Kylie A. Pitt · Cathy H. Lucas
Editors

Jellyfish Blooms

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We would like to thank all the contributing authors for their commitment in producing excellent chapters. Without you, we would not have a book! We would also like to thank the many anonymous reviewers for their time and for providing invaluable comments that have enhanced the quality of the chapters.

Many of us have just returned from the 4th International Jellyfish Blooms Symposium held in Hiroshima, Japan, which was attended by 120 delegates from 28 countries. This represents a significant increase from the 60 or so delegates who attended the first two symposia. It was heartening to see so many Ph.D. students and early career researchers studying the science of jellyfish blooms. Recognition of both the scientific and socioeconomic importance of jellyfish blooms is clearly growing.

Finally, we would both like to acknowledge the support and encouragement provided by our families as we oversaw the production of the book.

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Chapter 1
Introduction: Understanding Jellyfish Blooms

Carlos M. Duarte, Kylie A. Pitt, and Cathy H. Lucas

Abstract Jellyfish blooms are a conspicuous feature of our oceans. Negative interactions between jellyfish and humans are widely publicised, such as jellyfish disrupting power supplies by clogging cooling water intakes of power plants or interfering with commercial fishing operations. Yet jellyfish have delivered many benefits to humans, such as being the original source of a unique molecule, the "green fluorescent protein", that has revolutionised biomedical research. Here we discuss the public and scientific perceptions of jellyfish blooms and emphasise the need for striking a balance in the way jellyfish blooms are portrayed.

Keywords Jellyfish blooms • Public perception • Marine ecosystem health • Biomedical applications • Green fluorescent proteins • Societal impacts

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Jellyfish are a polyphyletic group of organisms with a body plan characterised by a high water and low carbon content. Most jellyfish species are members of the Cnidaria, an ancient phylum of organisms including about 10,000 species, many of which have a bipartite life history that incorporates a benthic polyp, and a pelagic medusa, phase. However, the phylum Cnidaria contains two types of organisms that polarise human perceptions, the corals and the jellyfish. Corals form habitats, coral reefs, which fascinate both scientists and the public, being iconic targets for biodiversity conservation (Duarte et al. 2008). In contrast, the jellyfish are organisms that the public often regards with attitudes ranging from disdain to fear (Baumann and Schernewski 2012; Condon et al. 2012).

As I open a local newspaper (El Mundo/El Dia de Baleares, Sunday June 16, 2013), in Mallorca, Spain, where this introduction was partially written, a photograph of a *Pelagia noctiluca* washed on a beach draws my attention. The heading of the article reads "The terror of the seas" and the subheading follows with "Medusae are benefitting from rising seawater temperature and nutrients and the decline in predators as turtle mortality rises. Humans punish the oceans with pollution and medusae, in turn, punish beach swimmers."

This portrayal of medusae as a plague is not an isolated exaggeration, but depicts a widespread perception summarising a paradigm rooted in the recent ecological literature that depicts the (supposed) rise of medusae as the consequence of the deterioration of the oceans (Jackson 2008; Jackson et al. 2001; Richardson et al. 2009). Indeed, the proliferation of medusae has been equated with the *rise of slime* (Jackson 2008). A recently released book on jellyfish addressed to the public entitled "Stung" (Gerswhin 2013) epitomises the narrative that the public has been receiving from scientists and the mass media where jellyfish are presented as the "creature that is thriving in this seasick environment." These negative perceptions of jellyfish contrast with the sympathy that their counterparts in the Cnidaria, the corals, meet among the public, which results in significant research efforts, generous funding and conservation programmes.

Yet, jellyfish have been pivotal to key developments in medical science. The neural system and the advanced eyes of some gelatinous organisms are prompting major advances in medical research worldwide, including possible applications of jellyfish toxins as anticancer compounds (e.g. *Chrysaora quinquecirrha*, Balamurugan et al. 2010) or antioxidant supplements in nutrition (e.g. *Rhopilema esculentum*, Yu et al. 2006). Biomedical research comprises a significant fraction of all published scientific papers on jellyfish over the past decade. Most of these papers assess the chemistry, properties and impacts of jellyfish toxins, but a substantial number of these involve research on jellyfish with potential beneficial applications (Nilsson et al. 2005), including applications for human health or diagnostics. For instance, research on jellyfish has delivered two Nobel Prizes. The Portuguese man o' war, *Physalia physalis*, is a colonial siphonophore and one of the most feared jellyfish because of its poisonous nature. However, this organism was the basis for the Nobel Prize in Medicine awarded to Charles R. Richet in 1913 for his discovery of anaphylaxis, or the property of a poison to reduce the resistance of organisms to this poison when applied in nonlethal doses, following experiments applying

Physalia extracts to animals conducted on board the research vessel of Prince Albert of Monaco. *Aequorea victoria*, the crystal jelly, is a bioluminescent hydromedusa found off the west coast of North America. This species produces flashes of blue light by a quick release of calcium that interacts with the photoprotein aequorin. The blue light produced is transduced to green by the green fluorescence proteins (Prasher et al. 1992). Chalfie and collaborators patented the green fluorescence proteins (GFPs) present in the species in 2000. GFPs and GFP-like substances can be used for automated live cell fluorescence microscopy systems, which are a broad array of applications as reporters of gene expression, tracers of cell lineage and as fusion tags to monitor protein localization within living cells (Cubitt et al. 1995). Shimomura, Chalfie and Tsien were awarded the 2008 Nobel Prize in Chemistry for the discovery and development of GFPs.

Hence, there is, therefore, an urgent need for scientists to strike a balance in their views on jellyfish as components of the global ocean ecosystem delivering both risks and benefits to society. This is particularly urgent as recent papers have questioned the predicament that jellyfish are globally rising (Condon et al. 2012), to show that they are likely to follow global oscillations, with some specific regions showing evidence of an increase (Condon et al. 2013). Whereas specialists in jellyfish ecology and biology, such as those that compose the list of authors of the various chapters in this book, are well aware of the complexity of changes and role of jellyfish in the marine ecosystem, there is a need for this knowledge to be passed on beyond the realm of the relative small community conducting research on jellyfish ecology.

The initiative to edit a balanced book on jellyfish biology and ecology was, therefore, long overdue. This book starts by addressing the difficult question of what is a jellyfish (Lucas and Dawson, this volume). Simple as this may seem, this is a question upon which jellyfish experts often get entangled in endless disagreement. The difficulty relies, as they explain, on the polyphyletic nature of gelatinous organisms, which span a broad diversity of evolutionary origins and habitats. Whereas many species are able to produce large blooms, this is not a universal trait for jellyfish. Lucas and Dawson (this volume) provide a comprehensive account of the life history and ecological traits that allow many species of gelatinous organisms to bloom. Whereas jellyfish blooms can generate significant problems to humans interacting with the ocean, bloom collapse plays an important ecological role, as these represent a burst of organic matter supplied to microbial and benthic communities (Yamamoto et al. 2008; Sweetman and Chapman 2011; Lebrato et al. 2012). This is the focus of the original chapter by Pitt and coworkers (this volume) which synthesises data on the duration and collapse of jellyfish blooms to provide a first understanding of this process.

The dynamics of bloom and collapse of jellyfish are described for some ecosystems, such as the Bering Sea (Decker et al. this volume), the Mediterranean Sea (Canepa et al. this volume) and for populations of *Chrysaora plocamia* in South American coastal waters (Mianzan et al. this volume), for which high-quality long-term data sets are available. The problems caused by outbreaks of the remarkable giant jellyfish in Japan are presented by Uye (this volume), providing an example of a case of increased jellyfish blooms with significant societal impacts. Cubozoans contain some of the jellyfish species most dangerous to humans, but their ecology is poorly understood. The chapter by Kingsford and Mooney (this volume) provides a much needed review of the ecology of cubozoans. However, jellyfish can also experience substantial declines and require conservation measures, as shown for *Rhopilema esculentum* in China, where stock enhancement actions were deployed in an effort to avert stock collapse (Dong et al. this volume).

In a series of chapters, this book addresses the problems caused by jellyfish. In addition, Bayha and Graham (this volume) review case histories of introduction of exotic jellyfish and their subsequent invasive behaviour and discuss both the traits that allow some jellyfish species to behave aggressively as invasive species when introduced beyond their range as well as the properties of the receiving ecosystems that may render these prone to experiencing such invasive episodes.

Nevertheless, a balanced assessment of jellyfish ecology requires that not only the impacts be addressed but also the ecological benefits associated with jellyfish be discussed. This is the goal of the chapter by Doyle et al. (this volume), which shows that jellyfish are key components of marine ecosystems responsible for important ecosystem services. Indeed, the impacts associated with jellyfish are to a large extent associated with the increased exposure of humans, as the diversity and extent of our activities in jellyfish habitats increases continuously. For instance, jellyfish fish can clog the intake of desalination and nuclear plants or harm fish in aquaculture cages (Purcell 2012). All of these uses of the marine environment were developed a few decades ago and have increased exponentially to date, thereby increasing the likelihood of these impacts even if jellyfish blooms remain unchanged. Hence, the development of management and policy options to minimise impacts of jellyfish blooms is an essential element of coping with the risks associated with increased exposure to these blooms, as discussed by Lucas et al. (this volume).

Interactions between humans and jellyfish are inevitable given humans' increasing utilisation of ocean habitats and the life history characteristics of jellyfish that facilitate their boom and bust dynamics. Scientists can influence the ways in which jellyfish blooms are perceived by the public and stakeholders of ocean environments and so must be vigilant to prevent sensationalising or overstating issues associated with jellyfish blooms. Here we present the good, the bad and the fascinating aspects of jellyfish blooms.

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Part I
Ecology of Jellyfish Blooms

Chapter 2
What Are Jellyfishes and Thaliaceans and Why Do They Bloom?

Cathy H. Lucas and Michael N. Dawson

Abstract The jellyfishes and thaliaceans comprise primarily planktonic species of cnidarians, ctenophores (jellyfishes) and chordates (thaliaceans or pelagic tunicates). Grouped together because of their gelatinous bodies, these diverse species nonetheless differ in their evolutionary histories and may have distinct morphologies, life histories, ecologies and other traits. Subsets of these species occur at some times and places in highly elevated concentrations, i.e. they accumulate, aggregate, bloom or swarm. Why jellyfishes and thaliaceans occur in such masses is, however, somewhat unclear; the reasons obscured in part by a tendency to treat many gelatinous zooplankton, including jellyfishes and thaliaceans, as a single functional group. Here we summarize the evolutionary relationships among gelatinous zooplankton and review the characteristics of blooms, before focusing on comparing and contrasting medusae, ctenophores and thaliaceans. We highlight some substantial knowledge gaps, emphasize biological factors that likely contribute to blooms and outline a population genetic framework for investigating the ecological causes of boom and bust population dynamics in the plankton.

Keywords Jellyfish blooms • Cnidarians • Ctenophores • Thaliaceans • Macroevolution • Microevolution • Phylogenetic analysis • Life histories • Body composition • Phenotypic plasticity • Growth rates

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2.1 Introduction

Detailed evolutionary and natural history studies of marine zooplankton, such as those practised by Ernst Haeckel and Alfred Goldsborough Mayer, were largely displaced by coarse-grained ship-based oceanographic surveys of abundance and biomass (e.g. Hensen 1887) during the late nineteenth and early twentieth centuries (Raskoff et al. 2003). Not until the development of blue-water diving (Hamner 1975) did field-based plankton biology and natural history, most specifically of jellyfishes and similar organisms, became recognized again as a discipline with something new and valuable to contribute. In the subsequent four decades, studies describing the functional biology of common species made way for studies of population dynamics and trophic ecology, setting the scene for the First International Jellyfish Blooms Symposium, in Alabama, USA, in 2000. The symposium galvanized research into the causes and consequences of mass occurrences or 'blooms' of jellyfishes and stimulated interest in gelatinous zooplankton more broadly (see Box 2.1 for definitions); the development of molecular techniques in the 1990s precipitated a parallel resurgence in evolutionary analyses of jellyfishes (e.g. Dawson and Jacobs 2001; Collins 2002). However, despite a dramatic increase in the number of papers on jellyfish blooms in the last decade (Condon et al. 2012), ecological and evolutionary studies remain poorly integrated (but see e.g. Dawson and Martin 2001; Dawson and Hamner 2009). Consequently, we are still a long way from understanding which extrinsic (abiotic and biotic environmental) characteristics of modern seas and which intrinsic (functional biological) traits of these evolutionarily diverse taxa interact to cause 'jellyfish blooms'.

The goal of this chapter is to bridge this divide, to clarify why—if we are truly interested in explaining the causes of jellyfish 'blooms'—it is essential to reintegrate the disciplines of plankton ecology and evolutionary biology. First, we use a phylogenetic framework to identify informative collective nouns for the organisms concerned (Fig. 2.1, Box 2.1) and a biophysical framework to distinguish how these organisms may 'bloom' (Box 2.2). We then move on to discuss the recent inferences from macroevolutionary studies and extend this perspective to provide a microevolutionary context for blooms (Sect. 2.3). We review the key life-history and physiological traits that enable large numbers of individuals to be produced (Sect. 2.4) and those new recruits to subsequently form large and consequential blooms of adults (Sect. 2.5) that are able to withstand and respond to environmental change (Sect. 2.6). Finally, we integrate the evolutionary, organismal and ecological perspectives in the form of the population-based study design that is needed to understand why jellyfishes and thaliaceans bloom (Sect. 2.7).

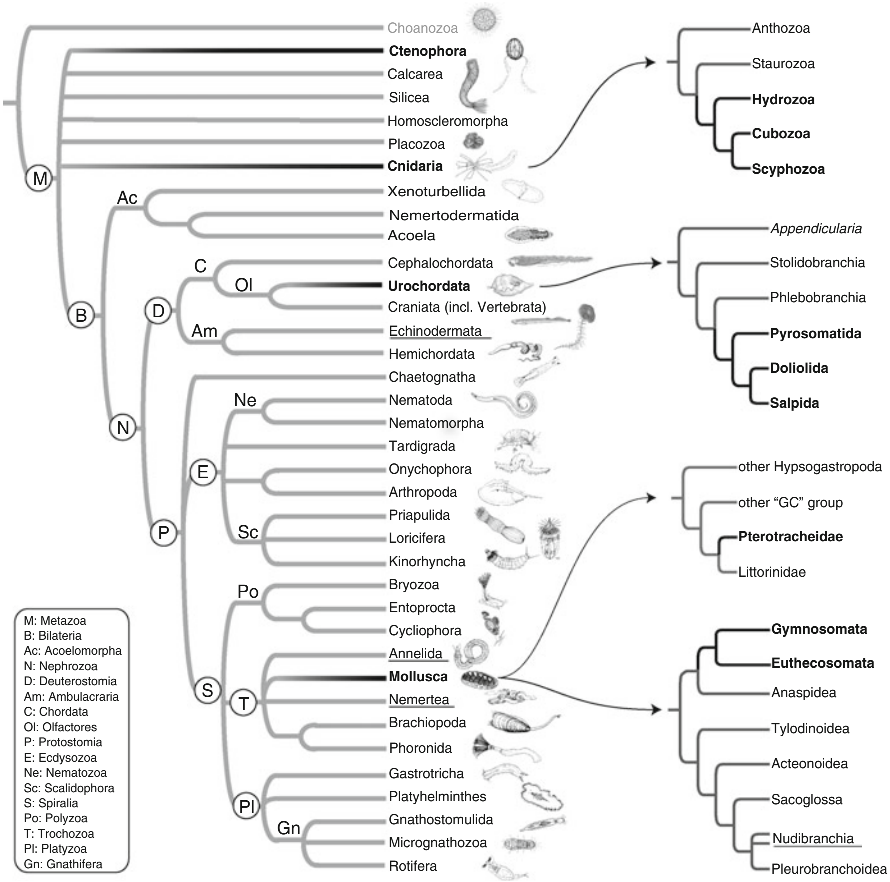
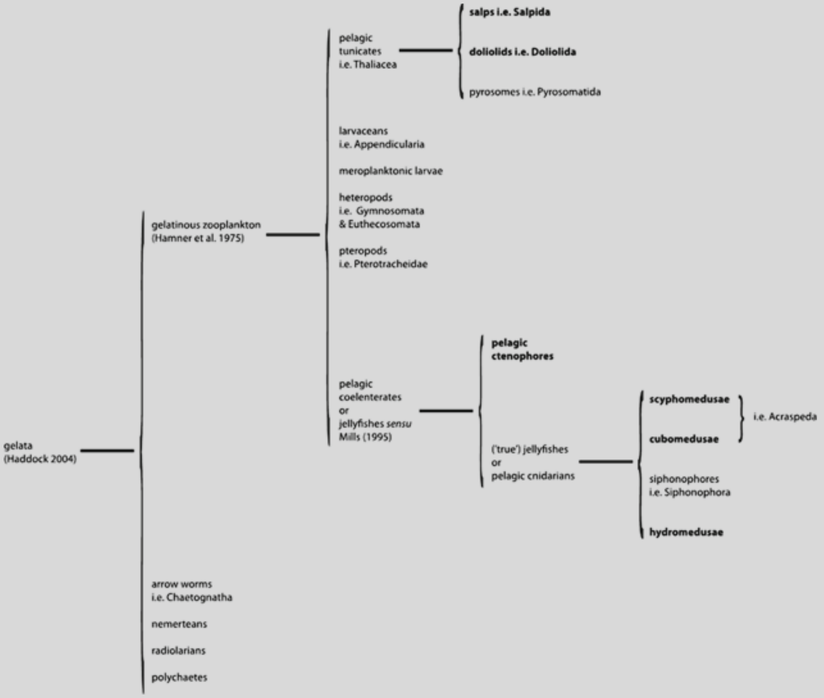


Fig. 2.1 The gelatinous planktonic ecotype arose at least nine separate times within Metazoa. Phylogeny of the metazoans (*left*, from Edgecombe et al. 2011) indicating the principal gelatinous zooplanktonic phyla (*black branches*, *bold*) and also other phyla in which there are occasional gelatinous zooplanktonic taxa (*underlined*). Relationships within the principal gelatinous zooplanktonic taxa are shown for Cnidaria (*right top*, e.g. Collins et al. 2006), for Urochordata (*right upper middle*, Govindarajan et al. 2011) and within Mollusca (*bottom*, Colgan et al. 2007; Klussmann-Kolb and Dinapoli 2006; Klussmann-Kolb et al. 2008; Jörger et al. 2010); the most recent common ancestor of all extant Ctenophora is inferred to have been gelatinous and planktonic with only the derived platyctenes being non-planktonic (Podar et al. 2001). Appendicularia is highlighted (italics) because, although the larvacean body is not gelatinous, the large mucous net they secrete conveys many of the functional attributes of other gelatinous zooplankton (Reproduced by permission from Elsevier)

Box 2.1 Jellyfish, Other Collective Nouns and Errors of Commission and Omission

The terms used to represent the taxa that bloom often are imprecise. Their nested and phylogenetic structures, represented below (groups that include species which bloom are in bold, common names equivalent with clades are marked 'i.e.'), regularly lead to errors of commission and/or omission. ***Errors of commission*** occur when use of a collective noun implies that members of that group all have a common characteristic, but in fact some members do not. Writing that 'jellyfishes are on the rise' includes an error of commission because, for example, some pelagic cnidarians are jellyfishes but are not increasing in abundance or frequency of blooms. ***Errors of omission*** occur when a collective noun includes some, but not all, of the taxa that do possess a particular characteristic. Writing that 'jellyfishes bloom' therefore may include an error of omission unless appended, for example, with a phrase that adds some salps and doliolids. Vernacular usage of imprecise collective nouns can provide useful shorthand when its limitations are common knowledge, but delineating research agenda imprecisely and inconsistently using vernacular can lead to errors of logic (Brotz et al. 2012; Condon et al. 2012). We recommend choosing the most precise collective noun(s) available with appropriate modifiers—such as some, many or most—until the relevant taxa have been identified and phenomena quantified. For example, all evidence indicates that some scyphomedusae, including many pelagiid species, form mass occurrences; moreover, this statement has been true of scyphomedusae and Pelagiidae for millions of years and will remain true even as we learn more about which scyphomedusae bloom, where and why.



Box 2.2 What Do We Mean by Blooms?

The vocabulary used to discuss blooms and related phenomena has grown as understanding of the factors influencing the distribution of jellyfishes has increased. Here, we summarize the current terms, following Mills (2001), Graham et al. (2001), Hamner and Dawson (2009) and Richardson et al. (2009; see also Miranda et al. 2012).

Accumulation**:** An increase in number relative to a different time or place. Used to refer collectively to, or when it is impossible to identify occurrences as, aggregations, blooms and swarms; describes a pattern without implying cause. In a more specific use, a gradual long-term summation.

Mass occurrence/occurrence en masse**:** Similar to ‘accumulation’ but necessarily very large in magnitude, also concerning biomass.

Aggregation**:** An accumulation of individuals that consequently likely interact; short-term concentrations, possibly, but not necessarily, within a natural or apparent bloom, due to passive drifting in currents, active behaviour of individual medusae or interaction of the two, in the absence of either increased population growth or mortality.

Swarm**:** A dense reaggregation of animals due to behaviour; animals in swarms are neither evenly spaced nor specifically oriented.

Blooms**:** A ***true bloom*** is in part a consequence of seasonal life cycles, and consequently, all metagenic organisms have the potential to bloom pending suitable environmental conditions; thus normal and/or abnormal seasonal biomass is directly attributable to population increase due to reproduction and growth, sometimes enhanced by anthropogenic activity. An ***apparent bloom***, in contrast, is a local increase in biomass of animals associated with temporary or transient chemical or physical phenomena (such as aggregation at fronts or local advection to a new location) or longer-term accumulation of large numbers in enclosed habitats; apparent blooms may, but do not necessarily, reflect true blooms that occurred elsewhere.

Outbreak**:** Exceptional, sudden, increases in biomass (seasonal or aseasonal), largely synonymous with ‘unnatural’ blooms associated with anthropogenic change in ecosystems.

Consistency of usage is essential for understanding the causes and consequences of blooms and may necessitate reinterpretation of scientific reports. For example, a deep-sea observation of an elevated local abundance of Stauromedusae was described as an ‘aggregation’ (Miranda et al. 2012, following Collins and Daly 2005) but better fits the definition of an accumulation. Miranda et al. (2012) also misinterpreted the reasons for the growing emphasis on biomass (c.f. number), and therefore on a subset of taxa of abundant-and-large animals, as a matter of ‘human convenience’, whereas it is rather a matter of their *ecological consequence*.

