	
			Overharvest					
			-1	-1	0	+1	0	+1
1	East Bering Sea					50.00		
2	Gulf of Alaska				27.34	6.25		~
3	California Current				43.75	29.69		23.10
4	Gulf of California					3.13		
5	Gulf of Mexico				25.00	6.25		12.50
6	Southeast US Continental Shelf				25.00	7.72		6.25
7	Northeast US Continental Shelf				3.13	60.89		~
8	Scotian Shelf				36.43			
9	Newfoundland-Labrador Shelf				50.00			
10	Insular Pacific-Hawaiian					25.00		20.53
11	Pacific Central-American Coastal					3.13		7.71
12	Caribbean Sea				9.18			9.18
13	Humboldt Current			50.00				3.13
14	Patagonian Shelf					25.00		6.25
15	South Brazil Shelf				25.00		12.50	6.25
16	East Brazil Shelf							6.25
18	West Greenland Shelf			1.56				
21	Norwegian Sea					12.50		1.56
22	North Sea			3.13	15.23	66.50		12.50
23	Baltic Sea				27.34			10.60
24	Celtic-Biscay Shelf				12.50	56.93		~
25	Iberian Coastal				25.00			1.56
26	Mediterranean Sea				12.50	42.58		53.06
28	Guinea Current					6.25		
29	Benguela Current					43.75		
30	Agulhas Current				23.44			~
31	Somali Coastal Current				12.50			
32	Arabian Sea		3.10		34.38	17.97		
34	Bay of Bengal		3.13	3.13	25.00	31.88		
35	Gulf of Thailand					1.56		
36	South China Sea		3.13		12.50	1.56		
40	Northeast Australian Shelf					6.15		
41	East Central Australian Shelf		3.13		23.44			
42	Southeast Australian Shelf				12.50	1.56		3.13
47	East China Sea					68.21		6.25
48	Yellow Sea					56.25		6.25
49	Kuroshio Current			3.13		47.27		1.56
50	Sea of Japan					53.86		
51	Oyashio Current			12.50	25.00			
52	Sea of Okhotsk				56.25	7.72		
53	West Bering Sea			25.00	25.00	12.50		
60	Faroe Plateau				50.00			
61	Antarctic					50.00		
62	Black Sea					50.00		50.00
63	Hudson Bay				12.50			