2.2 What Do We Mean by Jellyfishes and Thaliaceans?

Jellyfish is the descriptive common name first attributed in the mid-1800s to various medusae[1] and since the 1990s also considered to include the ctenophores and siphonophores on the basis of trophic equivalence (Mills 1995). The great benefit of the term—its figurative simplicity—however has led to confusion as 'jellyfish' also has been applied ad hoc to other gelatinous aquatic animals (e.g. Brotz et al. 2012). The problem is that occasional broader usage can imply functional or other equivalence that does not exist, increase ambiguity about the attributes of jellyfishes and blur potentially important distinctions from other gelatinous aquatic animals already known collectively as gelatinous zooplankton (Hamner et al. 1975). In asking why jellyfishes and thaliaceans bloom, therefore, it is essential to provide a clear description of the taxa concerned and to distinguish them unambiguously from others and then to ask what we can learn from comparisons within and between these groups. We thus start by contextualizing the jellyfishes and thaliaceans in relation to other gelatinous zooplankton.

Gelatinous zooplankton is one of four classes proposed in an ecological classification of marine pelagic organisms (Hamner et al. 1975). The gelatinous zooplankton is comprised of those organisms that are 'large but transparent', i.e. difficult to see in situ despite being big enough to resolve with the naked eye (> ~1 mm) (Hamner et al. 1975) and, for consequent physical reasons, slow moving (e.g. see Aleyev 1977). Thus, the ecological class gelatinous zooplankton includes distinct groups of related organisms (i.e. independent clades) from throughout the metazoan tree of life (Fig. 2.1), including clades within the annelid worms (specifically polychaetes), the molluscs, nemerteans (Haddock 2004; Bone 2005), occasional deep-sea fauna including holothurian echinoderms (Miller and Pawson 1990), the thaliaceans (salps and doliolids) and the larvaceans (appendicularians) in phylum Chordata, the comb jellies (phylum Ctenophora) and the medusae and siphonophores in phylum Cnidaria (Hamner et al. 1975; Mills 1995; Castro and Huber 2003: 337). Some organisms may have attributes of more than one ecological category, leading to other possible groupings which may or may not be fungible. Thus, gelatinous zooplankton does not include the chaetognaths, in contrast to the 'Gelata' (Haddock 2004), because while arrow worms predominantly are transparent and pelagic (Brusca and Brusca 2003: 841), they are neither slow nor gelatinous. Rather, the arrow worms are fast strike predators with a compact body form including cuticle and well-developed musculature (Brusca and Brusca 2003: 842–844). Likewise, more subtle differences among or within clades of gelatinous zooplankton also may be important.

Although all gelatinous zooplankton scattered across the metazoan branch of the tree of life have converged on phenotypes including low-carbon growth strategies

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[1] http://www.oed.com/view/Entry/101029?redirectedFrom=jellyfish#eid 'The popular name of various acalephs, medusas, or sea-nettles, from their gelatinous structure.' Here, we use 'jellyfish' to refer to one or more individuals within a single species and 'jellyfishes' to refer to multiple species.

(Arai 1997; Wrobel and Mills 1998: 79), transparency (Hamner 1985), drifting or natation, and buoyancy (Bone 2005), each has many unique characteristics due to their distinct evolutionary histories and, presumably, different selective landscapes. Thus, while being gelatinous and planktonic are considered generally important to their success (Hamner et al. 1975; Hamner 1985; Harbison 1992), other characteristics also may be important. Mills (1995) broadened the definition of jellyfishes based on trophic position and related characteristics, to include siphonophores and ctenophores as well as the traditional medusae. Whereas the majority of ctenophores, medusae and siphonophores are nonvisual generalist predators of meroplanktonic vertebrate and invertebrate larvae and holoplankton such as copepods and other gelatinous zooplankton (either as species or communities; Mills 1995), heteropods are adept visual predators (Wrobel and Mills 1998: 70); gymnosomes are predators primarily on the cosomes (Wrobel and Mills 1998: 75); the cosomes are 'indiscriminate omnivores' trapping copepods, larvae, phytoplankton and bacterioplankton (Wrobel and Mills 1998: 72); and salps and doliolids feed on particles between <1 and 10 µm (Sutherland et al. 2010). There also may be distinctions within clades, for example, among different classes, suborders and families of medusae (Dawson and Hamner 2009; Hamner and Dawson 2009; Bayha and Dawson 2010). What concerns us here is that these evolutionary differences among taxa appear to be related to different ecological patterns of abundance, biomass and distributions (e.g. Pagès et al. 2001; Zavolokin 2010). Understanding the evolutionary background of extant ecological differences therefore should help explain differences among species' population dynamics, their causes and perhaps consequences.

For the rest of this chapter, we use the term jellyfishes to describe cnidarian medusae and ctenophores, as proposed by Mills (1995) (see Box 2.1). Thaliaceans are considered separately due to their greatly different evolutionary and trophic status. We focus on scyphomedusae, hydromedusae, ctenophores, salps and doliolids as these contain the main bloom-forming taxa for which most literature is available. Pyrosomes and siphonophores are not included in our discussion.

2.3 Evolutionary Context of Blooms

Many questions in biology—including those about blooms—can be, and have been, asked without referring to evolution, but the evolutionary context is essential for a complete answer (Dobzhansky 1964, 1973). Evolutionary context is provided by comparing species, genera or other higher taxa typically considering 'deep' timelines (i.e. macroevolution) or by studying populations within species and typically considering 'shallow' timelines (i.e. microevolution). A macroevolutionary perspective, which typically uses the tools of phylogenetics, has been outlined previously (Dawson and Hamner 2009; Hamner and Dawson 2009). The microevolutionary perspective, which typically uses the theory and analytical approaches of population genetics, remains undeveloped as a strategy for understanding blooms, even though this perspective can unify population biology and ecological genetic processes to improve understanding of the causes of modern blooms. After recapping briefly the macroevolutionary perspective and some of its implications, we focus on developing the microevolutionary perspective in the remainder of this chapter.

2.3.1 Macroevolution

Macroevolutionary analyses of medusae have provided four insights into modern jellyfish blooms. (1) Blooms are not a new phenomenon, but rather have been a characteristic of, for example, medusae for hundreds of millions of years (Hagadorn et al. 2002; Condon et al. 2012). (2) Phylogenetic mapping identified independent origins of blooms and (3) putative stages in evolution of blooming, as well as (4) characteristics of clades that bloom versus those that do not bloom, i.e. suggested causal characteristics (Dawson and Hamner 2009; Hamner and Dawson 2009). Phylogenetic analysis provides two additional benefits: (5) it allows hypotheses to be constructed about which characteristics cause blooms, allowing tests to be made using independently evolved taxa—such as other gelatinous zooplankton—and (6) because characters often are shared among closely related species, it allows predictions to be made about taxa for which we have little or no data.

The hypothetical and predictive benefits of the phylogenetic approach, which were not emphasized previously, are illustrated by Fig. 2.2. Of the species of ctenophores, medusae and salps reviewed by Brotz et al. (2012) and that occur en masse, 2.6 % are cubozoans, though data were available only for Chirodropida (Chiropsalmidae+ Chirodropidae, 0.9 % of blooms) and a subset of Carybdeida (Tripedaliidae, 0 %; Carybdeidae, 1.7 %). If traits that influence blooming are evolutionarily conserved within closely related taxa, then we predict that Alatinidae, Carukiidae and Tamoyidae also rarely occur en masse (Fig. 2.2, right panel). This prediction, which is consistent with the inference of Hamner and Dawson (2009) (Fig. 2.2, left panel), can be used to guide future studies and/or tested by making new field observations. If future studies remain consistent, then our confidence in this inference increases. If tests instead show that many species of Alatinidae, Carukiidae and Tamoyidae occur en masse or that some species frequently occur en masse, then we might reassess our inference for other cubozoans and/or look for characteristics in the mass-occurring cubozoans that are similar to (i.e. homoplasious with) characteristics of other mass-occurring taxa, i.e. primarily the shallow-water semaeostomes and daktyliophoran rhizostomes. Candidate characteristics identified by phylogenetic analyses as likely causes of mass occurrences of scyphozoans relate to podocyst formation, strobilation, form of the oral arms, large size and shallow-water habitat (Dawson and Hamner 2009, see also Arai 2009).

These traits of scyphozoans—which include aspects of morphology and life history—are inferred to have favoured survival during periods of few resources, feeding on pulsed resources and increased fecundity. (Notably, podocysts since have been highlighted by ecological observations and experiments as a key life-history phase in the population persistence or dynamics of *Aurelia* and *Nemopilema* (Kawahara et al. 2012; Thein et al. 2012) which frequently form severe blooms

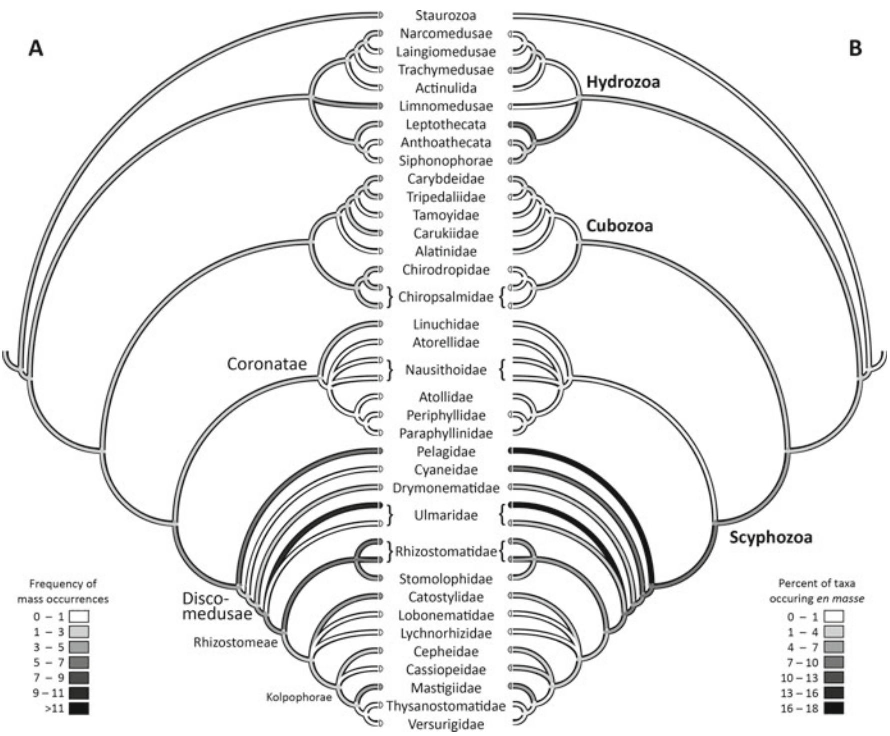

Fig. 2.2 (**a**, **b**) The macroevolutionary context of blooms: the phylogeny of Tesserazoa (i.e. non-anthozoan cnidarians) and the evolution of mass occurrences. This analysis shows the phylogenetic distribution of clades with many species that occur en masse (*darker shading*). The phylogeny is a composite of trees reported for Cnidaria (Collins et al. 2006) and Scyphozoa (Bayha et al. 2010). The evolution of mass occurrences was inferred from (**a**) accumulations, aggregations, blooms, swarms and outbreaks of extant taxa as summarized principally by Hamner and Dawson (2009) and (**b**) the percentage of mass occurrences summarized by Brotz et al. (2012) attributable to each family. Character states scored for extant taxa are shown in the semicircles between the tree tips and taxon names; ancestral states and states for taxa that were not scored (i.e. no semicircle at the tip) were inferred using least-squares parsimony reconstruction of continuous characteristics in Mesquite v.2.75 (Maddison and Maddison 2011). Note that hydrozoans are grouped by order, whereas cubozoans and scyphozoans are grouped by family; this graphical simplification does not skew the visual pattern that emerges in the trees. Seventy percent of reported mass occurrences are attributable to scyphozoans (47 % to semaeostomes, 22 % to rhizostomes); of the remaining 30 % of mass occurrences, only 16 % are attributable to hydrozoans (principally leptothecates, siphonophores, Trachymedusae), 8 % to ctenophores, 3 % to cubozoans and 2 % to salps. In the right panel, light grey shading on branches leading to taxa that were not scored in this analysis indicates an ambiguous character state and/or inferred infrequent mass occurrence

(Fig. 2.2).) Such adaptations then appear to have been co-opted by selection for reproductive success which favoured mass occurrence (Dawson and Hamner 2009). Mass occurrence, therefore, is an emergent property of species and higher taxa arising from processes affecting individuals and populations, i.e. mass occurrence is a phenomenon that arose via the processes of microevolution.

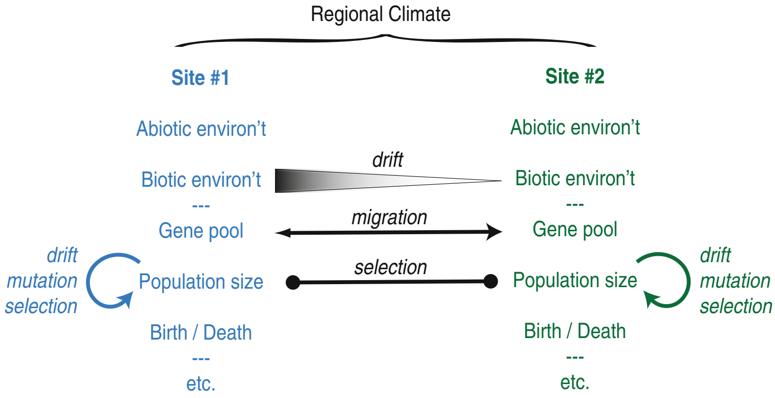

Fig. 2.3 Population dynamics and population genetics are influenced by overlapping suites of processes; population genetics, therefore, provides insight into factors influencing population dynamics. Four of the five mechanisms of microevolution—genetic drift, migration, natural selection and mutation—have parallels in autecology: ecological drift (random changes in relative frequencies of species), migration (movement among communities of species), natural selection (processes that favour particular species over others) and speciation (Vellend and Geber 2005; Roughgarden 2009; Vellend 2010). Interaction of local and regional process influences local population dynamics—e.g. through birth, death and immigration—and their effects can be distinguished with time series in population biology and data describing population genetic structure (Sect. 2.7)

2.3.2 Microevolution

Microevolutionary studies often explore the interface of ecological and evolutionary processes (Fig. 2.3). A microevolutionary perspective can bring together population biological and population genetic perspectives and thus is particularly well positioned to clarify the scales and causes of modern blooms.

A simple framework for illustrating this integration is provided by the population growth equation: $N_{t+1} = N_t + (B + I) - (D + E)$, where N is the number of individuals (e.g. medusae) in a population, t is the time step, B is the number of births, I the number of immigrants, D the deaths and E the emigrants during the preceding time step. In the context of most populations of scyphozoan medusae—excepting many deep-sea species and *Pelagia*—N_t is initially zero each year, i.e. the medusa population size is a function of births (i.e. strobilation), immigration, death and emigration. In the simple situation of a 'closed' population, migration by definition is absent, so birth and death alone influence the size of the medusa population. In a closed population, therefore, an increase in population size is always a result of demographic processes and therefore a true bloom or accumulation. In contrast, in 'open' populations, all four processes—strobilation, immigration, death and emigration—may influence the abundance of adult medusae. Notably, the abundance of medusae at a particular place and time could be a function of solely immigration and emigration, i.e. an apparent bloom.

This framework makes three important links between population biology and population genetics. First, dynamics in a closed population result only from processes at that location. Second, over generations, local closed (or largely closed) populations will adapt to local conditions, and the alleles at a location should reflect these processes of isolation and adaptation, i.e. there should be one or more alleles specific to that location (i.e. 'private' alleles). Third, dynamics in open populations may result from processes occurring at other locations, for example, if *I* far exceeds *B* and *D*. If *I* is large relative to *B*, then the alleles at a location will be principally alleles from a different location, and they will illustrate gene flow and may not be locally adapted (unless by chance). Thus, some insight into the processes driving dynamics in a population of jellyfish (or other taxon) can be gained through population genetic analyses (Sect. 2.7). We'll return to this integration later, after looking at the basic life-history factors that may influence the number of individuals in a population (*N*)—particularly factors influencing *B*—and the sizes of those individuals, i.e. whether blooms may be large in terms of biomass and therefore likely to be ecologically consequential (Fig. 2.4).

2.4 Life Histories

As noted above, local recruitment (*B*) has potential to be a strong determinant of adult density. Life-history and behavioural traits that enable large numbers of individuals to be produced quickly, assuming high survivorship through to the adult (reproductive) phase, will predispose a species to form numerically large populations and potentially 'blooms' or 'outbreaks', given the right environmental conditions. In the marine environment, traits that may facilitate high *B* include asexual reproduction resulting in rapid rates of population increase (Madin and Deibel 1998), aggregation of sexually mature adults, synchronized spawning, selfing in hermaphrodites and high fecundity which circumvent the dilution effect of the watery environment and enhance fertilization success (Ghiselin 1969; Strathmann 1990; Purcell and Madin 1991; Hamner et al. 1994) and ecophysiological and reproductive flexibility (Hadfield and Strathmann 1996; Lucas 2001, Deibel and Lowen 2012) that enables populations to respond quickly and positively to variability in the environmental conditions encountered. Mortality (*D*), and also emigration (*E*), may be kept low by brooding or production of short-lived lecithotrophic larvae which reduce the risk of predation and may promote local recruitment (Pechenik 1999; Uthicke et al. 2009), rapid growth and short generation times (Heron 1972) and gregarious settlement of larvae (Underwood and Keough 2001). Marine taxa that share some of these life-history traits and which are able to undergo rapid population growth leading to outbreaks, include several phytoplankton and macroalgae groups (Smayda 1997; Valiella et al. 1997), echinoderms (Uthicke et al. 2009), larvaceans (Troedsson et al. 2002) and some members of the Cnidaria, Ctenophora and Thaliacea covered in this chapter (Dawson and Hamner 2009; Hamner and Dawson 2009; Deibel and Lowen 2012).

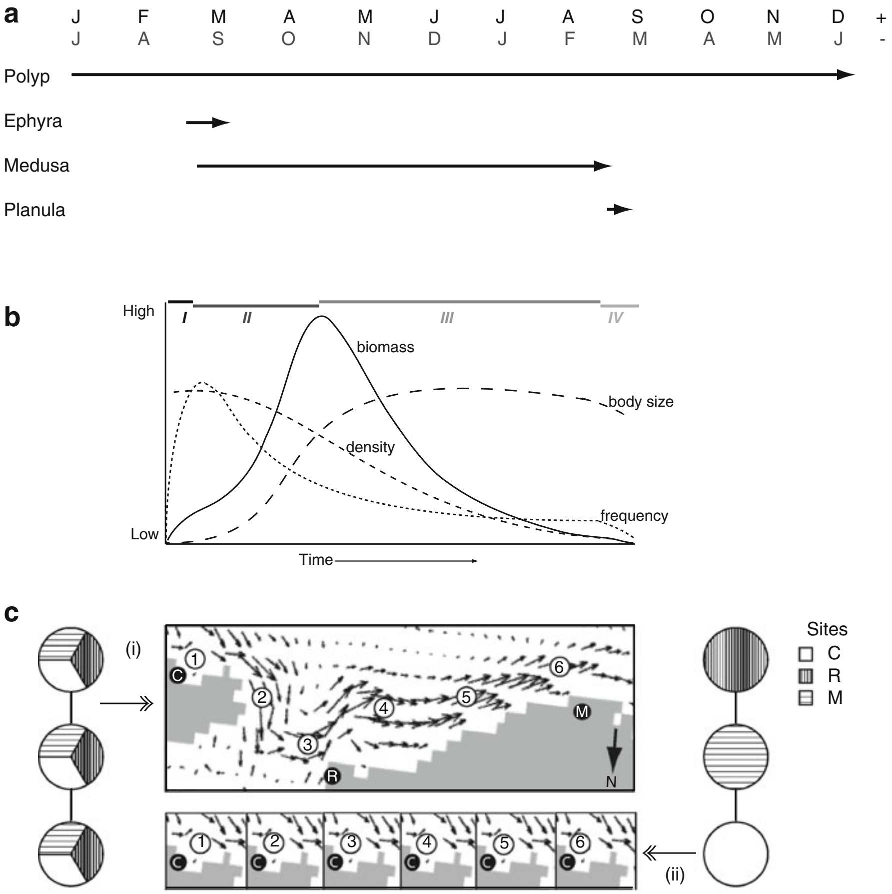

Fig. 2.4 (**a**–**c**) Timeline and stages of jellyfish blooms (**a**) Generalized timeline of principal life-history stages of scyphozoans (after, e.g. Hamner and Jensen 1974; Thein et al. 2012). *Upper row* of letters indicates northern hemisphere months, and *lower row* indicates southern hemisphere months. In tropical latitudes, timing may be more closely allied with monsoon seasons than with boreal/austral seasons. Polyp stages also will produce recruits into planuloid or podocyst subpopulations and likewise recruit from those stages. (**b**) How the life history causes changes in biomass (and other properties such as population-level clearance rates, respiration) and how their interactions translate into the stages of jellyfish blooms. Stage *I*: Strobilation increases the abundance (frequency) of ephyrae and smallest medusa, causing biomass to increase only nominally due to the very small mass of these life stages. Because strobilation occurs over an extended period of time, surveys of numbers may not generate the idealized type III survival curve. Stage *II*: Strobilation subsides as the mechanism of numerical increase of medusae is overtaken by growth of medusae causing rapid increase in biomass. Growth is so rapid that losses of mass due to mortality (*D*, see Sect. 2.3.2) or advective losses (emigration, *E*) of ephyrae and medusae are insufficient to limit increases in biomass. Stage *III*: With the reduction of growth rate of large medusae ceasing to offset numerical losses due to mortality and advection (or diffusion), biomass begins to decrease/disperse, and the bloom, while still a phenomenon, begins to decrease in intensity. Stage *IV*: Degrowth and senescence emphasize any losses attributable to advective losses, and the population becomes unnoticeable, absent and inconsequential. This graphical representation makes it clear that stages *I* and *II* are the 'critical stages' (sensu Hjort 1914 cited by Stenseth et al. 2002; see also

2.4.1 Asexual Reproduction

2.4.1.1 Cnidarians, Primarily Discomedusae

Many of the cnidarian jellyfish have complex, metagenic life cycles, alternating between sexual and asexual generations. Within Cnidaria, the cubozoans, majority of scyphozoans and several orders of hydrozoans (e.g. Anthomedusae and Leptomedusae) also alternate between (asexual) polypoid and (sexual) medusoid body forms. While metagenesis and strobilation are not prerequisites for a cnidarian jellyfish to be a bloom-forming species (see e.g. *Pelagia noctiluca*; Dawson and Hamner 2009), asexual reproduction is an 'efficient, effective and inexpensive' (Crow 1994) means of reproducing which enables blooming by increasing the source (polyps) and supply (ephyrae) of new recruits to the medusa population.

Scyphozoan polyp populations may increase in size (i.e. N_p) via several asexual methods (Holst et al. 2007: Table 1, Arai 2009 for Rhizostomeae; Kakinuma 1975; Arai 2009; Han and Uye 2010 for the Semaeostomeae). Laboratory experiments on *Aurelia*, the most commonly studied and widespread bloom-forming genus, reveal that individual polyps can produce between 0.03 and 1.15 buds d^{-1} at temperatures ranging between 5 °C and 30 °C (see Purcell et al. 2012: Table 2). Rates of budding are positively correlated with temperature and food, both independently and interactively (Han and Uye 2010; Purcell et al. 2012), although the actual temperature required for peak budding rates is likely to be species- and location-specific, reflecting thermal tolerances and geographic distribution of the population (Lucas et al. 2012) which may signal local adaptation. Budding rate data for other semaeostome

◄

Fig. 2.4 (continued) e.g. Cushing 1984; Ottersen and Loeng 2000) in the formation of blooms. Because growth can increase biomass of medusae far more rapidly and many more orders of magnitude than can strobilation, the primary stage of 'blooming' is stage *II*. Stage *III* may be critical in the maintenance of blooms principally as a consequence of oceanographic factors and the biological responses of large natatory medusae. (**c**) Two ways in which the life-history timeline may translate into geographic patterns (based on an oceanographic simulation from Lee et al. (2013)) and expected genetic patterns. *(i) Upper centre*, a true bloom in March at site C is advected westward during the subsequent 5 months. It is perceived as an apparent bloom at site R in May, but this demographic population is depleted by mortality and advective losses by August and is not noted as a bloom at site M. *(ii) Lower centre*, a true bloom in March at site C is retained during the subsequent 5 months and appears as a bloom sometime during April–May as the population increases rapidly in biomass. Section 2.7 of the main text relates this schematic representation also to spatial dynamics and an ecological genetic understanding of the dynamics of blooms. *Left* and *right*, simplified schematics of the expected genetic patterns for samples collected at locations C, M and R under these two scenarios. *Left*, under scenario *(i)*, medusae sampled at site C in March, R in May and M in August would share the same neutral alleles in approximately the same proportions; also see Fig. 2.5b. *Right*, under scenario *(ii)*, assuming locally recruiting populations occur also at sites R and M, then samples of medusae at site C, R and M in any month would have distinct, or 'private', neutral alleles; also see Fig. 2.5a. Scenarios between these extremes, for example, involving incomplete isolation of populations or admixture, are also possible and distinguishable genetically; polyp populations should be included in analyses when possible. A similar suite of figures is conceivable for other taxa such as ctenophores, doliolids and salps, in which case the life-history stages in part (**a**) would be amended, and the dynamics in (**b**) and (**c**) may be altered and rhizostome species are scarce, but values are typically less than 0.25 (often <0.10) buds polyp^{-1} d^{-1} (see Purcell et al. 2012: Table 2). Single polyps of *Chrysaora quinquecirrha* also have been reported to produce >50 podocysts in under 3 months (Cargo and Schultz 1966).

The published maximum rates of asexual budding equate to approximately one new polyp every 1–3 days, highlighting the potential for rapid growth of source polyp populations, yet the few published abundances of natural polyp populations vary greatly, ranging between 0.0005 (Ishii and Katsukoshi 2010) and 88 cm^{-2} (Miyake et al. 2002) for *Aurelia* spp. This high variance suggests other limiting factors. In addition to changes in the rate of asexual reproduction of polyps triggered by environmental cues, polyp abundance also is affected by available habitat (e.g. on shells inhabited by other biota; Lucas et al. 2012), recruitment of planula larvae and mortality due to intra- and interspecific competition, predation and physiological stress. Polyp populations consequently can be very patchily distributed over small (cm) and large (m, km) spatial scales, and existing estimates made on relatively small spatial scales, from centimetres to a few metres, cannot simply be extrapolated linearly to estimate polyp population size. Although polyp population size generally is presumed to be very large, populations of only tens of medusae that recur for years and decades (e.g. in coves in Palau, Dawson pers. obs.) suggest large polyp populations are not essential for long-term viability.

Strobilation of scyphopolyps generates ephyrae that may recruit into the medusa population. Each strobilation cycle may be monodisc or polydisc—usually depending on the species—and each polyp may have several (2–5) strobilation cycles over the course of a season, depending on species and environmental conditions (temperature, salinity, light, O_2, food). Polydisc strobilation appears to be an ancestral trait in Discomedusae, characterizing the majority of semaeostomes and daktyliophoran rhizostomes (Dawson and Hamner 2009). Semaeostomes are prolific strobilators. *Aurelia labiata* may yield as many as 42 ephyrae per strobilation in larger, well-fed polyps (Purcell 2007). The daktyliophoran rhizostomes produce only 2–6 ephyrae per polyp per strobilation (see Lucas et al. 2012: Table 4), but this relatively low strobilation rate is offset by repeated strobilation cycles. *Lychnorhiza lucerna*, for example, produces 50–60 ephyrae over a 4-month period (Schiariti et al. 2008). The kolpophoran rhizostomes are primarily monodisc strobilators and, notably, mostly non-blooming species (Dawson and Hamner 2009).

Absolute temperature and magnitude of temperature change are important factors influencing the timing and rate of ephyra production in scyphozoans as they initiate strobilation (e.g. Kawahara et al. 2006; Prieto et al. 2010) and affect the rate of development, the number of ephyrae per polyp, the frequency of strobilation cycles and the proportion of polyps strobilating (e.g. Purcell 2007; Holst 2012). Warmer temperatures generally lead temperate species to produce more ephyrae (Purcell 2007) although polyps of some tropical species may not tolerate greatly elevated temperatures (e.g. *Mastigias*; Dawson et al. 2001). Laboratory experiments have shown that the total number of buds and ephyrae produced per *Aurelia labiata* polyp over 142 d ranged between 16.6 at 7 °C and 74.1 at 15 °C (Purcell 2007).

The presumed high numerical abundance of scyphopolyps coupled with their ability to propagate asexually and produce sometimes many tens-of-ephyrae per polyp per year suggests polyp populations have potential to produce very large numbers of recruits into the medusa population over a matter of weeks or months. The enormous number of planula larvae produced during sexual reproduction (giving rise to polyps) coupled with the rapid formation of podocysts and repeated polydisc strobilation producing >100 ephyrae polyp^{-1} over 2 months may have accounted for the population explosion of *Rhopilema nomadica* in the Eastern Mediterranean during the early 1990s (Lotan et al. 1992).

2.4.1.2 Salps and Doliolids

All of the thaliaceans have complex, metagenic life cycles characterized by an obligatory alternation of generations between asexual and sexual phases. As very little is known of the life history of pyrosomes, we focus here on the salps and doliolids. In salps, solitary oozoids reproduce asexually to form a chain of ~50–200 blastozooids, with multiple chains being produced at ~2–4-d intervals. Following internal fertilization of each hermaphroditic blastozooid, typically a single embryo is released following a period of brooding, which develops directly into a solitary oozoid (see Loeb and Santora 2011: Fig. 3). Doliolids have polymorphic asexual stages. The oozoid asexually produces colonies of feeding trophozooids and phorozooids. The smaller phorozooids are released as individuals, which then asexually produce a cluster of gonozooids at their base. Following their release the hermaphroditic gonozooids produce up to three eggs and release sperm into the water. The resulting larva develops into an oozoid (see Paffenhöfer and Gibson 1999: Fig. 1, Paffenhöfer and Köster 2011: Fig. 1).

High survival of sexually produced embryos is favoured by direct development, internal brooding and viviparity in the salps and by internal fertilization in doliolids (reviewed by Deibel and Lowen 2012). High asexual reproductive capacity, however, is the principal life-history trait of the Thaliacea thought to account for the capacity of some species to form dense swarms of >1,000 m^{-3} for salps and up to 48,000 m^{-3} for doliolids in only a few weeks (reviewed by Andersen 1998; Deibel and Paffenhöfer 2009). Asexual progeny dominate these mass occurrences which may span tens of thousands of square kilometres in regions of sustained high primary production such as shelf seas, upwellings and intrusions and along tidal fronts.

In salps, each oozoid during its lifespan may produce several chains of blastozooids, releasing a total of up to 800–900 buds. The number of chains and blastozooids per chain depend on oozoid size and generation time, both of which are affected by latitudinal and seasonal differences in temperature and food availability (Foxton 1966; Heron 1972; Heron and Benham 1985; Deibel and Lowen 2012).

The asexual fecundity of doliolids is 3–4 orders of magnitude higher than salps, as a result of asexual reproduction occurring in two sequential stages of the life history: oozoid–phorozooid–gonozooid. A single oozoid of *Dolioletta gegenbauri* can produce an average of 35.6 phorozooids d^{-1} over 5 d, each of which can then produce an average of 11.0 gonozooids d^{-1} over 11.2 d (Paffenhöfer and Gibson 1999), giving a total of 21,930 gonozooids arising asexually from a single oozoid in its lifetime (average 20.5 d at 20 °C).

2.4.2 Hermaphroditism and Self-Fertilization

All thaliaceans and the majority of ctenophores are hermaphroditic, whereas the cnidarian jellyfishes are dioecious. The convergence of thaliaceans and ctenophores on an hermaphroditic life history suggests they gain a benefit specific to their circumstances that is unimportant, or constrained, in medusozoans. Benefits of simultaneous hermaphroditism may include self-fertilization or selfing in low-density populations (Tomlinson 1966) and/or organisms that are sessile or have low motility (Brazeau et al. 1998), where opportunities for encountering a mate and successful cross-fertilization are constrained as a result of low adult abundance and sperm limitation and dilution (Ghiselin 1969). For species that broadcast spawn into the water column, self-fertilization assures reproductive success and may help establish and maintain populations where densities of conspecifics are low. The potential benefits of self-fertilization are a trade-off against the risk of reduced genetic diversity.

Salps and doliolids are protogynous hermaphrodites (Godeaux et al. 1998), so self-fertilization does not occur, although it is possible that eggs in young clones are fertilized by sperm released by older clones (i.e. salp blastozooids or doliolid gonozooids), within a clonal chain. Hermaphroditism—and internal fertilization, brooding and viviparity—likely favours reproductive success during the sexual phase of the life cycle but does not contribute directly to the blooms which, as noted above, are composed primarily of ramets.

The majority of ctenophores are simultaneous hermaphrodites capable of self-fertilizing and producing viable offspring (Pianka 1974). Exceptions include the oceanic *Ocyropsis* sp. (Harbison and Miller 1986) and mesopelagic *Bathocyroe fosteri* (Miller et al. 2000) which are dioecious for all or part of their life cycle. It would appear that Ghiselin's 'low-density model' (Ghiselin 1969) does not apply to *Ocyropsis* sp. or *Bathocyroe fosteri* even though they are likely to experience low population density and sperm dilution in the open ocean. Nevertheless, self-fertilization, together with direct development, high fecundity and growth, is often cited as the reason why coastal and shelf sea ctenophores such as *Mnemiopsis* and *Pleurobrachia* spp. form large blooms and successfully invade new habitats (Martindale 1987; Purcell et al. 2001b).

2.4.3 Generation Time

Generation time, defined as the time taken to develop from egg to maturity or age at first reproduction, is an important determinant of the rate of population increase in a species (Cole 1954). The relevance of generation time is illustrated by the equation for 'maximal intrinsic rate of increase', r_{max}, of a population:

r_{max} (d^{-1}) = ln lifetime fecundity (b)/generation time (T, d)
b is total lifetime egg production
T is development time (d) from egg to maturity or age at first reprodution

While increasing fecundity will increase the rate of increase (see next section), r_{max} clearly is more sensitive to the effect of a change in generation time. Fecundity may be increased most likely in response to food by organisms referred to as 'clutch manipulators' (Aksnes and Giske 1990), and generation time may be reduced in response to increased temperature by 'time manipulators' such as *Oikopleura dioica* (Troedsson et al. 2002). Semelparous organisms tend to minimize generation time, unless they have evolved such that generation time is synchronized with a specific environmental factor such as a spring bloom (Troedsson et al. 2002). Unfortunately relatively little is known about these trade-offs in gelatinous zooplankton. Generation time is difficult to measure in gelatinous species. Their fragility makes controlled laboratory measurements difficult to obtain, and they often lack morphological features by which to age individuals. Moreover, unlike the general trend among metazoans that generation time scales positively with body wet mass (Blueweiss et al. 1978; Hulbert et al. 2007), body size is a poor indicator of generation time in cnidarian medusae and ctenophores. Neither jellyfish longevity nor size at maturity correlates with body size (Lucas 2001; Pitt et al. 2013), and individuals may grow, degrow and regrow in response to food availability (Hamner and Jensen 1974). Nevertheless, it is clear that, in general, many gelatinous organisms are semelparous, reproduce at a population-specific upper size range and die shortly after a period of spawning (Mills 1993; Lucas 2001; Deibel and Lowen 2012).

2.4.3.1 Cnidarians and Ctenophores

Some interesting life-history strategies adopted by a minority of gelatinous zooplankton include paedogenesis (reproduction by larvae or juveniles), dissogony (sexual maturity of larvae and adults with a period of gonad regression in between) and repeated spawning in ctenophores such as *Mnemiopsis leidyi* (Martindale 1987), *Bolinopsis microptera* and *Pleurobrachia bachei* (Hirota 1974; Pianka 1974). Many scyphozoan jellyfishes, including *Aurelia*, *Catostylus* and *Mastigias,* also mature precociously (Martin 1999; Pitt and Kingsford 2003; Dawson 2005). For example, generation time in *Catostylus mosaicus* is estimated to be 2–3 months, after which they spawn continuously and produce multiple cohorts over their estimated lifespan of >1 year (Pitt and Kingsford 2003). Mesopelagic coronate jellyfish such as *Periphylla periphylla* release eggs semi-continuously over several years (Jarms et al. 2002). All these strategies allow fecundity to be greater due to repeated spawning and could in theory lead to evolution of reduced generation time relative to longevity; however, in the vast majority of cases, most obviously in temperate coastal situations, generation time appears to be constrained by synchronization with annual patterns of environmental change. Thus, the majority of cnidarian medusae have generation times and lifespans of <1 year, even though laboratory-maintained individuals often live longer (2–4 years; Raskoff et al. 2003). The giant jellyfish, *Nemopilema nomurai*, develops from a 2–3 mm ephyra to a sexually mature adult >1 m diameter and ~95 kg wet weight in 6–7 months (Kawahara et al. 2006), and many of the bloom-forming coastal species such as *Aurelia aurita*, *Chrysaora quinquecirrha*, *Cyanea* spp. and *Rhopilema nomadica* also reach sexual maturity and diameters of ~150–500 mm within ~2–5 months of ephyra release (Cargo and Schultz 1967; Lotan et al. 1992; Lucas and Lawes 1998). Common bloom-forming ctenophores such as *Pleurobrachia bachei* can produce eggs between 24 and 47 d, and again from 69 d, while *Mnemiopsis* spp. can produce eggs in 13–17-d post-hatch (Hirota 1974; Pianka 1974; Reeve and Walter 1978).

2.4.3.2 Salps and Doliolids

Generation times in thaliaceans are temperature- and food-dependent (see Deibel and Lowen 2012: Table 2). In the temperate salp *Thalia democratica*, for example, generation time ranges between 14 and 23 days at 14–22 °C. Cold-water species such as *Salpa thompsoni* have ~7-week generation times as aggregates and ~7-month when solitary (Loeb and Santora 2011). Total development time of all life stages in the doliolid *Doliolum gegenbauri* is estimated to range between 29 and 41 d at 20 °C/low food and ~21 d at 20 °C/high food (Paffenhöfer and Gibson 1999). Extremely rapid generation times have also been recorded, between ~2 and 11 d (Heron 1972; Madin and Deibel 1998: Table 5.7). These lowest values are among the shortest yet reported for metazoans which may be one of the main reasons why many thaliaceans are able to exploit favourable conditions and attain extremely high densities very rapidly.

Estimates of r_{max} are available primarily for the pelagic tunicates, which are more easily raised than cnidarians and ctenophores under controlled laboratory conditions. Precisely estimated generation time and lifetime fecundity in salps give r_{max} values of typically $<0.2\ d^{-1}$ ($\sim 0.1–1.9\ d^{-1}$; Deibel and Lowen 2012: Table 2). The tendency for longer generation times of doliolids to reduce r_{max}, relative to salps, is countered by the 3–4 orders of magnitude greater fecundity of their sequential asexual life stages; thus r_{max} of *Doliolum gegenbauri* is similar: $0.26\ d^{-1}$ (Deibel and Lowen 2012: Table 3).

2.4.4 Lifetime Fecundity

In favourable conditions, jellyfishes and thaliaceans, with their high water and low-carbon contents, grow rapidly and attain large sizes disproportionate to their carbon content, relative to non-gelatinous taxa (Madin et al. 1981; Larson 1986, Pitt et al. 2013). The potential for rapid growth, maturation and large size typical of jellyfishes and thaliaceans can result in high reproductive output in a short space of time. With repeated spawning—as in the case of many scyphozoans, ctenophores and doliolids—considerable lifetime fecundity can be achieved. Fecundity, like many other physiological and life-history traits, is strongly correlated with body size (see Stearns 2000). Significantly fewer and smaller eggs are produced by small and juvenile individuals, with continuous egg production occurring in larger adults.

Therefore lifetime fecundity can be increased by enlarging body size and by repeated or continuous spawning. Yet within the limits defined by the bioenergetics and life-history strategy of an organism, fecundity is a highly plastic character, and environmental factors such as temperature and food quality or quantity significantly affect reproductive output (Ramirez-Llodra 2002). Additionally, some species display sexual size dimorphism with females larger than males consistent with, but not necessarily evidence of, Darwin's 'fecundity advantage' model (Shine 1988). Preliminary analyses of scyphomedusae *Aurelia* and *Catostylus mosaicus* showed that female medusae were larger than contemporaneous conspecific males (Dawson and Hamner 2009).

2.4.4.1 Cnidarians and Ctenophores

Assuming a water temperature of 22 °C and development time of 7.1 d, Ishii and Takagi (2003) estimated planula production of an *Aurelia* in Tokyo Bay to be 58,3000 medusa^{-1} d^{-1}. Lucas and Lawes (1998) counted ~65,000 planula larvae in the oral arms of a 110–120 mm diameter *A. aurita* from a productive stretch of Southampton Water. While these numbers indicate that lifetime fecundity can be very high, empirical estimates are scarce. Also, actual fecundity may fall far short of the maximum; fewer than 5,000 (often <500) planula larvae were counted in the oral arms of small, severely food-limited *A. aurita* inhabiting Horsea Lake, and Horsea Lake medusae had 30-fold fewer planula larvae than medusae of comparable size in Southampton Water (Lucas and Lawes 1998).

Egg production by the invasive lobate ctenophore *Mnemiopsis* also varies with body size, temperature and food availability (e.g. Reeve and Walter 1978; Reeve et al. 1989; Purcell et al. 2001b). Somatic growth continues after the onset of maturity, and appreciable and continuous reproductive output only occurs in larger, well-fed individuals. In laboratory experiments, the largest ctenophores maintained at the highest food concentrations produced 2,000–3,000 eggs d^{-1} over a period of ~8 d (Reeve et al. 1989), giving a total fecundity of ~16,000–24,000 eggs ind^{-1}. Both Baker and Reeve (1974) and Finenko et al. (1995) reported *Mnemiopsis* to produce up to 12,000 eggs ind^{-1} over a 10-d period. Notably, egg production is extremely sensitive to food supply, even though carbon investment in egg production is low (<2 % of body carbon). Egg production ceases 2–4 days following starvation, but resumes in a similar time frame once food becomes abundant again (Reeve et al. 1989), consistent with the idea that the gelatinous body plan is a specialized adaptation to a marginal niche.

2.4.4.2 Salps and Doliolids

Asexual fecundity in thaliaceans has already been covered in Sect. 2.4.1.2. Both salps and doliolids produce several chains of buds over a period of ~5–20 d, resulting in high lifetime asexual fecundity (Deibel and Lowen 2012). This reproductive longevity is shorter than that of copepods, which range from approximately 10 to 42 d (Gibson and Paffenhöfer 2002). Regarding sexual fecundity, salp blastozooids only produce one egg, while doliolid gonozooids produce between two and six eggs over a period of just a few days (Paffenhöfer and Köster 2011). Thus, asexual fecundity appears to be the reproductive trait in these organisms with greatest potential for a plastic response to environmental conditions.

2.5 Body Composition, Growth and Feeding

While many of the life-history traits of jellyfish and thaliaceans enable large numbers of new individuals to be produced rapidly under favourable conditions, these new recruits constitute only the *potential* for a bloom of great ecological consequence (Dawson and Hamner 2009). Life-history models appropriate for gelatinous zooplankton (i.e. type III) predict that the vast majority of individuals die early, before they grow substantially or mature (Rauschert 2010), and thus 'match/mismatch' dynamics during critical stages may have very large consequences for the significance of blooms (Dawson and Hamner 2009; Fig. 4). Blooms that have visible and significant ecological and socio-economic impacts are typically those composed of adult individuals of larger species. Questions regarding the larger bloom-forming species are as follows: how do the surviving juveniles grow so large in such a short space of time, and does their large watery body relative to carbon confer physiological and ecological advantages over non-gelatinous counterparts, particularly with respect to their growth, body size, future fecundity, feeding ecology and vulnerability to predation, and which enable them to form visible blooms?

2.5.1 Implications of Watery Bodies and Low Carbon on Growth Rate and Body Size

Most marine animals are composed of approximately 75 % water and 8–10 % carbon per unit wet weight (Vinogradof 1953). In contrast, gelatinous members of the Cnidaria, Ctenophora and Thaliacea have an average water content of 96 % and carbon content of 0.5 % (Arai 1997; Lucas et al. 2011). Specific growth rates (k, day^{-1}) of cnidarian medusae (0.05–0.24 d^{-1}) are significantly faster (3.5x) than non-gelatinous organisms of equivalent size (measured as equivalent spherical diameter, ESD) and 2.2x faster when ESD is adjusted for carbon content ($P<0.001$; Pitt et al. 2013). Similarly, the metabolic rates of medusae, ctenophores and thaliaceans are many times slower than other organisms of comparable size, but the carbon-corrected metabolic rates are comparable (Schneider 1992), and the assimilation efficiencies and net growth efficiencies of gelatinous zooplankton are similar to other carnivores (Arai 1997; Møller and Riisgård 2007; Pitt et al. 2009). In this context, the distinguishing feature of jellyfishes and thaliaceans is that they do not invest substantial amounts of carbon and energy in constructing and maintaining skeletons, structures for gaseous exchange or transport of metabolites around the body typical of large metazoan animals. Rather, they use low-carbon structures requiring correspondingly low-energy input, such as the largely acellular extracellular matrix of mesoglea as a hydrostatic skeleton, and gaseous and metabolic exchange takes place via simple diffusion across thin body walls. The limited carbon and energy that are available therefore can be directed primarily towards essential tissue layers such as muscle for movement, gastric and oral surfaces for prey capture and digestion and gonads which take advantage of the fecundity increases of rapidly attaining large body sizes usually unattainable by other organisms of equivalent carbon content but small size (Arai 1997; Dawson and Hamner 2009).

Published bioenergetic and growth data for thaliaceans are scarce and imprecise, so were not included by Pitt et al. (2013) in their analysis of allometric relationships in gelatinous and non-gelatinous organisms. Growth rates in the Ctenophora (0.09–0.47 d^{-1}, Møller et al. 2010) are similar to those of the cnidarian medusae ($k = 0.05$–0.24 d^{-1}), but both usually are slower than the growth rates of thaliaceans and larvaceans. The doliolid *Dolioletta gegenbauri* has $k = 0.15$–0.70 d^{-1} (Gibson and Paffenhöfer 2000). Salps such as *Cyclosalpa* spp., *Pegea* spp. and *Salpa* spp. have hourly linear growth rates of <5 % h^{-1} (Madin and Deibel 1998: Table 5.6), while the small temperate salp *Thalia democratica* has $k = 4.2$–9.2 d^{-1}which is equivalent to increasing in length by up to 28 % h^{-1} (Heron 1972; Deibel 1982; Heron and Benham 1985; Tsuda and Nemoto 1992). Larvaceans such as *Oikopleura dioica* can have rates as high as $k = 3$–23 d^{-1}(Hopcroft and Roff 1995). It should be noted that there are a number of caveats to consider with published growth data for thaliaceans, and care should be taken to note the method used to measure growth (see Deibel and Lowen 2012). Heron's 1972 rate value of 28 % h^{-1} for *T. democratica* was based on cohort tracking which makes a large number of assumptions. In the laboratory the same author measured rates of only 10 % h^{-1}. Nevertheless, growth rates of thaliaceans are among the fastest reported for any multicellular animals and, combined with short generation times (Sect. 2.4.3.2) and high rates of asexual reproduction (Sect. 2.4.1.2), allow population biomass increases of up to 2.5x per day (Heron 1972; Alldredge and Madin 1982). Blooms of *Thalia democratica*, *Salpa fusiformis*, *S. aspera* and *S. thompsoni*, containing millions of individuals, can be produced within just 2–3 weeks under favourable feeding conditions. Although mass occurrences of salps are found in all oceans, true blooms are most commonly associated with periods of sustained high productivity in nutrient-rich upwellings, cold-core eddies and at water-mass frontal regions typically found along the continental shelf break and slope.

2.5.2 Feeding

The watery, low-carbon bodies combined with the feeding and physiological ecology typical of many cnidarians and ctenophores provide them with a competitive advantage in the heterogenous food environment found in many pelagic ecosystems.

Growth that leads quickly to large body size confers several advantages for gelatinous zooplankton (Dawson and Hamner 2009) including a larger search volume which enhances prey encounter rates and feeding rates (Acuña et al. 2011). Feeding rates of gelatinous zooplankton, usually are measured as ingestion rate [prey consumed ind^{-1} d^{-1}] or clearance rate [litres cleared ind^{-1} d^{-1}]), increase with body size (Kremer and Reeve 1989; Arai 1997; Purcell 2009) and are equivalent to visually orienting predatory fishes and greater than those of crustacean zooplankton of equivalent carbon content (Acuña et al. 2011). The capacity of gelatinous zooplankton for rapid growth, however, may give them an edge over fishes in effectively exploiting fast-growing prey populations.

2.5.2.1 Cnidarians and Ctenophores

Many medusozoans and ctenophores are characterized by type I feeding responses in relation to food concentration (Purcell 1997; Purcell and Arai 2001), with little or no reduction in ingestion rate, even at very high prey concentrations in excess of those found in the field (Møller et al. 2010). Large species such as *Aurelia* and *Cyanea* feeding at high prey densities (>100 prey l^{-1}) may consume hundreds or thousands of prey items per day (Båmstedt 1990; Purcell and Arai 2001; Purcell 2003). Thus, jellyfish are able to utilize dense patches of prey effectively. The possibility for jellyfish to feed at maximum clearance rate in either very high prey concentration for a short time or low prey concentration for a long time has also been demonstrated by Hansson and Kiørboe (2006) using *Sarsia tubulosa* fed on copepods in prey concentrations of variable heterogeneity. The stomachs of many cnidarians and ctenophores are large relative to prey size, capable of accumulating food, and this allows individuals to feed at maximum clearance rate in a wide range of food concentrations. The ability of jellyfish to capture prey at maximum clearance rate under different prey concentrations, and to accumulate relatively large amounts of food in their guts, suggests that they would thrive in both homogenous and patchy food distributions. This ability to feed at high prey densities seems also to be complemented by an ability to feed at exceptionally low prey densities. By examining the scope for growth in fish, jellyfish and their crustacean prey, Acuña et al. (2011) concluded that fishes and jellyfish could thrive at lower prey concentrations than their crustacean counterparts, with jellyfish utilizing their large size and feeding area to increase prey encounter rates and achieve high clearance rates, equivalent to those of fish on a g^{-1} C basis, even in very dilute prey concentrations.

The flexibility of jellyfishes to exploit different feeding environments does not mean, however, that they feed indiscriminately. Studies of scyphomedusae that occur en masse (e.g. *Aurelia aurita*, *Chrysaora quinquecirrha* and *Cyanea* spp.) and of the invasive lobate ctenophore *Mnemiopsis* spp. show that feeding rates are affected by the morphology (e.g. tentacle length and spacing, body shape) of the predator and by the size and swimming behaviour of the predator and the prey (e.g. Costello and Colin 1995; Sørnes and Aksnes 2004; Titelman and Hansson 2006). Particularly, large body size increases encounter rates in taxa that utilize a slower swimming 'cruising' method of food capture, such as scyphomedusae, some hydromedusae and lobate ctenophores (Bailey and Batty 1984; Gerritsen and Strickler 1997; Acuña et al. 2011). Taxa such as tentaculate ctenophores, siphonophores, box jellyfish and coronates that employ a more stationary 'ambush entangling' or 'fishing' style of prey capture using long tentacles are likely to be less strongly influenced by body size as the body surface area itself is not being used to capture prey, but rather the length of tentacles. For ambush predators such as *Pleurobrachia* spp., prey size and motility (swimming speed and escape response) and detection distances of the predator and prey are more important determinants in the predator–prey encounter rate and prey selection (Gerritsen and Strickler 1997; Greene et al. 1986).

2.5.2.2 Salps and Doliolids

Salps and doliolids have several feeding adaptations that enable them to be highly efficient omnivores capable of clearing large volumes of water in both low- and high-food environments: a highly efficient filtering mechanism capable of non-selectively removing particles from small bacteria to large phytoplankton chains and very high filtration rates (Acuña 2001). Both salps and doliolids pump water in through their oral siphon, doliolids using ostial cilia and salps using contractions of their muscular bands as part of their jet propulsion swimming (Madin and Deibel 1998). The inflowing particles are trapped by the pharyngeal filter, a fine mucous mesh sieve which fills up most of the body cavity and is continually generated. The mucous sieves of salps have some of the smallest diameter mesh elements and mesh spacing of all marine filter feeders (Bone et al. 2003). Salps are able to achieve higher filtration rates, 1–10 ml s^{-1} (Sutherland and Madin 2010), and can feed on smaller-sized particles than most other planktonic filter feeders, giving salps a competitive advantage in a unique niche. Indeed, Sutherland et al. (2010) demonstrated that small particles < 1 µm can satisfy a salp's energetic needs. Although retention efficiencies appear to decline for particles <2 µm (Madin and Deibel 1998), this is likely to vary between salp species and size of food items (Vargas and Madin 2004). Nevertheless salps are able to capture a very wide range of particles between <1 µm and 1 mm with clearance rates of between 35 and 1429 ml ind^{-1} h^{-1} (Madin and Deibel 1998). Grazing studies on doliolids are rather scarce. The ultrastructure of the pharyngeal filter has not been examined in doliolids, but it is suggested that they are able to retain very small particles (<1 µm) more efficiently than salps and achieve filtration rates of ~21 ml ind^{-1} h^{-1} at moderate to high food concentrations (Madin and Deibel 1998; Gibson and Paffenhöfer 2000).

As well as forming occasional large blooms in productive regions of the world's oceans, thaliaceans also inhabit oligotrophic subtropical gyres where productivity can remain low for prolonged periods of time. They are able to maintain normal feeding and swimming activities in these nutritionally poor subtropical waters (Acuña 2001) as well as during seasonal periods of food scarcity in temperate seas without having lipid storage (Deibel et al. 1992), diapause eggs or dormant stages.

Harbison (1992) suggested that a large, gelatinous body may involve some feeding advantage at very low concentrations, as they could develop a large and delicate feeding structure due to reduced gravitational and turbulent shear stresses in their natural environment. Later, Acuña (2001) proposed that the gelatinous body was an evolutionary strategy to increase body size and supportive structure for the filter-feeding mechanism while maintaining the same low-carbon content. Based on a semi-empirical approach using filtration theory and allometric relationships, he estimated that a hypothetical *Pegea confoederata* salp with the same carbon content but 'normal' water content (i.e. the same as a copepod) would starve in a large proportion of the world's oceans.

2.6 How Jellyfishes Withstand and Respond to Environmental Change

The rapid growth and development, early reproduction, high fecundity and condensed period of sexual reproduction typical of gelatinous zooplankton suggest they evolved in relatively unpredictable and ephemeral environments (Deibel and Lowen 2012). The attributes of modern gelatinous zooplankton which respond rapidly to the onset of favourable conditions, enabling some to occur en masse, may also underwrite population outbreaks that may result from anthropogenic perturbations of the environment (Purcell et al. 2012). Cnidarians, ctenophores and thaliaceans also display great plasticity in key traits such as feeding and physiology (Acuña 2001; Hansson and Kiørboe 2006), allocation of energy towards reproductive or somatic growth (Lucas 2001) and age and size at maturity (Lucas 2001) in relation to temperature and food availability, all of which presumably help individuals to persist through bad times, take advantage of good times and maximize lifetime fitness.

These traits, and their plasticity, may help to explain why several cnidarians and ctenophores are highly successful invasive species capable of forming significant blooms in non-native regions (Graham and Bahya 2007). The classic example is the translocation of *Mnemiopsis leidyi* from North America into the Black Sea in the mid-1980s and its subsequent spread into the Mediterranean Sea in the 1990s (Fuentes et al. 2010), followed by new introductions into the Baltic and North Seas in the 2000s (Costello et al. 2012; Lehtiniemi et al. 2012). *M. leidyi* is known to have wide tolerance for temperature (2–32 °C), salinity (2–38) as well as polluted and eutrophic waters, which enables effective spreading to new regions (Fuentes et al. 2010). Other established invasive species include *Rhopilema nomadica* in the Mediterranean in the early 1990s (Lotan et al. 1992) and the spread of *Phyllorhiza punctata* from SE Asia into the central and eastern Pacific, Atlantic coast of North America and Mediterranean Sea (Verity et al. 2011).

Additional features that enable jellyfishes to survive through more prolonged periods of stress likely have been important complements to the high clearance rates and rapid growth coupled with short generation times and annual lifespans which allow them to respond rapidly in highly variable food environments. Proteins, rather than lipids, are thought to provide some energy storage capacity, and during periods of starvation, jellyfish degrow, a process that is reversible once food becomes available again (Hamner and Jensen 1974). The mesoglea gel may act as a short-term storage tissue, providing energy to metabolically active tissues during periods of starvation (Thuesen et al. 2005a). During this period of degrowth, reproductive tissues remain relatively unaffected (Hamner and Jensen 1974). Population studies of *Aurelia aurita* indicate that during periods of food limitation, medusae direct available resources into reproduction. In the semi-enclosed Horsea Lake, for example, medusae remained small and became sexually mature during periods of food shortage, but following increased zooplankton abundance grew larger in size. During years of very high medusa abundance and severe food limitation, *A. aurita* as small as 19 mm diameter was sexually mature (Lucas 2001).

Another reproductive trait that aids survival is the production of chitin-covered podocysts by the Scyphozoa (Arai 2009). While podocysts are thought to be a normal mechanism of increasing numbers via asexual reproduction in several species such as *Cyanea* spp., several authors (Cargo and Schultz 1967; Thein et al. 2012, Lucas unpubl. data) have found that cysts only form following periods of starvation and high or low temperature, depending on species. Podocysts are reported to be able to survive for over 3 years on organic-rich reserves (Thein et al. 2012, Uye pers. comm.) and are thought to be an important mechanism in aiding survival during adverse conditions such as hypoxia, sediment burial and extreme temperature (Uye pers. comm.) and as protection against predation by nudibranchs (see Arai 2009). In her review, Arai also noted the similarity between lists of species known to produce podocysts and form blooms (e.g. *Aurelia*, *Chrysaora*, *Cyanea*, *Nemopilema*, *Rhopilema* and *Rhizostoma*). Phylogenetic analysis also indicated the podocyst as possible cause of mass occurrences (Dawson and Hamner 2009), presenting a hypothesis pending more data on the benthic phase of other scyphozoans.

Several estuaries and coastal seas where jellyfish are abundant (e.g. Tokyo Bay, Chesapeake Bay, Mljet Lake, the Black Sea and Mediterranean Sea) are seasonally dysoxic (≤ 2 ml l^{-1} O_2; Sen Gupta and Machain-Castillo 1993) or anoxic, often as a result of eutrophication (Purcell et al. 2001a). Dysoxia and anoxia, which are most severe during the summer months when density stratification is most pronounced, can directly or indirectly affect feeding, growth, reproduction and survival. (NB Following the paleontological literature, we use dysoxia and anoxia to describe environment conditions, which may or may not induce hypoxia (<30 % O_2 saturation) or anoxaemia (<10 % O_2 saturation) of blood, haemocoel or tissues. Although unorthodox for the physiological literature, it is essential in an evolutionary context to distinguish the environment from the organism's response to that environment.) Nevertheless, several of the mass-occurring Cnidaria (e.g. *Aurelia*, *Chrysaora quinquecirrha*, *Cyanea capillata*) and Ctenophora (e.g. *Mnemiopsis leidyi, Pleurobrachia bachei*) are able to tolerate dissolved oxygen levels as low as 0.5 mg l^{-1}, in both the polyp and medusa phases of the life cycle in the case of scyphozoans (Condon et al. 2001; Thuesen et al. 2005a, b; Ishii et al. 2008).

When exposed to increasingly dysoxic conditions, metazoans generally show one of two categories of response: oxyregulation or oxyconformation. Animals that oxyregulate maintain a relatively constant rate of oxygen consumption during progressive dysoxia, whereas oxyconformers consume oxygen at a proportionately decreasing rate. Experiments on several common species of scyphomedusae and ctenophores show they can maintain steady oxygen consumption down to <10 % air saturation for ≤2 h and oxyregulate by using the intragel oxygen gradient (i.e. gradient in oxygen between the mesoglea, metabolically active tissues and surrounding seawater) to meet the metabolic needs of the individual (Thuesen et al. 2005a). In the hypereutrophic waters of Tokyo Bay, natural populations of *Aurelia* polyps colonize the deeper hypoxic waters where they are able to outcompete the more sensitive benthic epifauna (Ishii et al. 2008; Ishii and Katsukoshi 2010). While experiments indicate that planula survival time is reduced in low dissolved oxygen due to the increased oxygen demand of swimming, settlement and metamorphosis into a sedentary polyp is enhanced at low dissolved oxygen (Ishii et al. 2008). Polyps of *C. quinquecirrha* inhabiting Chesapeake Bay are able to survive and asexually reproduce even in prolonged exposure to 0.5 mg O_2 l^{-1} (Condon et al. 2001).

Predation by *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* on zooplankton and *C. quinquecirrha* predation on *M. leidyi* remain unchanged or increase at oxygen concentrations that reduce feeding rates of co-occurring finfish (Breitburg et al. 1997; Decker et al. 2004). The tolerance of *C. quinquecirrha* and *M. leidyi* to exposure to low oxygen, and their high feeding rates under dysoxic conditions, may be partly responsible for the high abundance of these gelatinous species in coastal ecosystems where dysoxia is common (Breitburg et al. 1997; Purcell et al. 2001a). But not all medusae are so tolerant. Some hydromedusae, including *Euphysa flammea* and *Eutonina indicans*, are oxyconformers rather than oxyregulators (Rutherford and Thuesen 2005). Interestingly, congeners of those species, *Euphysa aurata* and *Eutonina scintillans*, used to occur in the Adriatic Sea but have since disappeared following increased frequency of anoxic events (Benović et al. 1987).

2.7 Why Do Jellyfishes and Thaliaceans Bloom?

The causes of jellyfish blooms include attributes of organisms, attributes of environments and organism–environment interactions. The multifaceted nature of the causes of jellyfish blooms was captured in the early definitions of 'true' and 'apparent' blooms (Graham et al. 2001) which were refined to include other situations (Box 2.2). Since the First International Conference on Jellyfish Blooms (Purcell et al. 2001c), progress has been made in identifying attributes of organisms—principally medusozoans—that likely contribute to blooms and other kinds of mass occurrence (Arai 2009; Dawson and Hamner 2009), and we have summarized similar attributes of doliolids and salps herein. The advances in our understanding of the biological causes of jellyfish blooms were enabled in part by application of phylogenetic tools which also indicated that mass occurrences likely had ancient origins in principally shallow-water taxa (Dawson and Hamner 2009); both inferences are consistent with the fossil record (Young and Hagadorn 2010). One other inference from phylogenetic analyses cannot currently be overstated: only a subset of species of jellyfishes have the suite of attributes that predispose them to occur often at very high density (Hamner and Dawson 2009; Fig. 2), and it is this subset of species on which notorious claims that jellyfish outbreaks are on the rise caused by global change are based (e.g. Jackson 2008; Richardson et al. 2009). That generic claim is oversimplistic (Purcell 2005; Daryanabard and Dawson 2008) and recently was questioned (Condon et al. 2012). The key question, though, is perhaps not whether 'the numbers of gelatinous zooplankton [is] rising in the world's oceans?' (Condon et al. 2012)—that answer we have known for some time (e.g. Mills 2001; Brodeur et al. 1999, 2008) is both yes and no (e.g. Brotz et al. 2012)—so much as which species are on the rise, where and why?

Answers to the first two parts of the question—i.e. which species are on the rise (or not) and where—are the purview of long-term research in quantitative ecology, backed up by some rigorous systematics. Rigorous, molecular, systematics is essential because of the prevalence of cryptic species of gelatinous zooplankton (e.g. Dawson 2004; Govindarajan et al. 2005; Appeltans et al. 2012). Answers to the third question 'why?' commonly are perceived also to be the purview of quantitative ecology, specifically macroecology (e.g. Brotz et al. 2012; Condon et al. 2012), but in fact they are first the purview of ecological genetics—the study of how ecologically relevant traits evolve in natural populations, often in the context of pressing social-ecological questions (Urban 2008). While it is appealing to try to address a perceived global issue with global analyses of higher taxa or regionally grouped species (Brotz et al. 2012), such a strategy is premature in the case of jellyfish blooms and perhaps never appropriate for discovering the causes of jellyfish blooms, because blooms (and other mass occurrences) are properties of populations. Jellyfish blooms are emergent phenomena resulting from interactions between the attributes of many organisms and the attributes of environments that share a common spatial and temporal context (Fig. 2.5). To study the phenomenon using a basic unit of larger scale than the population is to blur response and explanatory variables (e.g. see Fig. 2.3).

The causes (and consequences) of blooms undoubtedly result from interactions among a suite of abiotic and biotic factors, which occur within populations along a specific time course and route (or in a single location). The relative strengths of, and interactions between, these factors certainly differ from place to place and from time to time. There is no single cause, nor any single consequence, of mass occurrences of jellyfishes or salps nor therefore of blooms or 'outbreaks'. To understand which causes are important in each case, it is essential that we unite the techniques of population biology and population genetics. These techniques should be integrated to study multiple populations in a diversity of taxa across a range of locations, repeatedly across years, allowing us to draw generalities about the relative frequencies and biological and environmental causes of mass occurrences, and to distinguish them as accumulations, aggregations, blooms, swarms and outbreaks.

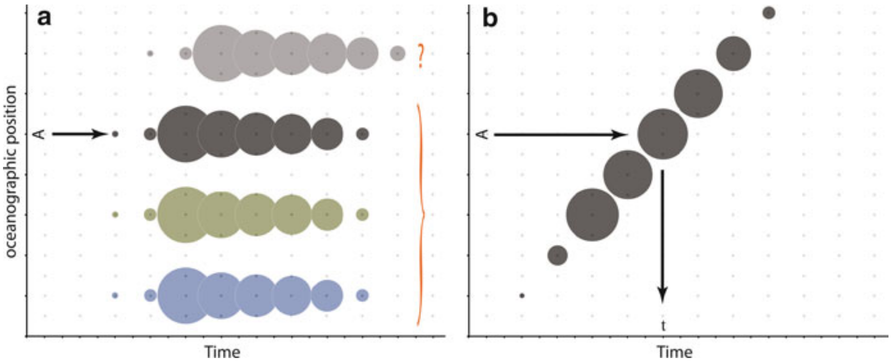

Fig. 2.5 (**a**–**b**) A preliminary quantitative evolutionary-ecological framework for identifying mass occurrences and their causes. For the purposes of orientation and scale in this schematic, the abscissa shows a single year, and the ordinate axis shows distance along an approximately northward flowing current, therefore approximating latitude from more southerly (*bottom*) to more northerly (*top*). (**a**) A quantitative ecologist observes an increase in both number and size of medusae (i.e. biomass, the area of plotted circles) and their subsequent demise, at a single location over a period of several months (*dark grey*). These observations suggest an endemic bloom. However, the same dynamics have been observed at two other upstream locations (i.e. to the south), raising the question of whether these are all observations of the same widespread population. This question can be answered by population genetic analysis and, in this case, shows three genetically distinct populations (*dark grey*, *green* and *blue*). In this case, the dynamics of each closed population could be described by the simplified population growth equation $N_{t+1} = N_t + B - D$ (see Sect. 2.3.2). Further environmental studies show that the three populations experience (are bracketed by) the same regional climate, suggesting the population dynamics are coordinated by regional, rather than distinguished by local, environmental dynamics and their interactions. A fourth population, to the north, shows a similar pattern of changes in biomass delayed to later in the year, raising questions about whether this is a genetically similar population in a different environment, a genetically distinct population in a similar environment or a genetically distinct population in a distinct environment. Again, this question is answerable by bringing together the approaches of ecology and population genetics. (**b**) A quantitative ecologist observes, during a limited period around time *t*, a very rapid increase in the number of large medusa and their rapid disappearance, suggesting an apparent bloom (i.e. described by the simplified population growth equation $N_t = N_{t-1} + I$ and $N_{t+1} = N_t - E$). This inference could be supported (or refuted) by genetic analyses of samples taken at other locations and times, which would (or would not) be statistically similar to samples collected earlier from upstream locations and later from downstream locations (see Sect. 2.3.2). Scenarios for other kinds of mass occurrence also can be hypothesized. A key point clarified by these graphs is that the cause(s) of blooms must precede in time *and* place (at ≥1 point) the observed 'bloom'. Thus, careful integration of ecological and genetic analyses at the population level along the relevant time course (stages I and II in Fig. 2.4) and in the right places—i.e. in the bloom location (**a**) or along the bloom trajectory (**b**)—is essential to identify the cause(s) of jellyfish mass occurrences. By repeating such studies in many places at many times, and integrating them through years, we can identify which species occur en masse, which species are on the rise (or not), where and why

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Chapter 3
Nonindigenous Marine Jellyfish: Invasiveness, Invasibility, and Impacts

Keith M. Bayha and William M. Graham

Abstract The marine jellyfishes (herein referring to pelagic scyphozoans, hydrozoans, and ctenophores) have been increasingly recognized as important nuisance species in ecosystems around the world, impacting fisheries, injuring swimmers, and clogging the intakes of power plants, among other effects. These animals have independently evolved life history and reproductive strategies that allow them to quickly reach large abundances and exert considerable ecological and economic impacts over their native ecosystems. However, many of these same adaptations have also led to the success of marine jellyfishes as bioinvaders, as many have established themselves as important predators in nonnative ecosystems around the globe. Here, we examine the role of marine jellyfishes as nonindigenous species. We begin by reviewing what is known about the invasion histories of the major nonindigenous jellyfishes and then analyze organismal attributes of marine jellyfishes that promote their success as bioinvaders (*invasiveness*) and characteristics of recipient ecosystems that increase likelihood of successful invasions by marine jellies (*invasibility*). We conclude by examining how these have interacted to determine which species have bloomed in their recipient ecosystems, exerting significant ecological and economic effects (*impacts*).

Keywords Jellyfish blooms • Nonindigenous species • Invasiveness • Invisibility • Scyphomedusae • Hydromedusae • Ctenophores • Reproductive strategies • Phenotypic plasticity • Anthropogenic disturbance

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3.1 Introduction

The marine jellyfishes, here referring to pelagic members of Phylum Cnidaria (hydrozoans, scyphozoans, and cubozoans) and Ctenophora (comb jellies), have independently evolved similar adaptations for rapid population growth and high predatory capacity that allow them to exert considerable ecological influence over their ecosystems (Burrell and van Engel 1976; Feigenbaum and Kelly 1984; Arai 1997; Dawson and Hamner 2009; Hamner and Dawson 2009). Jellyfish exhibit reproductive and life history strategies (e.g., single-parent reproduction, high reproductive capacity, short maturation times) that allow them to quickly reach "bloom concentrations" ("blooming" is here defined as suddenly and rapidly occurring en masse) in the pelagic phase when environmental conditions are favorable (Hyman 1940; Mayer 1912; Arai 1997; Dawson and Hamner 2009; Hamner and Dawson 2009, see also Lucas and Dawson, Chap. 2). The controlling predatory influence jellyfish blooms can exert on zooplankton populations often results in cascading effects throughout the local food web (Burrell and van Engel 1976; Feigenbaum and Kelly 1984). In addition, jellyfish blooms can have detrimental economic effects on fisheries, sting swimmers, and clog intakes of power and water desalinization plants (Arai 1997; Mills 2001; Hay 2006; Purcell et al. 2007).

Many of the organismal attributes that make marine jellyfishes effective blooming species also make them exceptional marine bioinvaders, while also complicating study of them as introduced organisms (Graham and Bayha 2007). Here, we delineate "introduced" species (those that simply occur in nonnative or nonindigenous regions) from "invasive" species (introduced species that impact recipient regions economically, environmentally, or ecologically). Some of the premier examples of jellyfish blooms involve gelatinous species native to other regions, including ctenophores (e.g., *Mnemiopsis leidyi*), scyphozoans (e.g., *Aurelia* spp. and *Phyllorhiza punctata*), and hydrozoans (*Blackfordia virginica* and *Maeotias marginata*) (Vinogradov et al. 1989; Mills and Sommer 1995; Dawson and Jacobs 2001; Graham et al. 2003). Their life history strategies of population explosions from small, cryptic populations (benthic or pelagic) (Mayer 1910; Arai 1997) likely allow them to be easily transported and established in new regions and exert significant ecological and economic impacts. The investigation of introduced populations is consequently hindered by the fact that small, cryptic populations probably go undetected until a population explosion occurs (Vinogradov et al. 1989; Graham et al. 2003; Oliveira 2007). Likewise, the propensity for species crypsis, phenotypic plasticity, and taxonomic uncertainty of marine jellyfishes make it more likely that nonindigenous species might be mistaken for native species and some original taxonomic descriptions do appear to be from introduced populations (e.g., *Blackfordia virginica* (Thiel 1935)). While taxonomic expertise regarding jellyfish among marine scientists has grown in recent years, as has the implementation and use of molecular techniques in ecological studies (Dawson and Jacobs 2001; Holland et al. 2004; Bayha and Graham 2011), it is likely that many more jellyfish invasions are occurring than are being recognized.

A major emphasis in invasion ecology is the study of the transition of organisms from native to invasive (Milbau and Stout 2008). Bioinvasions are broken down into four general stages: introduction to novel environment, establishment in novel environment, spread, and impact (Sakai et al. 2001). Each of these stages has a suite of biotic and abiotic barriers that a species must overcome before transition to the subsequent stage (Lodge 1993; Sakai et al. 2001; Milbau and Stout 2008).

Many recent studies of bioinvasions have focused on three general topics: invasiveness, invasibility, and impacts (Alpert et al. 2000). Invasiveness deals with organismal characters that enhance a species' ability to be introduced to a new environment and become invasive, while invasibility refers to the environmental and ecological conditions of individual ecosystems that make one more susceptible to invaders than another, including the role of anthropogenic disturbances. Lastly, impacts deal with how the first two interact with one another to determine whether or not a species will reach abundances capable of effecting ecological change or exerting economic damage and whether these changes or damages will be ephemeral or persistent.

In this chapter, we explore the roles of jellyfishes as nonindigenous and invasive species. We begin by summarizing the more notable nonindigenous jellyfish species by major taxonomic group, updating the literature on each species since the review by Graham and Bayha (2007). We then examine the attributes that make a particular jellyfish an effective invasive species (*invasiveness*) and describe characteristics of those recipient ecosystems that have promoted jellyfish invasions (*invasibility*). We conclude by addressing how these interact in determining which species bloom and exert ecologically and economic impacts (*impacts*) and whether these nonindigenous species add to the overall magnitudes of jellyfish blooms worldwide.

3.2 Case Studies of Introduced Jellyfish

3.2.1 Scyphozoan Jellyfishes

The Scyphozoa is a class of pelagic cnidarians comprised of approximately 200 species (Mayer 1910; Kramp 1961; Russell 1970) and containing most of the worst nuisance blooming species, such as the moon jellyfish *Aurelia*, the mauve stinger *Pelagia noctiluca*, and Nomura's jellyfish *Nemopilema nomurai*. The majority of scyphozoan species exhibit a bipartite life history, consisting of a benthic polyp stage that asexually produces ephyrae, cysts, or additional polyps, followed by a pelagic medusa stage that sexually produces planulae that subsequently develop into medusae (Mayer 1912; Hyman 1940; Arai 1997). While many genera were historically thought to have cosmopolitan distributions (Kramp 1961), recent genetic studies have revealed that most are actually composed of multiple locally adapted species (Dawson and Jacobs 2001; Holland et al. 2004; Dawson 2005a). The Scyphozoa contains the greatest number of confirmed nonindigenous jellyfish species worldwide.

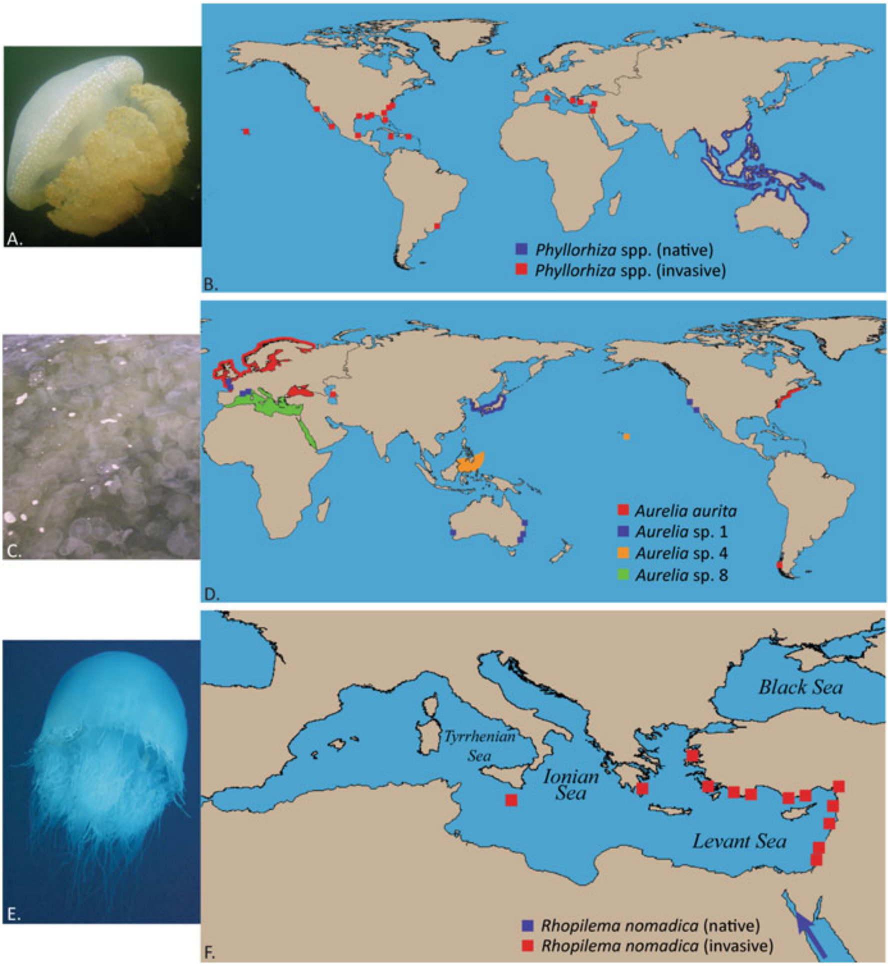

Fig. 3.1 (**a**–**f**) (**a**) *Phyllorhiza punctata* from Laguna Joyuda, Puerto Rico (Photographic credit: L Rodriguez); (**b**) native and invasive ranges of *Phyllorhiza* spp.; (**c**) bloom of *Aurelia* sp. 1 from the Seto Sea, Japan (Photographic credit: S-I Uye); (**d**) current ranges of *Aurelia* species with nonindigenous distributions; (**e**) *Rhopilema nomadica* from the Israeli coast (Photographic credit: A Yurman); (**f**) invasive extent of the Lessepsian immigrant *R. nomadica* into the Mediterranean Sea

The Australian spotted jellyfish *Phyllorhiza punctata* (Fig. 3.1a, b; Table 3.1) is the most successful nonindigenous scyphozoan species (geographically), having been introduced to all nonnative water bodies except the Arctic and Antarctic (Fig. 3.1b). Native to Australia, Japan, and the eastern Indian Ocean (Agassiz 1862; Haeckel 1880; Von Lendenfeld 1884; Uchida 1954, Kawahara, pers. comm.), *Phyllorhiza* was first found in Hawaii, possibly brought there by post-World War II shipping (Doty 1961; Devaney and Eldredge 1977) and was thereafter found in the eastern Pacific, Mediterranean, Atlantic, Caribbean, and Gulf of Mexico

Table 3.1 Sightings of jellyfish either identified as *Phyllorhiza* or later attributed to *Phyllorhiza* from the animal's introduced range

Region (major water body)	Reference
Pearl Harbor, Hawaii (Pacific USA)	Doty (1961)[a]
Southern Brazil (Atlantic)	Moreira (1961)[b]
Jamaica (Caribbean)	Vannucci (1964)
Israeli coast (Mediterranean)	Galil et al. (1990)
Puerto Rico (Caribbean)	Cutress (1971)
San Diego, California (Pacific USA)	Larson and Arneson (1990)
Puerto Rico (Caribbean)	Garcia (1990) Garcia and Durbin (1993)
Northern Gulf of Mexico	Graham et al. (2003)
Florida coast (Atlantic USA)	Graham et al. (2003)
Bahia State (Atlantic Brazil)	Silveira and Cornelius (2000)
Sao Paulo State (Atlantic Brazil)	Migotto et al. (2002)
Greek coast (Mediterranean)	Abed-Navandi and Kikinger (2007)
Galveston, Texas (Gulf of Mexico, USA)	Barord et al. (2007)
North Carolina (Atlantic USA)	B. Kirby-Smith pers. comm.
South Carolina (Atlantic USA)	Calder (2009)
Veracruz, Mexico (Gulf of Mexico, Mexico)	Ocaña-Luna et al. (2010)
Georgia (Atlantic USA)	Verity et al. (2011)
Israeli coast (Mediterranean)	Galil et al. (2009)
Italian coast (Mediterranean)	Boero et al. (2009)
Gulf of California (Mexico)	Gomez-D'aglio and Dawson (2009)
Jamaica (Caribbean)	L. Brotz pers. comm.
Turkish coast (Mediterranean)	Çevik et al. (2011)
Spanish coast (Mediterranean)	V. Fuentes pers. comm.

[a] Originally identified as *Cotylorhizoides pacificus*, it was later attributed to *Phyllorhiza* (Devaney and Eldredge 1977)

[b] Originally identified as *Mastigias scintillae*, it was later attributed to *Phyllorhiza* (Mianzan and Cornelius 1999)

(Fig. 3.1b; Table 3.1). In the summer of 2000, an extremely large bloom of *P. punctata* was encountered in the northern Gulf of Mexico (Graham et al. 2003).

While transport vector(s) and source region(s) are equivocal for *Phyllorhiza*, transport appears tied to global ship traffic, either through the transport of ballast water (ephyrae and medusae) or as hull-fouling organisms (benthic polyps and cysts). Johnson et al. (2005) suggested that the *Phyllorhiza* medusae in the northern Gulf of Mexico were transported via water currents from the Caribbean Sea. However, Bayha et al. (unpublished data) used molecular data to uncover three distinct species of *Phyllorhiza*, two of which (*P. punctata* and *Phyllorhiza* sp. 1) have invaded worldwide. These molecular data indicated that *Phyllorhiza* sp. 1 is present in Brazil, originating from the vicinity of Indonesia, while all other introduced populations are *P. punctata* and a Caribbean source for the Gulf of Mexico animals was not supported (Bayha et al. unpublished data).

The moon jellyfish *Aurelia* spp. (Fig. 3.1c, d) has been studied intensively for centuries. While historically thought to encompass three widely distributed species

Table 3.2 Sightings of *Rhopilema nomadica* from the animal's introduced range

Region (major water body)	Reference
Israeli coast (Mediterranean)	Galil et al. (1990)
Lebanese coast (Mediterranean)	Lakkis and Zeidane (1991)
Syrian coast (Mediterranean)	Lakkis and Zeidane (1991)
	Lotan et al. (1992)
Turkish coast (Mediterranean)	Kideys and Gücü (1995)
	Ozturk and Isinibilir (2010)
Turkish coast (Aegean)	Gülşahin and Tarkan (2011)
Greek coast (Aegean)	Siokou-Frangou et al. (2006)
Malta (Mediterranean)	Deidun et al. (2011)

(Kramp 1961), molecular studies have indicated the presence of as many as 14 locally adapted species of *Aurelia* worldwide (Dawson and Jacobs 2001; Schroth et al. 2002; Dawson 2003; Dawson et al. 2005; Bayha and Graham 2009). Four of these species appear to have been dispersed anthropogenically into distant water bodies (Fig. 3.1d). Indo-Pacific native *Aurelia* sp. 4 is established in Hawaii, possibly as a result of post-World War II shipping, like *Phyllorhiza* (Dawson and Jacobs 2001; Dawson et al. 2005). Likely a Red Sea native, *Aurelia* sp. 8 appears to be a Lessepsian migrant, appearing throughout the Mediterranean Sea (Dawson et al. 2005). *Aurelia aurita* is native to the northern Atlantic and Black Sea (Dawson and Jacobs 2001; Schroth et al. 2002; Dawson et al. 2005) yet can now be found in the Caspian Sea (Korsun et al. 2012) and Chile (Häussermann et al. 2009). Most widespread is *Aurelia* sp. 1, native to the northwestern Pacific, but which is now established in Australia, California, and Europe (Dawson and Jacobs 2001; Schroth et al. 2002; Dawson et al. 2005).

Rhopilema nomadica (Fig. 3.1e, f; Table 3.2), a rhizostome jellyfish first found (1976) and described in Israeli waters (Galil et al. 1990), represents another likely Lessepsian jellyfish invader (although ship transport cannot be fully discounted). The jellyfish has subsequently spread west in the Mediterranean, as far as Malta (Fig. 3.1f; Table 3.2). Given the temperature dependence of the polyp stages (Lotan et al. 1994), Deidun et al. (2011) hypothesize that the invasion may be relegated to the eastern half of the Mediterranean under current water temperature regimes.

The genus *Cassiopea* (Fig. 3.2a, b; Table 3.3) consists of photosymbiotic rhizostome jellyfishes collectively called upside-down jellyfish, common to most tropical and subtropical waters. The medusa stage of this jellyfish is epibenthic, remaining in place on the sandy or muddy surfaces with its algal symbiont-containing oral arms facing the surface sunlight. While the taxonomy of this group has been in flux for decades, genetic work done by Holland et al. (2004) revealed that there were at least six species of *Cassiopea*, where there were previously three, and that two represented worldwide species invasions. *Cassiopea* sp. 3 is found in the Indo-Pacific (Papua New Guinea) and Hawaii, appearing just after World War II, indicating that post-World War II shipping may have played a role (Doty 1961). *Cassiopea andromeda* is a Lessepsian invader, as it is a common in the Red Sea and previously invaded the Mediterranean just after the opening of the Suez Canal (Keller 1888).

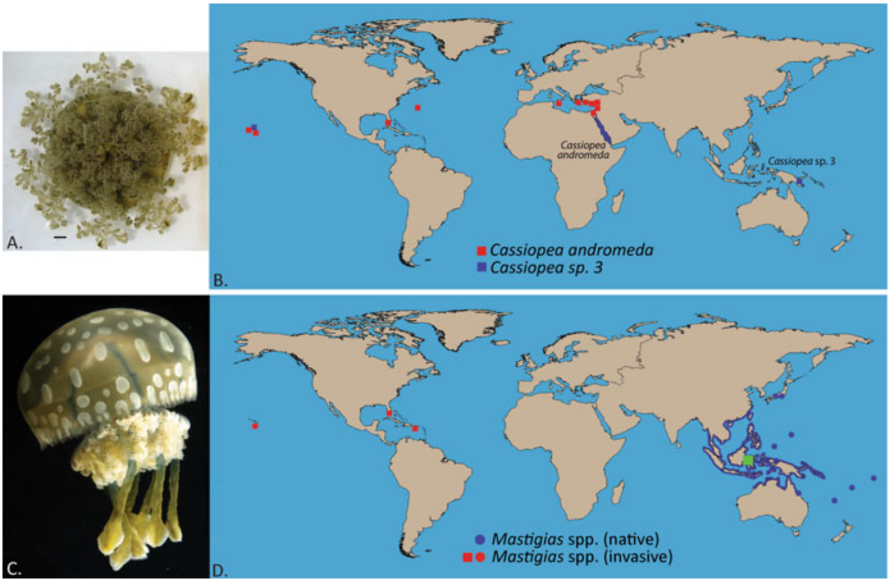

Fig. 3.2 (**a**-**d**) (**a**) *Cassiopea andromeda* from Key Largo, Florida, USA (Photographic credit L Chiaverano). Species identity was confirmed by DNA sequencing (Chiaverano and Bayha unpublished). Scale bar is 10 mm; (**b**) native and invasive ranges of *C. andromeda* and *Cassiopea* sp. 3; (**c**) *Mastigias* sp. 1 from No Name Key, Florida, USA (Photographic credit ME Miller); (**d**) native and introduced ranges of *Mastigias* spp. *Squares* represent regions established genetically as having *Mastigias* sp. 1, and the *green square* represents the region (Kakaban, Indonesia) where the specimen most genetically similar to Caribbean *Mastigias* sp. 1 animals was taken (Dawson 2005b)

Table 3.3 Sightings of *Cassiopea andromeda* from the animal's introduced range

Region (major water body)	Reference
Egypt (Mediterranean)	Keller (1888)
Cyprus (Mediterranean)	Maas (1903)
Greek coast (Aegean)	Schäfer (1955)
Lebanese coast (Mediterranean)	Goy et al. (1988)
Israeli coast (Mediterranean)	Spanier (1989)
Turkish coast (Mediterranean)	Kideys and Gücü (1995)
	Çevik et al. (2006)
	Özgür and Öztürk (2008)
Turkish coast (Aegean)	Galil and Zenetos (2002)
Malta (Mediterranean)	Schembri et al. (2010)
Bermuda (Atlantic)	Holland et al. (2004)
Florida Keys (Atlantic USA)	Holland et al. (2004)

Since entering the Mediterranean Sea, *C. andromeda* has moved progressively westward in the Mediterranean, with its westernmost sighting in Malta (Fig. 3.2b; Table 3.3). In addition, *C. andromeda* can also be found in Hawaii (USA), Bermuda, and the Florida Keys (USA) (Holland et al. 2004).

Mastigias (Fig. 3.2c, d) is native to the Indo-Pacific (Kramp 1961) but has been observed in other ocean basins, indicating anthropogenic dispersal. Like *Aurelia*, *Cassiopea*, and *Phyllorhiza*, *Mastigias* was first encountered in Hawaiian waters (Eldredge and Smith 2001), though how long it has been in Hawaii is not clear. More recently, *Mastigias* was found in a marine lake in Puerto Rico and a salt water-filled quarry in the Florida Keys (USA) (Bayha and Graham 2011). Molecular analysis of medusae from Puerto Rico and the Florida indicated they likely have a common source and are most genetically similar to *Mastigias* sp. 1 from Indonesia (Bayha and Graham 2011). While the typical culprits for transport of *Mastigias* have been proposed (ballast water transport, hull fouling, etc.), an additional possibility is the transfer of "live rock" for the aquarium industry, since such rock, harvested from living reefs (Wabnitz et al. 2003), can sometimes contain viable jellyfish polyps (Bolton and Graham 2006).

3.2.2 Hydromedusae

Medusae of the Class Hydrozoa are typically very small, inconspicuous jellyfish species that, in most cases, exhibit a metagenic life history consisting of a benthic colonial hydroid stage and a sexually reproducing hydromedusa stage (Fautin 2002). In contrast to the scyphozoans, which are comprised by 200 or so species (Kramp 1961), there are more than 800 recognized valid species of hydromedusae (Bouillon and Boero 2000). While there are several species that have clearly been anthropogenically dispersed (Fig 3.3; Tables 3.4 and 3.5), the sheer number of hydromedusae species, their small size, and a general dearth of taxonomic expertise among marine scientists likely mean that many more introductions have gone unrecognized.

Three species of hydromedusae have spread worldwide with significant overlap in dispersal patterns: the Leptomedusa *Blackfordia virginica* Mayer 1910 (Fig. 3.3a, b; Table 3.4) and the Limnomedusae *Maeotias marginata* Modeer 1791 and *Moerisia* sp. (Fig. 3.3b; Table 3.4). Although one species of *Moerisia* (*M. lyonsi*) and *B. virginica* were described from elsewhere (Boulenger 1908; Mayer 1910), all three hydrozoans are thought to be native to the region of the Black Sea, Sea of Azov, and Caspian Sea (Theil 1935; Kramp 1961; Calder and Burrell 1967; Mills and Sommer 1995). *M. marginata* has since been found in various regions of the Atlantic and Pacific basins, as has *Moerisia* sp. (Fig. 3.3b; Table 3.5). Currently, *Blackfordia virginica* is significantly more widespread than *M. lyonsi* and *M. marginata*, occurring in the Atlantic, Pacific, and Indian Oceans (Fig. 3.3b; Table 3.4), though genetic analyses revealed that one population previously identified as *B. virginica* in Brazil is a different species (Harrison 2010). Given the tenuous taxonomies of these animals, their extensive invasive abilities, and inconspicuous natures, it is likely that all have invaded considerably more geographic regions and some populations around the world identified as novel species of *Maeotias*, *Moerisia*, and *Blackfordia* may also actually be invaders (Rees and Gershwin 2000).

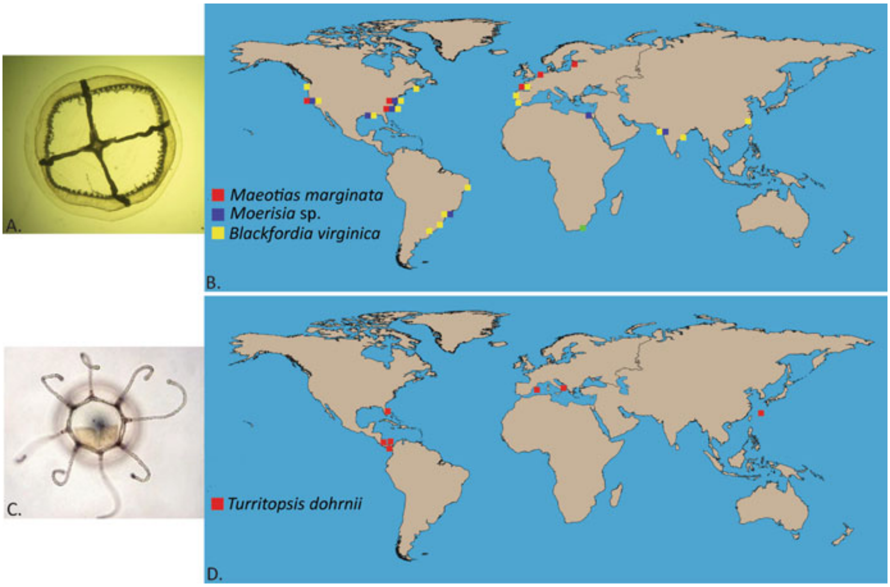

Fig. 3.3 (**a**–**d**) (**a**) *Blackfordia virginica* from Lake Pontchartrain, Louisiana, USA (Photographic credit: G Harrison); (**b**) global distribution of *Maeotias marginata*, *B. virginica*, and *Moerisia* sp.; (**c**) *Turritopsis dohrnii* from Panama (Photographic credit: MP Miglietta); (**d**) worldwide distribution of *Turritopsis dohrnii*

Table 3.4 Sightings of *Blackfordia virginica* from the animal's introduced range

Region (major water body)	Reference
France (Atlantic)	Denayer (1973)
Delaware Bay, USA	Cronin et al. (1962)
South China Sea	Zhang (1982)
Nova Scotia (Atlantic)	Moore (1987)
Ganges estuary, India (Indian)	Sai Sastry and Chandramohan (1989)
Chesapeake Bay, USA	Mills and Sommer (1995)
Upper San Francisco Bay, USA	Mills and Sommer (1995)
Coos Bay, Oregon (Pacific)	Mills and Sommer (1995)
Portugal (Atlantic)	Re (1996)
	Chicharo et al. (2009)
Bombay, India (Indian)	Santhakumari et al. (1999)
Chiapas, Mexico (Pacific)	Alvarez-Silva (1999)
	Alvarez-Silva et al. (2003)
South Africa (Indian)	Buecher et al. (2005)
Brazilian coast (Atlantic)	Genzano et al. (2006)
	Nogueira and de Oliveira (2006)
	Bardi and Marques (2009)
Argentina/Uruguay (Atlantic)	Genzano et al (2006)
Lake Pontchartrain (USA, Gulf of Mexico)	Harrison et al. accepted

Table 3.5 Sightings of *Maeotias marginata and Moerisia sp.* from the animal's introduced ranges

Region (major water body)	Reference
Maeotias marginata	
Netherlands (North Sea)	Hummelinck (1941)
Chesapeake Bay (USA)	Calder and Burrell (1969)
France (Atlantic)	Denayer (1973)
Upper San Francisco Bay (USA)	Mills and Sommer (1995)
South Carolina (Atlantic USA)	Mills and Sommer (1995)
Baltic Sea	Väinölä and Oulasvirta (2001)
Moerisia sp.	
Chesapeake Bay (USA)	Calder and Burrell (1967)
Lake Pontchartrain (Gulf of Mexico, USA)	Poirrier and Mulino (1977)
South Carolina (Atlantic USA)	Sandifer et al. (1974)
Upper San Francisco Bay (USA)	Rees and Gershwin (2000) Mills and Rees (2000)
Brazilian coast (Atlantic)	Nogueira and de Oliveira (2006)[a]
Bombay, India (Indian)	Santhakumari et al. (1999)[a]

[a] These were identified as *Moerisia inkermanica*

Apart from Harrison (2010) and Meek et al. (2013), few genetic studies have examined worldwide populations of these hydrozoans, and future such studies will greatly improve our knowledge of their taxonomies and invasion histories.

The genus *Turritopsis* (Fig. 3.3c, d) consists of small hydromedusae that occur worldwide in temperate, subtropical, and tropical waters (Kramp 1961). This genus is well known due to a unique life history in which starving medusae can revert back to the benthic polyp stage, something that has earned *Turritopsis* a reputation as "the immortal jellyfish" (Bavestrello et al. 1992; Piraino et al. 1996). Molecular genetic analyses confirmed the presence of six valid, localized species of *Turritopsis*, with one of these species (*T. dohrnii*) likely introduced, since it occurred in the Mediterranean and Pacific (Miglietta et al. 2007). Miglietta and Lessios (2009) then employed molecular techniques to show *T. dohrnii* exists in the Caribbean Sea (Panama), Atlantic coast of the USA (Florida), Mediterranean (Mallorca and Italy), western Pacific (Japan), and eastern Pacific (Panama Bay).

3.2.3 Ctenophores

The ctenophores, or "comb jellies," are gelatinous zooplanktivores of the Phylum Ctenophora. Entirely holoplanktonic, the vast majority of them are simultaneous hermaphrodites capable of producing an extremely large number of embryos by self-fertilization or outcrossing (Reeve et al. 1989). Unlike the Scyphozoa, molecular studies have indicated extremely large native ranges, with molecular studies confirming the presence of some species in multiple ocean bodies (Podar et al. 2001; Bayha 2005).

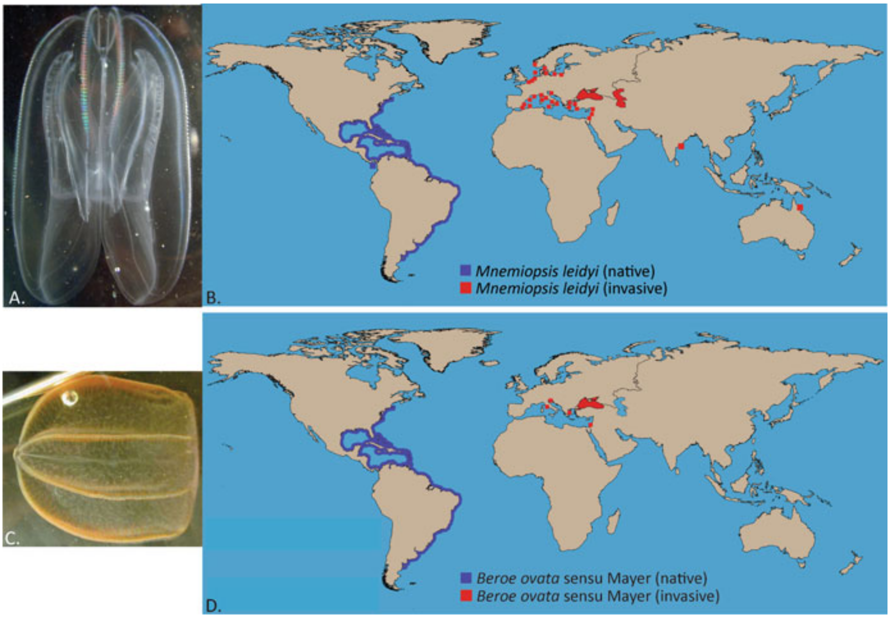

Fig. 3.4 (**a**–**d**) (**a**) *Mnemiopsis leidyi* collected from Fort Pierce, Florida. USA (Photographic credit K Bayha); (**b**) native and introduced ranges of *Mnemiopsis leidyi*. Literature identification of *M. leidyi* from Panama Bay (Agassiz 1892) is assumed to be a native population left over from the closing of the Isthmus of Panama, since it pre-dates the construction of the Panama Canal (1881–1914). Presence in Indian waters is uncorroborated, but presence in Australia was confirmed by photographic evidence (J. Seymour and K Bayha); (**c**) *Beroe ovata* sensu Mayer collected from Punta Gorda, Florida, USA (Photographic credit: K Bayha); (**d**) native and invasive ranges of *B. ovata* sensu Mayer

While few ctenophore species have been confirmed as introduced, the ctenophore *Mnemiopsis leidyi* is one of the most notorious of all gelatinous invaders.

Mnemiopsis leidyi (Fig. 3.4a, b; Table 3.6) is a lobate ctenophore native to estuarine and coastal waters of the Atlantic coasts of the Americas (GESAMP 1997). As a result of its high reproductive rate (Reeve et al. 1989) and predatory capabilities (Kremer 1979; Feigenbaum and Kelly 1984; Purcell et al. 1994; Purcell and Decker 2005), *Mnemiopsis* can exert controlling predation pressure on zooplankton populations (Feigenbaum and Kelly 1984; Kremer 1994; Purcell and Decker 2005) and impact economically important fish and shellfish species through competition for food and predation on their early life history stages (Purcell et al. 1991, 1994).

However, *Mnemiopsis* has gained a notorious reputation as an invasive species, as it has invaded multiple regions of Eurasia over the past 30 years (GESAMP 1997; Purcell et al. 2001b; Faasse and Bayha 2006). First encountered in the Black Sea in the 1980s, *Mnemiopsis* populations exploded in the 1980s, reaching a staggering average biomass of 1 kg m^{-2} (Vinogradov et al. 1989). From the Black Sea, *Mnemiopsis* spread to the adjacent Sea of Azov and Sea of Marmara, then into the

Table 3.6 Sightings of *Mnemiopsis leidyi* from the animal's introduced range

Region (major water body)	Reference
Crimean coast	Pereladov (1988)
Entire Black Sea	Vinogradov et al. (1989)
Sea of Azov	Vinogradov et al. (1989)
Sea of Marmara	Shiganova (1993)
Aegean Sea	Kideys and Niermann (1993)
Turkish coast (Northeastern Mediterranean)	Kideys and Niermann (1994)
Caspian Sea	Ivanov et al. (2000)
Israel (Mediterranean)	Galil et al. (2009)
Northern Adriatic Sea	Shiganova and Malej. (2009)
Italian coasts (Mediterranean)	Boero et al. (2009)
Spain (Mediterranean)	Fuentes et al. (2010)
Netherlands (North Sea)	Faasse and Bayha (2006)
Germany (North Sea)	Boersma et al. (2007)
Kiel Bight, Germany (Baltic Sea)	Javidpour et al. (2006)
Sweden (Baltic and North Sea)	Hansson (2006)
Norway (North Sea)	Oliveira (2007)
Denmark (North and Baltic Seas)	Tendal et al. (2007)
Belgium (North Sea)	Van Ginderdeuren et al. (2012)
Cairns, Australia (Pacific)	J. Seymour pers. comm.[a]

[a] This report was confirmed based on morphological analysis of photographs (K Bayha, pers. obs.)

Caspian Sea and the Mediterranean (Fig. 3.4b; Table 3.1). *Mnemiopsis* also appeared in the North Sea and Baltic Sea in 2006, with subsequent range expansions in both seas (Fig. 3.4b; Table 3.6). There have also been observations of *Mnemiopsis* in small numbers in the Pacific, including an uncorroborated sighting from India (Sai Sastry and Chandramohan 1989), Australia (with photographic corroboration; Bayha personal observation), and Panama (Agassiz 1892).

As *Mnemiopsis* is holoplanktonic, it was presumed from the beginning that *Mnemiopsis* arrived into Eurasian waters via ballast water from somewhere in the native range (Vinogradov et al. 1989). Several molecular studies have attempted to trace various introduced populations of *Mnemiopsis* to their native range(s), with two studies (Ghabooli et al. 2010; Reusch et al. 2010) showing the Black/Caspian and North/Baltic Sea invasions to be independent of each other. Both studies indicated the Black Sea invaders originated from the vicinity of the Gulf of Mexico, while the only study to include the southeast US Atlantic (Bayha 2005) indicated a potential source range between Cape Hatteras and the Gulf of Mexico. Both Reusch et al. (2010) and Ghabooli et al. (2010) showed the North/Baltic Sea invaders originated from New England waters in the USA.

Following the introduction of *Mnemiopsis leidyi* into the Black Sea came the introduction of another species of ctenophore, *Beroe ovata* sensu Mayer[1] (referred

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[1] We use the term *Beroe ovata* sensu Mayer in accordance with Bayha et al. (2004) to differentiate this species from *Beroe ovata* sensu Chun applied by Chun (1880), which is identical to the species *Beroe cucumis* Fabricius 1780. The commonly used term *Beroe ovata* Mayer 1912 is taxonomically incorrect since Mayer applied the name but did not describe the species.

to as *B. ovata* herein) (Fig. 3.4c, d), a species that feeds exclusively on *M. leidyi* (Mayer 1912; Mianzan 1999). Native to the eastern coast of the Americas, *B. ovata* can exert significant population pressure on *M. leidyi* populations (Burrell and van Engel 1976). In 1997, *B. ovata* was discovered in the Black Sea (Vinogradov et al. 2000) and subsequently in the Mediterranean Sea, the Aegean Sea (Shiganova et al. 2007), the northern Adriatic (Shiganova and Malej 2009), Italy (Occhipinti-Ambrogi et al. 2011), and Israel (Galil et al. 2011).

3.3 Invasiveness: Which Traits Make Jellyfish Effective Invasive Species?

Numerous studies on the ecology of bioinvasions have cataloged organismal traits that facilitate species' invasiveness (Lodge 1993; Kolar and Lodge 2001; Sakai et al. 2001; Milbau and Stout 2008), as well as empirically assessing their effectiveness (Kolar and Lodge 2001). Traits that facilitate invasiveness generally include reproductive and life history strategies, environmental tolerance, and trophic plasticity.

3.3.1 Reproductive and Life History Strategies

Jellyfish have the ability to reproduce rapidly, which likely facilitates their invasive capabilities. Invasiveness has been associated with high fecundity, rapid maturation, and single-parent reproduction (asexual reproduction and hermaphroditism) (Lodge 1993; Kolar and Lodge 2001; Sakai et al. 2001; Funk and Vitousik 2007).

The ability to reproduce uniparentally is likely paramount to the success of jellyfish as marine invaders, as the abilities to reproduce asexually or as a simultaneous hermaphrodite are common among successful bioinvaders (Lodge 1993; Kolar and Lodge 2001). Successful establishment in a new region is predicated upon sufficient propagule pressure or sufficient supply of individuals to overcome abiotic and biotic barriers and to form a self-sustaining population (Lockwood et al. 2005; Von Holle and Simberloff 2005; Simberloff 2009). Jellyfish reproductive strategies may decrease the propagule pressure necessary for successful establishment since hypothetically a single medusozoan polyp or ctenophore could establish an invasive population.

Sexual maturation in jellyfish can be rapid, and reproductive output can be extremely high, both typical characteristics of successful invasive species (Lodge 1993; Kolar and Lodge 2001; Funk and Vitousik 2007). Polyps form in a matter of days after settlement in the medusozoa (Rippingale and Kelly 1995; Rees and Gershwin 2000), and asexual reproduction can begin within 1–2 weeks (Rees and Gershwin 2000). Asexual propagation of additional polyps typically occurs continuously and can be extremely rapid, allowing medusozoan species to greatly increase benthic coverage (Purcell et al. 1999; Han and Uye 2010). While asexual reproductive output of ephyrae or medusa buds may differ based on how many are released at a time (Arai 1997; Fautin 2002; Rees and Gershwin 2000; Holst et al. 2007), many species are capable of releasing ephyrae or medusae multiple times throughout the year (Sugiura 1963; Hofmann and Honegger 1990; Lotan et al. 1992). For instance, *R. nomadica* may strobilate as many as 3–4 times per year (Lotan et al. 1992), and *Moerisia lyonsi* is capable of producing as many as 22 medusa buds day^{-1} almost continuously under the correct conditions (Purcell et al. 1999). Sexual reproductive output of medusae is directly related to medusa size in most species (Lucas 1996), but Ishii and Takagi (2003) estimated daily planulae production at as much as 58,300 planulae medusae^{-1} day^{-1} in *Aurelia* sp. 1. As for the ctenophores, larval reproduction in *Mnemiopsis leidyi* can occur as early as 8 days after hatching (Martindale 1987), but sexual maturation typically occurs as early as 14 days (Reeve and Walter 1978). Once sexually mature, *M. leidyi* is capable of producing thousands of eggs per day (Baker and Reeve 1974; Reeve et al. 1989) with very little energy investment, either through self-fertilization or outcrossing (see also Lucas and Dawson, Chap. 2).

The reproductive strategies employed by the medusozoa may also confer some evolutionary advantages, allowing for the maintenance of high genetic diversity, rapid propagation, and superior abilities to adapt to new conditions. The ability to reproduce both sexually and asexually has been associated with invasion success (Kolar and Lodge 2001; Sakai et al. 2001; Burns 2008). In a genetic study of *Maeotias marginata* and *Moerisia* sp. in San Francisco Bay, Meek et al. (2013) reported both high levels of genetic diversity and high indexes of asexual reproduction, with clonal lineages found geographically separated from one another. Their interpretation was that the combination of asexual and sexual reproduction allows the species to maintain high levels of genetic variation, allowing for the genetic flexibility to spread and adapt to new environmental conditions, while also providing the ability to rapidly propagate through asexual reproduction.

Life history strategies exhibited by jellyfish may make them exceptionally adept at surviving transport to and successfully establishing themselves in nonnative regions. Increased international shipping has been blamed for many recent marine bioinvasions in general, with ballast water transfer typically seen as the predominant dispersal mechanism (Carlton 1985; Carlton and Geller 1993; Wonham et al. 2001). Hull fouling or the transport of encrusting organisms on exposed surfaces of ocean-going cargo ships, slow-moving barges, floating dry docks, or oil rigs is mostly overlooked as a significant dispersal mechanism, even though it has been implicated in many invasions (Coles et al. 1999; Wasson et al. 2001; Godwin 2003; Drake and Lodge 2007), and estimates indicate the risk of invasion from hull fouling may be equal to or even greater than that posed by ballast water transport (Drake and Lodge 2007).

Ballast water transfer is likely the main vector only in holoplanktonic organisms such as ctenophores. Given self-fertilization, short generation times, ability to withstand long periods of starvation, and high reproductive output with little metabolic requirement (Baker and Reeve 1974; Reeve and Walter 1978; Martindale 1987), ctenophores could be pumped into ballast tanks as adults or larvae, withstand transit in a depressed feeding environment, and even reproduce further during transport. On the other hand, medusozoans are more likely to be transported as hull-fouling organisms (as polyps or cysts) on the exposed surfaces of ocean-going vessels. The cyst stage, specifically, could be vitally important, since this stage is extremely hardy and can withstand extreme environmental stress, metamorphosing into polyp form once environmental conditions are favorable (Arai 1997; Arai 2009). As some have noted, transport of the benthic stage seems a more logical vector for organisms with a bipartite life cycle (Larson and Arneson 1990; Calder 1993; Graham et al. 2003). The transport of ephyrae or medusae would necessitate an additional step, requiring sexual reproduction among invaders and effective settlement of planulae into polyps. The process of taking on and releasing ballast water might critically damage all but the smallest medusae.

The probability that the medusozoans invade in the benthic polyp stage is supported by two other arguments. The first line of evidence is the corridor of marine bioinvasions that existed between the Indo-Pacific and Hawaii following World War II. Shipping between these two regions, including slow-moving tugs and floating dry docks, has been implicated in the introduction of benthic hydroids, sponges, and anemones (Coles et al. 1999; Eldredge and Smith 2001). The appearances of at least two species of scyphozoans (*Cassiopea* and *Phyllorhiza*), one of which is benthic even as an adult, occurred during this time and may have invaded through this shipping exchange. Second, if the transport of a small number of asexually reproducing benthic polyps (or cysts) were to seed a long-term invasive population, perhaps a clonally reproducing one, genetic variation would likely decrease significantly due to a founder effect. A few established or likely invasions of the scyphozoan *Phyllorhiza* (Moreira 1961; Graham et al. 2003) and the hydrozoan *Moerisia* (Boulenger 1908) reported only male medusae, indicating possible clonal populations, though the fact that Meek et al. (2013) found high genetic diversity in *Moerisia* in San Francisco Bay could be explained by multiple invasions or one large event involving many individuals. In addition, Bayha et al. (unpublished data) encountered no genetic diversity in most nonnative populations of *Phyllorhiza*, each consisting of a single mitochondrial haplotype. In contrast to other medusozoans, the hydrozoan *Turritopsis* could either be introduced as a benthic polyp or via ballast water as a medusa then revert back to polyp form once in the introduced region (Bavestrello et al. 1992; Piraino et al. 1996).

3.3.2 Environmental Tolerance

The ability to survive over a wide range of environmental conditions and/or exhibit phenotypic plasticity in response to conditions is also common to invasive organisms (Lodge 1993; Milbau and Stout 2008; Richards et al. 2006; Smith 2009). Many jellyfish species exhibit considerable eurytopic properties that likely aid their abilities to survive and reproduce in a range of environmental conditions. The scyphozoan *A. aurita* can be found in salinities of 13–33 and temperatures of −2 to 23 °C

(Lucas 2001). The ctenophore *M. leidyi* can survive in waters of 1.3–32 °C and salinities of 3.4–75 (reviewed in GESAMP 1997), though its lower reproductive limit appears to be about 10 °C (Purcell et al. 2001b, Costello et al. 2006). The widespread hydrozoans *B. virginica* and *Moerisia* sp. can tolerate salinities of 3–35 and 1–40, respectively (Moore 1987; Purcell et al. 1999), although optimal recruitment in San Francisco Bay was 14.9–22.2 for *B. virginica* and 4.6–21.8 for *Moerisia* sp. (Wintzer et al. 2011c). Laboratory experiments on *B. ovata* have indicated that it would successfully survive and reproduce in the lower salinity waters (~12) of the Caspian Sea, where there are calls for intentional introduction to control *Mnemiopsis leidyi* populations (Kideys et al. 2004; Finenko et al. 2011). In addition, many jellyfish species have been shown to be extremely tolerant of low dissolved oxygen levels (Condon et al. 2001, Purcell et al. 2001a, Decker et al. 2004; Shoji et al. 2005; Thuesen et al. 2005; Ishii et al. 2008). On the other hand, some species, such as *Phyllorhiza punctata* (Rippingale and Kelly 1995), *Rhopilema nomadica* (Lotan et al. 1992), and *Mastigias papua* (Dawson et al. 2001), have shown evidence of more narrow salinity and/or temperature tolerances, potentially restricting invasion possibilities to environments similar to their native ranges.

3.3.3 Feeding Strategies

Many species of jellyfish are generalist feeders, allowing them to take advantage of a wide range of novel prey items in a new environment, something also correlated with invasion success (Lodge 1993). One of the best examples is *M. leidyi*, which can consume microplankton as small as tintinnids and other ciliates, as well as larval copepods and bivalves, large adult copepods, and fish larvae (Larson 1987; Monteleone and Duguay 1988; Tzikhon-Lukanina et al. 1991, 1992; Granhag et al. 2011). Likewise, *Aurelia aurita* feeds on planktonic ciliates, all stages of copepods, and fish larvae (Möller 1980; Stoecker et al. 1987). Both *Maeotias marginata* and *Moerisia* sp. were found to ingest a wide range of planktonic organisms in San Francisco Bay, from copepod and barnacle nauplii to adult copepods, mysids, cumaceans, and fish larvae (Wintzer et al. 2011b). While Purcell et al. (1999) did not find ciliate predation in laboratory experiments by *Moerisia* sp., it cannot be discounted since Wintzer et al. (2011b) showed predation on prey items (barnacle nauplii) not ingested in laboratory studies of Purcell et al. (1999). *Phyllorhiza punctata* primarily feeds on invertebrate larvae, but it can also feed on ciliates and adult copepods (Garcia and Durbin 1993; Graham et al. 2003; Peach and Pitt 2005). In addition, three nonindigenous genera of rhizostome jellyfishes (*Cassiopea*, *Mastigias*, and *Phyllorhiza*) are capable of photosymbiosis through symbiotic zooxanthellae in their oral arms, allowing for energy procurement in addition to what they obtain through predation (Mayer 1910; Arai 1997). An exception to this pattern of polyphagy, however, is *Beroe ovata*, which feeds solely on *Mnemiopsis leidyi* and, therefore, has only been introduced to areas with *M. leidyi* populations (Fig. 3.4b).

3.4 Invasibility: Which Characteristics Make Ecosystems More Susceptible to Jellyfish Introductions, and Do Human Activities Increase the Invasibility of Ecosystems?

Another focus of invasion ecology has been to examine the characteristics of heavily invaded ecosystems in order to determine which characteristics might make one ecosystem more susceptible to invasion than another (invasibility) and, conversely, which characteristics might result in an ecosystem being resistant to invasions (Lodge 1993; Lonsdale 1999; Alpert et al. 2000; Sakai et al. 2001). Here, we will consider how community structure and ecological interactions and disturbance regimes, all factors in community invasibility (Lodge 1993; Alpert et al. 2000; Sakai et al. 2001; Arenas et al. 2006), might impact an ecosystem's invasibility to marine jellyfishes.

3.4.1 Community Structure and Ecological Interactions

Highly invaded ecosystems commonly have lower than average species diversity, something that led many to conclude that high species diversity necessarily makes a community less invasible (Elton 1958; Lodge 1993; Kolar and Lodge 2001). However, other analyses have not supported this argument (Levine and D'Antonio 1999), and some have focused more on the role of a community's functional diversity or "trait spectrum" in determining invasibility (Sakai et al. 2001, Symstad 2000). Along the same lines, high resource availability has been correlated with invasion success (Tilman 1999; Alpert et al. 2000). Therefore, a high strength of competitive interactions within a community might render it less susceptible to invasion, as a diverse community with intense levels of competition among consumers would likely result in a lowered level resource availability. Additionally, less diverse communities may lack the diversity of predators and/or parasites to control invaders (Sakai et al. 2001; Torchin and Lafferty 2009). In many cases, being functionally "novel" or different from native organisms makes an invader more successful in the recipient ecosystem, and the chance to be "novel" is higher for regions with low functional diversity (Strayer 2012). These factors have been invoked to explain higher than average invasions in "naïve" island ecosystems (Elton 1958; Lonsdale 1999), but may also come into play regarding sheltered estuarine and inland sea ecosystems (Paavola et al. 2005; Preisler et al. 2009).

These hypotheses may explain the success of a few jellyfish invasions in estuarine and inland seas. The ctenophore *Mnemiopsis leidyi* invaded a Black Sea ecosystem devoid of predators and parasites (Purcell et al. 2001b), with relatively weak competition from native zooplanktivores. Competition from zooplanktivorous fishes in the late 1980s was likely low as a result of overharvesting (Daskalov et al. 2007) (see Sect. 3.4.2), and competition from other zooplanktivores, such as the scyphomedusa *Aurelia aurita* and chaetognath *Sagitta setosa*, was also likely weak, since *Mnemiopsis* outcompeted them handily in the early years of the *Mnemiopsis* bloom, such that *Aurelia* abundances dropped precipitously and *Sagitta* disappeared almost completely (Vinogradov and Shushkina 1992). However, the later introduction of *Beroe ovata*, an effective *Mnemiopsis* predator, helped control *Mnemiopsis* populations (Shiganova et al. 2001; Shiganova et al. 2004). In contrast, the *Mnemiopsis*-invaded North and Baltic Seas contain two native predators, the scyphozoan *Cyanea capillata* and the ctenophore *Beroe gracilis*, that actively feed on *Mnemiopsis*, as well as an invasive parasite (the larvae of *Edwardsia lineata*), all of which may have mitigated the animal's blooming magnitudes and overall impacts (Hosia and Titelman 2010; Selander et al. 2010; Hosia et al. 2011). Brackish waters of the upper San Francisco Estuary previously contained no hydromedusae before *Blackfordia virginica*, *Maeotias marginata*, and *Moerisia* sp. were introduced, and their abundances have increased over the past 10 years, with concomitant decreases in many species of zooplankton and zooplanktivorous fishes (Schroeter 2008; Wintzer et al. 2011a). A functional equivalent did not exist in the Mediterranean Sea before the introduction and spread of *Cassiopea andromeda* (Fig. 3.2b), though more ecological studies are required to determine if the success of *Rhopilema nomadica* and *Phyllorhiza punctata* in the Mediterranean may be related to any novel functional aspects or competitive superiority compared to native zooplanktivores.

3.4.2 Disturbance Regimes

Disturbance, especially anthropogenic disturbance, increases ecosystem invasibility (Byers 2002), and there is strong evidence that jellyfish populations thrive in such degraded systems (reviewed in Purcell et al. 2007; Purcell 2012). Overharvesting of fish and shellfish may decrease the competitive or predatory influence of the fished species, which may increase the ecosystem's susceptibility to invasion, such as the release of competition from zooplanktivorous fishes of *Mnemiopsis leidyi* in the Black Sea (Daskalov et al. 2007). Overharvesting of shellfish may have a similar effect, as Sullivan et al. (1991) showed that a reduction in benthic consumers benefits gelatinous zooplankton.

Eutrophication and resultant hypoxia may favor invasive organisms by detrimentally affecting natives (Byers 2002). In the case of jellyfishes, nutrient loading may benefit jellyfish populations by increasing their prey populations of herbivorous zooplankton. Populations of the photosymbiotic jellyfish *Cassiopea* are larger adjacent to urban areas with increased nutrient runoff (Stoner et al. 2011). Coastal eutrophication has been shown to lead to smaller zooplankton sizes, which would likely favor nonvisual predators (jellyfishes) over visual predators (zooplanktivorous fishes) (Uye 1994; Purcell et al. 2007). Increased turbidity from coastal eutrophication has been shown to benefit *Aurelia* sp. 1 over jack mackerel when comparing abilities to feed on anchovy larvae (Ohata et al. 2011). Jellyfish appear to be less susceptible to low dissolved oxygen levels (Purcell et al. 2001a), so hypoxic conditions resulting from eutrophication may affect gelatinous organisms to a much lesser extent than other organisms, giving them a competitive and predatory advantage (Shoji et al. 2005). Benthic scyphozoan polyps are tolerant of low oxygen levels (Condon et al. 2001), and Miller and Graham (2012) indicate that seasonal hypoxia may enhance jellyfish populations in the Gulf of Mexico by benefiting their benthic polyp populations.

Elevated ocean temperatures from global climate change may promote distributional expansion and new invasion vectors (Occhipinti-Ambrogi 2007; Lonhart 2009). While it is difficult to generalize about the potential effects of climate change on global jellyfish populations, given that optimal temperature ranges vary among species (Purcell 2005), it is likely that any increases in seawater temperatures may strengthen invaders' abilities to invade waters currently at their temperature minimum, potentially allowing *R. nomadica* and *C. andromeda* to disperse further west in the Mediterranean beyond the current extent thought to be limited by temperature tolerance (Lotan et al. 1992; Deidun et al. 2011). Similarly, while the invasion of *Mnemiopsis* into the Baltic Sea was predicted years ago (Gollasch and Leppäkoski 1999), its success in the North and Baltic Seas followed years of increasing North Sea temperatures, indicating that temperature may have reached a minimum threshold allowing for successful *Mnemiopsis* population increases (Faasse and Bayha 2006).

3.5 Impacts: Which Nonindigenous Jellies Exert Ecological and Economic Impacts, and Do Nonnative Jellies Significantly Enhance the Intensity of Global Jellyfish Blooms?

Organismal traits of invaders (invasiveness) and environmental and ecological aspects of the invaded ecosystem (invasibility) interact to determine whether or not nonindigenous species will establish themselves in the long term and/or reach population magnitudes that have ecological impacts on the recipient ecosystem. Many species of introduced jellyfishes have reached high population abundances in recipient ecosystems, resulting in substantial ecological and economic impacts.

3.5.1 Impacts of Invasive Jellyfish Populations

The most cited example of a jellyfish invasion exerting negative impacts on an ecosystem is *Mnemiopsis leidyi* in the Black Sea (GESAMP 1997; Purcell et al. 2007; Costello et al. 2012). When populations reached bloom magnitudes throughout the Black Sea in the late 1980s (Vinogradov et al. 1989), the populations of mesozooplankton fed on by *Mnemiopsis* plummeted (Vinogradov and Shushkina 1992) and harvest of zooplanktivorous fishes such as the anchovy *Engraulis encrasicolus* declined dramatically (Kideys 1994; GESAMP 1997; Kideys 2002). In the Caspian Sea, zooplankton biomass and diversity decreased markedly (Stone 2005; Finenko et al. 2006), and harvest of *Clupeonella* sp. dropped precipitously (Kideys 2001a, b as cited in Kideys 2002; Stone 2005) following the introduction of *Mnemiopsis*. Food competition and direct predation on fish eggs and larvae were blamed (Vinogradov and Shushkina 1992; Tzikhon-Lukanina et al. 1992; Zaika 1993; GESAMP 1997), with attributed losses estimated in the hundreds of millions of US dollars in the Black Sea (GESAMP 1997, reviewed in Knowler 2005). However, later analyses have indicated a more complex interplay between environmental variables, overfishing, and pollution, in addition to the *Mnemiopsis* invasion (Gücü 2002; Bilio and Niermann 2004; Oguz et al. 2008), and economic losses directly attributed to *Mnemiopsis* have been calculated to be far less than previous estimates (Knowler 2005). While the situation in the Black Sea has generally improved (Kideys 2002), the effects of *Mnemiopsis* populations are likely still significant, given its ecological and economic influence even in its native range (Feigenbaum and Kelly 1984, Purcell et al. 2001b). Although *Mnemiopsis* does reach bloom proportions in the North Sea and Baltic Sea, given the presence of native predators and an invasive parasite that will feed on *Mnemiopsis* (Sect. 3.5.1), there is hope that it will not inflict the ecological and economic damage scientists feared when it was found in 2006 (Faasse and Bayha 2006; Javidpour et al. 2006). The main concern was that *Mnemiopsis* predation would impact the catches of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*), two economically important species (Haslob et al. 2007). However, laboratory experiments (Hamer et al. 2011; Jaspers et al. 2011) and stable isotope data (Hamer et al. 2011) have shown that these fish stocks are not vulnerable to direct *Mnemiopsis* predation.

The appearance of *Rhopilema nomadica* on the Mediterranean side of the Suez Canal resulted in a constant spread of the animal across the Levantine coast, forming large, yearly blooms in the eastern Mediterranean, with major repercussions to fishing and tourism industries, as well as power plants (Galil 2007, 2010). These large blooms can extend for kilometers during the summer months and clog fishing nets and temporarily close fishing grounds (Galil 2007; Ozturk and Isinibilir 2010). Also, *R. nomadica* packs an extremely painful sting (Gusmani et al. 1997), and blooms can close beaches with economic loss to the tourist industry (Galil et al. 1990; Kideys and Gücü 1995; Galil 2010; Ozturk and Isinibilir 2010). Lastly, large blooms of *R. nomadica* have clogged seawater intakes, necessitating the temporary closure of power plants in the eastern Mediterranean in 2001 and 2010 (Galil 2007, 2010).

While the jellyfish *Phyllorhiza punctata* has been introduced to regions in the Pacific, Atlantic, and Mediterranean, it has really only reached blooming magnitudes in two regions. The blooms encountered in the northern Gulf of Mexico in 2000 were responsible for closing local fisheries and resulted in economic impacts approaching $10 million (Graham et al. 2003), though significant blooms have not been reported since in the Gulf of Mexico or adjacent US Atlantic coasts. The reappearance of *Phyllorhiza* in the Mediterranean (Abed-Navandi and Kikinger 2007;

Galil et al. 2009) has resulted in the animal spreading further west, and it appears that *Phyllorhiza* is assuming a role as a blooming nuisance species in the Mediterranean similar to that shown by *Pelagia noctiluca* (Goy et al. 1989) and *Rhopilema nomadica* (Galil 2007). Blooms of *Phyllorhiza* recently have closed beaches along the Spanish coast (V. Fuentes pers. comm.).

While *Aurelia* is one of the most studied jellyfish genera and its impacts around the world are well known (Purcell et al. 2007), many of the species that have been introduced around the world have yet to be adequately studied in their introduced ranges. In its various native ranges, *Aurelia* is well known as a blooming species that can reach concentrations great enough to have significant anthropogenic effects, such as clogging fishing nets and blocking power plant intakes (reviewed in Purcell et al. 2007). The invasive species *Aurelia* sp. 1 is especially notorious for shutting down power plants, having done so in its native range in Japanese waters (reviewed in Purcell et al. 2007) as well as in its introduced range in California waters (Stewart 2008). Whether or not nonindigenous populations of *Aurelia* sp. 4 (Mediterranean), *Aurelia* sp. 7 (Hawaii), or *Aurelia aurita* (Chile and Caspian Sea) will exert ecological and economic pressure is unknown, though the presence of a novel gelatinous organism, such as *A. aurita*, in the Caspian Sea, an extremely isolated water body with a high level of endemic species, is definitely worrisome.

The three Pontocaspian hydrozoan species discussed here (*Blackfordia virginica*, *Maeotias marginata*, and *Moerisia* sp.) have spread widely around the world, though actual economic and ecological impacts have only been documented in a few regions. While previous indications were that these three species exhibited minor effects on invaded ecosystems (e.g., Graham and Bayha 2007), apart from fouling culturing mesocosms (Sandifer et al. 1974), they have shown a more recent propensity for reaching high abundances, exhibiting significant predatory pressure and competing with fish populations. Abundances of all three species have steadily increased in the upper San Francisco Bay (Schroeter 2008). Wintzer et al. (2011a) indicated that *Moerisia* sp. and *M. marginata* may exert a controlling influence over their prey, as indicated by a negative correlation between medusae density and prey abundance. Additionally, food competition with zooplanktivorous fishes was indicated by a negative correlation between *Moerisia* sp. density and fish stomach fullness (Wintzer et al. 2011a), potentially adding to other stressors (urban development, nutrient runoff, water management, and other invasive species) driving a sharp decline in copepod abundances and populations of various fish species in the San Francisco Estuary (reviewed in Wintzer et al. 2011a). In a Portuguese estuary, *B. virginica* feeds voraciously on eggs of the anchovy *Engraulis encrasicolus*, and large medusae density coincided with extremely low abundances of all zooplankton prey, as well as anchovy eggs, indicating the medusae blooms may heavily impact this ecologically and economically important fish (Chicharo et al. 2009).

While *Beroe ovata* (Fig. 3.4b, c) populations have been relatively modest where they have been introduced, they likely have an ameliorating effect on their invaded ecosystems, regions that also include its only prey item, *Mnemiopsis* (Mayer 1912; Mianzan 1999). When *B. ovata* was introduced to the Black Sea, *Mnemiopsis* populations decreased significantly (Shiganova et al. 2001; Shiganova et al. 2004). There was a concomitant increase in zooplankton populations, including fish eggs and larvae, the conclusion being that predation on *M. leidyi* may have released some of the predation pressure it had placed on the zooplankton populations (reviewed in Purcell et al. 2001b, Shiganova et al. 2004; Gordina et al. 2005). Given the impact *B. ovata* has had in the Black Sea, the possibility of purposeful introduction into the Caspian Sea has been considered, and studies have indicated that *Beroe* can successfully survive, feed on *Mnemiopsis*, and reproduce in Caspian Sea water (Kideys et al. 2004; Finenko et al. 2011).

The swift spread of the epibenthic *Cassiopea* sp. through the Mediterranean with large local abundances in some areas has some people advising the species be monitored closely. However, a compelling case for it having massive impacts in introduced ranges has not been made. Özgür and Öztürk (2008) found high abundances near Fethiye, Turkey, on the Mediterranean coast and postulated that *Cassiopea* abundance and stinging ability might impact tourism. Stoner et al. (2011) found denser populations and larger sizes of *Cassiopea* sp. near urban areas on Abaco Island, Bahamas, as opposed to nonurban areas, and postulated that these higher abundances might compete with other zooplanktivores for food, compete with benthic flora for light, and affect nutrient cycling in these regions.

3.5.2 Do Nonindigenous Jellyfish Significantly Contribute to the Intensity Global Jellyfish Blooms?

There is comparatively little information on whether or not nonnative jellies actually are adding to jellyfish bloom magnitudes in the ecosystems they have invaded. There has been increasing interest regarding whether or not jellyfish blooms are increasing in magnitude worldwide in response to anthropogenic perturbations (Mills 2001; Purcell et al. 2007; Brotz et al. 2012; Condon et al. 2012; Purcell 2012). Condon et al. (2012) found that current data sets are inconclusive in supporting this hypothesis, but Brotz et al. (2012) analyzed historical data from Large Marine Ecosystems (LMEs) and found that about 42 % of them (28 of the 66 analyzed) showed increasing trends in jellyfish blooms since the 1950s. The analyses found that, for six of the LMEs, the inclusion of nonindigenous species was the difference in declaring the regions as increasing in jellyfish bloom magnitude (Gulf of Mexico, Southeast US Continental Shelf, Caribbean Sea, Baltic Sea, East Brazil Shelf, and Insular Pacific-Hawaiian LME) (Brotz et al. 2012).

Of the 13 species of jellyfish we have profiled, six of them have been shown to reach bloom magnitudes in at least one nonnative region (Sect. 3.2). However, apart from *M. leidyi* in the Baltic Sea and *P. punctata* in the Gulf of Mexico, Brotz et al. (2012) did not attribute overall increases in jellyfish bloom magnitudes to introduced jellies in regions where these invaders have bloomed. It is possible that in many cases, blooms of invaders may simply be substituting themselves for native jellyfish species, as was the case for *Mnemiopsis* taking the place of *Aurelia aurita* at the beginning of the Black Sea invasion (Vinogradov and Shushkina 1992), though additional studies are necessary to fully examine this possibility.

3.6 Conclusions

In recent years, there has been increased interest in jellyfish bloom formations that can incur significant ecological and economic impacts, including analyses of biological adaptations, as well as ecological features and anthropogenic alterations that support bloom formation. However, many of the most important jellyfish blooms have involved species occurring in regions outside their native ranges. Many of the biological and environmental factors that allow marine jellyfishes to establish themselves in new regions and exert ecological and/or economic impacts also make them ideal marine bioinvaders. As scientific expertise for studying the marine jellyfishes, either through traditional morphological/ecological techniques or the use of molecular genetic analyses, has increased, our ability to identify, track, and examine jellyfish invasions has also increased. Future use of these techniques will undoubtedly fundamentally alter our understandings of currently recognized invasive species, their impacts on invasive ranges, and roles in jellyfish blooms as well as uncover previously unrecognized invasions.

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Chapter 4
Bloom and Bust: Why Do Blooms of Jellyfish Collapse?

Kylie A. Pitt, Ariella Chelsky Budarf, Joanna G. Browne, and Robert H. Condon

Abstract Research on jellyfish blooms has focused heavily on the factors influencing the production of blooms. Identifying the factors that cause blooms to collapse, however, is important for predicting the duration of blooms and when they are likely to disappear. We assembled studies from the literature to assess the persistence of populations of medusae, the timing of the disappearance of the populations and the potential cause of the populations' declines. We found 76 observations that met our criteria for inclusion that were derived from 33 studies and included 47 different taxa. Most populations exhibited strongly seasonal patterns of occurrence, but the population dynamics of the same or closely related species varied greatly across small spatial and temporal scales. Duration of occurrence was negatively related to latitude, but latitude explained only 8 % of the total variability, and no relationship existed when tropical species were excluded from the analysis. Senescence after spawning, infestations of parasites, food limitation, disease, low salinity, extreme water temperatures, predation and intertidal stranding were most commonly cited as causing blooms to collapse. Improving understanding of when and why blooms collapse will benefit coastal industries that are affected by blooms and greatly improve our understanding of how jellyfish blooms impact the ecology of the systems they inhabit.

Keywords Jellyfish blooms • Cnidarians • Biogeochemical cycling • Jelly-falls • Population dynamics • Feeding ecology • Parasitism • Hyperiid amphipods • Digenean trematodes • Physiological tolerance • Catabolism

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4.1 Introduction

Jellyfish (i.e. cnidarian medusae and ctenophores) are renowned for their ‘boom and bust’ population dynamics. Prolific rates of production, coupled with growth rates (based on wet weight) that are two to three times those of non-gelatinous pelagic taxa (Pitt et al. 2013), can result in the seemingly sudden appearance of conspicuous, and often spectacular, population blooms. The biomass of blooms regularly exceeds 10 t wet weight 100 m^{-3} (Lilley et al. 2011). Typically, however, blooms are short-lived, sustained for periods of weeks to months, after which the populations disappear, often abruptly (i.e. collapse).

Concern regarding the perceived global increase in jellyfish blooms, coupled with their potential negative ecological and socioeconomic impacts, has, over the past two decades, seen a surge in studies that have tried to identify the causes of blooms (see Condon et al. 2012). Identifying natural and anthropogenic causes of blooms is important for predicting bloom events, developing potential management or eradication strategies and forecasting how jellyfish populations may respond to changing ocean conditions. However, such enormous fluctuations in biomass (both appearance and disappearance) are likely to have major influences on the ecology of marine systems. For example, the disappearance of what is often the dominant predator of zooplankton releases predation pressure on zooplankton and may initiate trophic cascades. Jellyfish also provide shelter to juvenile fish and invertebrates and, therefore, may influence recruitment and population dynamics of such taxa (see Doyle et al., Chap. 5). The sudden disappearance of jellyfish also has major implications for biogeochemical cycling because jellyfish turn over large quantities of assimilated material as carbon-rich dissolved organic material, which is shunted toward rapid uptake and respiration by specific microbial phylotypes (Condon et al. 2011). Because microbial respiration converts potential food web energy into a form that can only be utilised by autotrophs (i.e. carbon dioxide), this detour of carbon represents a diversion of carbon away from higher trophic levels. Following the collapse of blooms, therefore, the transfer of carbon to higher trophic levels may be restored. Moreover, microbial respiration associated with decomposition of medusae can create an oxygen demand that exceeds the rate of oxygen resupply, resulting in localised hypoxia or anoxia (Pitt et al. 2009a). Consequently, understanding the causes of declines, the timing and locations where blooms collapse and the ecological and biogeochemical consequences of bloom collapses is equally as important as understanding the production of blooms.

Senescing jellyfish typically exhibit increased rates of physical damage, loads of parasites and rates of infection (Mills 1993). The pattern of mortality varies little among taxa and usually involves degeneration of the tentacles, oral structures and gonads, reduced swimming ability and, finally, necrosis of the epithelial tissues of the bell (Brewer 1989; Kikinger 1992). The fate of moribund jellyfish is poorly known, but their specific density exceeds that of seawater and also living jellyfish (Yamamoto et al. 2008) suggesting that they are likely to sink rapidly. The observation of largely intact moribund jellyfish on the seafloor, so-called jelly-falls (Lebrato et al. 2012), supports this argument. Rapid sinking of medusae may accelerate regional rates of carbon export from surface waters in open ocean regions (Yamamoto et al. 2008; Lebrato and Jones 2009) and increase transfer efficiency of the biological pump to the deep sea (Billett et al. 2006). For example, Billett et al. (2006) observed in the Arabian Sea the massive 'jelly-flux' of *Crambionella orsini* carcasses at 3,000 m following a surface bloom, which contained an order of magnitude more carbon than the total annual carbon flux as measured by sediment traps. Given the dearth of long-term time series of jellyfish communities and their biogeochemical influences in the open ocean (Condon et al. 2012), it is unclear on what spatial and temporal scales jelly-falls occur and how they are linked to 'boom and bust' dynamics of jellyfish blooms, although recent information suggests that jelly-falls are prevalent in coastal areas and oligotrophic gyres (Yamamoto et al. 2008; Lebrato et al. 2012) and have occurred over geological timescales (Hagadorn et al. 2002; Condon et al. 2012). Similarly, information on how jelly-falls relate to carbon export processes are sparse (but see Lebrato et al. 2013) but jellyfish size, density and shape, physical advection and microbial decomposition (Riemann et al. 2006; Tinta et al. 2012; Lebrato et al. 2013) are likely the primary driving factors influencing sinking of jellyfish blooms (Lebrato et al. 2011).

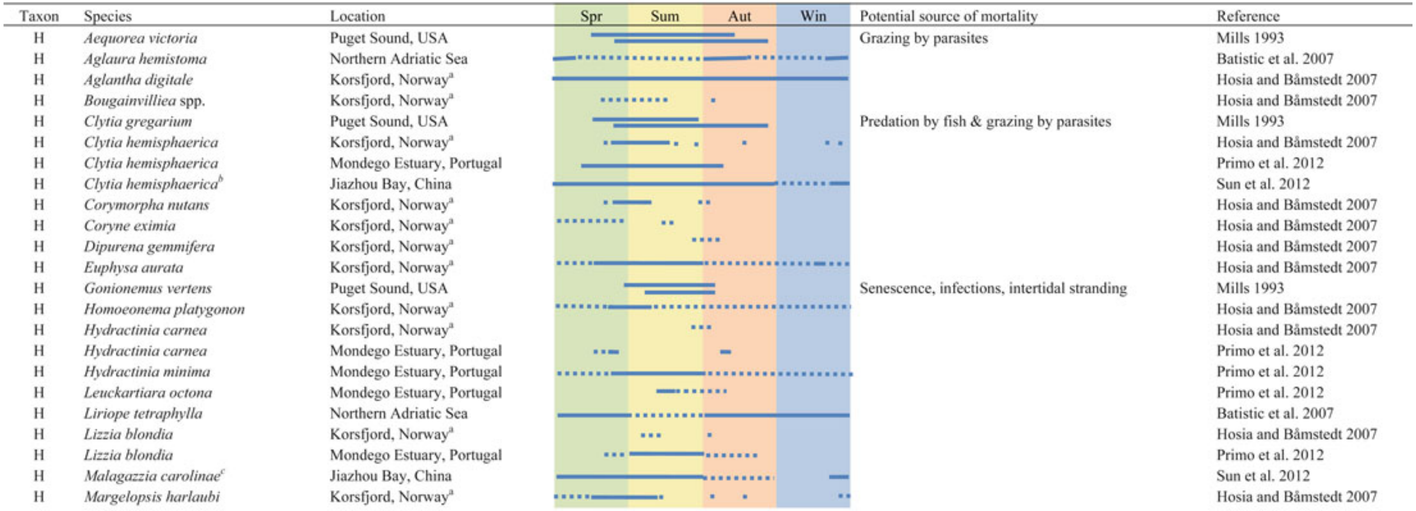
The major objective of this chapter is to analyse the literature to elucidate temporal and spatial trends in the persistence of jellyfish populations and to identify the major causes of declines in jellyfish populations. The major drivers identified as causing blooms to collapse are then reviewed.

4.2 Literature Analysis

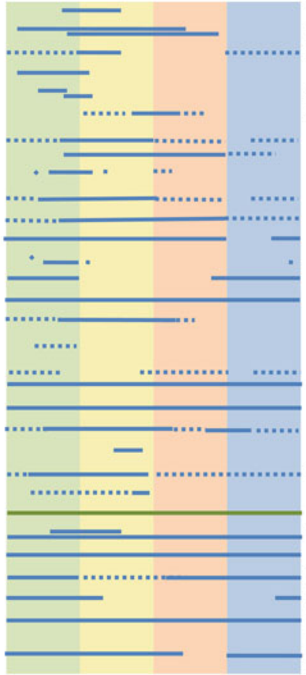
We searched the literature for studies of population dynamics to assess the persistence of the population, timing of the disappearance of the population and the potential cause of the population's decline. Although ctenophores are usually considered 'jellyfish', they were not included in the analysis because their populations are typically restocked annually from overwintering populations (Costello et al. 2006) indicating that at least some of the population is perennial. Only studies that sampled medusae at intervals of less than 2 months and that sampled for ≥1 year, or that sampled from before the initial appearance of the population and until after the population had disappeared, were included. A linear regression was used to test whether the duration of the occurrence of populations was related to latitude. The duration of the population was determined by the period when medusae were abundant (i.e. rare occurrences were excluded; Table 4.1).

Our analysis found 76 observations that met our criteria and included 44 observations of hydrozoans (including four siphonophores) and 32 observations of scyphozoans (Table 4.1). The observations were derived from 33 studies and included 47 different taxa. Only eight observations were derived from the southern hemisphere

Table 4.1 Patterns of occurrence of medusae (and ephyrae when reported) and potential source of mortality for the population or for individuals within the population. Lines indicate duration of occurrence. *Dashed lines* indicate that medusae or ephyrae were rare (as defined or stated by author). *Blue lines* = northern hemisphere, *green lines* = southern hemisphere (seasons in the table refer to the appropriate season in the respective hemisphere). A single line per entry indicates that only 1 year was sampled; patterns were identical between years or indicate a general pattern if ≥ 2 years sampled. Two lines for a given entry represent differences in patterns of occurrence during each year



Taxon	Species	Location	Spr	Sum	Aut	Win	Potential source of mortality	Reference
H	*Aequorea victoria*	Puget Sound, USA					Grazing by parasites	Mills 1993
H	*Aglaura hemistoma*	Northern Adriatic Sea						Batistic et al. 2007
H	*Aglantha digitale*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Bougainvilliea* spp.	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Clytia gregarium*	Puget Sound, USA					Predation by fish & grazing by parasites	Mills 1993
H	*Clytia hemisphaerica*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Clytia hemisphaerica*	Mondego Estuary, Portugal						Primo et al. 2012
H	*Clytia hemisphaerica*[b]	Jiazhou Bay, China						Sun et al. 2012
H	*Corymorpha nutans*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Coryne eximia*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Dipurena gemmifera*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Euphysa aurata*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Gonionemus vertens*	Puget Sound, USA					Senescence, infections, intertidal stranding	Mills 1993
H	*Homoeonema platygonon*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Hydractinia carnea*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Hydractinia carnea*	Mondego Estuary, Portugal						Primo et al. 2012
H	*Hydractinia minima*	Mondego Estuary, Portugal						Primo et al. 2012
H	*Leuckartiara octona*	Mondego Estuary, Portugal						Primo et al. 2012
H	*Liriope tetraphylla*	Northern Adriatic Sea						Batistic et al. 2007
H	*Lizzia blondia*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007
H	*Lizzia blondia*	Mondego Estuary, Portugal						Primo et al. 2012
H	*Malagazzia carolinae*[c]	Jiazhou Bay, China						Sun et al. 2012
H	*Margelopsis harlaubi*	Korsfjord, Norway[a]						Hosia and Båmstedt 2007



H	*Mitrocoma cellularia*	Saanich Inlet, Canada	Warm water temperature	Larson 1986
H	*Mitrocoma cellularia*	Puget Sound, USA	Grazing by parasites	Mills 1993
H	*Mitrocomella polydiademata*	White Sea, Russia	Died post-spawning	Pertsova et al. 2006
H	*Mitrocomella polydiademata*	Saanich Inlet, Canada		Larson 1986
H	*Mitrocomella polydiademata*	Puget Sound, USA	Possible medusivory by *Aequorea victoria*	Mills 1993
H	*Moerisia* sp.d	San Francisco Bay, USA	Cool water & senescence	Wintzer et al. 2011
H	*Muggiaea atlantica*	Mondego Estuary, Portugal		Primo et al. 2012
H	*Muggiaea atlantica*	Jiazhou Bay, China		
H	*Obelia* spp.	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
H	*Obelia* spp.	Mondego Estuary, Portugal		Primo et al. 2012
H	*Obelia* sp.	Jiaozhou Bay, China		Sun et al. 2012
H	*Podocorynoides minima*[e]	Jiaozhou Bay, China		Sun et al. 2012
H	*Rathkae octopunctata*	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
H	*Rathkae octopunctata*	Jiaozhou Bay, China		Sun et al. 2012
H	*Rhopalonema velatum*	Northern Adriatic Sea		Batistic et al. 2007
H	*Solmaris corona*	Mondego Estuary, Portugal		Primo et al. 2012
H	*Tiaropsis multicirrata*	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
SP	*Diphyes* spp.	Mondego Estuary, Portugal		Primo et al. 2012
SP	*Dimophyes arctica*	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
SP	*Lensia conoidea*	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
SP	*Nanomia cara*	Korsfjord, Norway[a]		Hosia and Båmstedt 2007
S	*Aurelia aurita*	Thames Estuary, UK		Attrill and Thomas 1996
S	*Aurelia aurita*	Elefsis Bay, Greece	Food limitation	Papathanassiou et al 1987
S	*Aurelia aurita*	southern North Sea		Barz and Hirche 2007
S	*Aurelia aurita*	Port Phillip Bay, Australia		Fancett 1986
S	*Aurelia aurita*	Tomales Bay, USA	Died post-spawning	Hamner and Jenssen 1974
S	*Aurelia aurita*	Jellyfish Lake, Palau		Hamner et al. 1982
S	*Aurelia aurita*	Tapong Bay, Taiwan	Low salinity	Lo and Chen 2008
S	*Aurelia aurita*	Southampton Water, UK	Died post-spawning	Lucas and Williams 1994
S	*Aurelia aurita*	Horsea Lake, UK	Died post-spawning	Lucas 1996
S	*Aurelia aurita*	Kiel Bight, Germany	Food limitation, grazing by parasites, dies post-spawning	Möller 1980

(continued)

Table 4.1 (continued)

Taxon	Species	Location	Spr	Sum	Aut	Win	Potential source of mortality	Reference
S	*Aurelia aurita*	Black Sea	━	━	━	━		Mutlu 2001
S	*Aurelia aurita*	Eckenford Bay, Germany[f]	━	━	━			Schneider and Behrends 1994
S	*Aurelia labiata*	Roscoe Bay, Canada	━	━	━	━	No visible mortality but some advection	Albert 2005
S	*Catostylus mosaicus*	New South Wales, Australia	━	━	━	━		Pitt and Kingsford 2000
S	*Catostylus mosaicus*[c]	Port Phillip Bay, Australia	┅	┅	┅			Fancett 1986
S	*Chrysaora quinquecirrha*	Chesapeake Bay, USA		━	━		Cool temperatures & low salinity	Decker et al. 2007
S	*Chrysaora quinquecirrha*	Chesapeake Bay, USA		━	━	━	Cold temperatures	Sexton et al. 2010
S	*Cotylorhiza tuberculata*	Bay of Vlyho, Greece	━	━ ━	━ ━			Kikinger 1992
S	*Cyanea capillata*	southern North Sea	━	━				Barz and Hirche 2007
S	*Cyanea capillata*	Port Phillip Bay, Australia	━	┅	┅	┅━	Died post-spawning	Fancett 1986
S	*Cyanea hyoscella*	southern North Sea		━	━			Barz and Hirche 2007
S	*Cyanea lamarckii*	southern North Sea	━	━		━		Barz and Hirche 2007
S	*Cyanea* sp.	Niantic River, USA	━	━		━	Died post-spawning	Brewer 1989
S	*Mastigias papua*	Jellyfish Lake, Palau	━	━	━	━	Warm water associated with ENSO event	Martin et al. 2006
S	*Pelagia noctiluca*[g]	Port Phillip Bay, Australia		┅	┅		Cool water temperatures	Fancett 1986
S	*Pelagia noctiluca*	Northern Adriatic Sea	━	━	━	━		Malej and Malej 1992
S	*Periphylla periphylla*	Lurefjord, Norway	━	━	━	━		Jarms et al 1999
S	*Phyllorhiza punctata*[d]	Laguna Joyuda, Puerto Rico	━	━	━	━	Food limitation (possibly)	Garcia 1990
S	*Phyllorhiza punctata*[d]	Gulf of Mexico, USA	━	━	━		Senescence, infection, intertidal stranding	Graham et al. 2003
S	*Phyllorhiza punctata*[d]	southern Brazil		━	━		Starvation, parasitism, predation, senesence	Haddad and Nogueira 2006
S	*Phyllorhiza punctata*[d]	Swann Canning Estuary, Australia		━	━		Low salinity	Rippingale and Kelly 1995
S	*Pseudorhiza haeckeli*	Port Phillip Bay, Australia		━	━		Cool water temperatures	Fancett 1986

Taxon: *H* hydrozoa, *SP* siphonophore, *S* scyphozoa

[a] Data were presented for two locations: Korsfjord and the nearby Fanafjord. To avoid over-representation of this one study in the table, only data for Korsfjord are presented because the Korsfjord was sampled more extensively than the Fanafjord. Medusae were considered to be rare when densities were <10 ind. 1,000 m^{-3}

[b] Reported as *Phialidium hemisphaerica*

[c] Reported as *Phialucium carolinae*

[d] Invasive species

[e] Reported as *Podocoryne minima*

[f] Sampled Kiel Bight and Eckernforde Bay from May to Sept. Only data for Eckernforde Bay are included because the occurrence of the population in Kiel Bight exceeded the duration of the sampling programme

[g] Mostly represented by ephyrae

(seven from Australia and one from Brazil). Two studies from Norway (Hosia and Båmstedt 2007) and Portugal (Primo et al. 2012) which sampled multiple hydrozoan taxa contributed 17 and 9 observations, respectively. Most populations exhibited strongly seasonal patterns with the majority exhibiting greatest abundances between mid-spring and mid-autumn in their respective hemispheres. Seventeen taxa occurred year-round, but at least one third of those still exhibited strong seasonal variations in abundances. Rarely was the cause of the decline in the population reliably identified; however, authors frequently speculated about the cause of mortality, which included senescence after spawning, infestations of parasites, food limitation, disease, low salinity, extreme water temperatures (low and high), predation, advection and intertidal stranding.

Surprisingly, populations of the same or closely related species sometimes exhibited different dynamics at different locations or times. For example, the most commonly sampled species, the scyphozoan *Aurelia aurita*, exhibited strong seasonal patterns of occurrence in six studies but occurred throughout the year in seven studies (Table 4.1). The pattern of occurrence of *A. aurita* also varied substantially among years at a single location. For example, in Tomales Bay, California, *A. aurita* exhibited a seasonal occurrence during 1 year, whilst the population persisted throughout the following year (Hamner and Jenssen 1974). Patterns of occurrence can also vary greatly over spatial scales of 10s of kilometres. In the southern UK, for example, *A. aurita* persists year-round in a man-made coastal lake but occurs seasonally nearby in Southampton Water (Lucas et al. 1997). However, some caution must be applied to these observations of *Aurelia* because the genus contains numerous cryptic species (Dawson and Jacobs 2001) and some variations (particularly among locations) could reflect taxonomic differences. The invasive rhizostome, *Phyllorhiza punctata*, occurs predominantly during summer and autumn in subtropical and temperature locations such as southern Western Australia (Rippingale and Kelly 1995), the Gulf of Mexico (Graham et al. 2003) and southern Brazil (Haddad and Nogueira 2006), but populations of medusae persist year-round in tropical Puerto Rico, despite still exhibiting distinct seasonal cycles of recruitment and mortality (García 1990). These observations suggest that populations of medusae may rarely achieve their potential maximum longevity and that environmental conditions are most likely the primary drivers of mortality. This conclusion is further supported by observations that medusae can survive much longer (sometimes several years) in captivity than they do in the field (Zahn 1981).

The persistence of populations was negatively correlated with latitude ($P = 0.02$), but latitude explained only a small amount of the total variability ($r^2 = 0.081$), and the relationship was largely driven by the year-round persistence of three of the four tropical species recorded (i.e. *Aurelia aurita* and *Mastigias papua* in Palau and *Phyllorhiza punctata* in Puerto Rico) (Fig. 4.1). When tropical species were excluded, no relationship with latitude existed ($r^2 = 0.006$; $P > 0.05$).

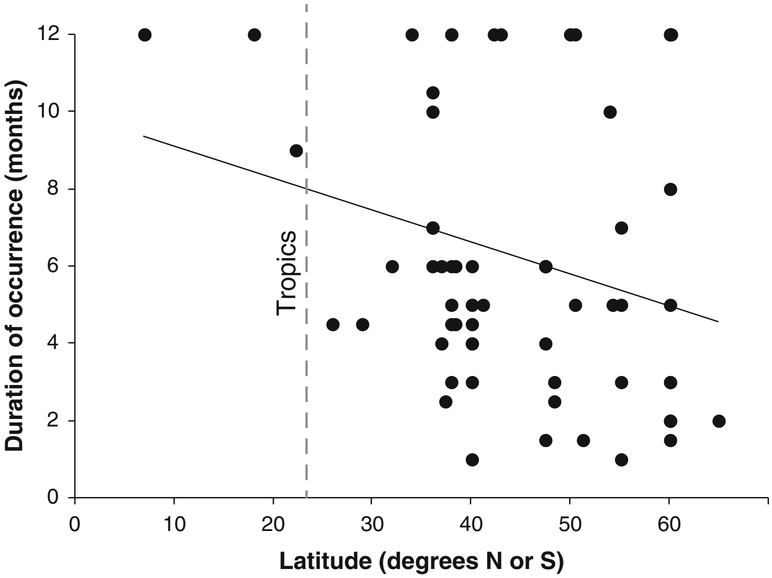


Fig. 4.1 Relationship between duration of occurrence of medusae and latitude

4.3 Common Causes of Mortality of Medusae

4.3.1 Food Limitation

Medusae can be voracious predators of zooplankton. The very high water content of medusae enables them to attain body sizes that are much larger than other planktivores of equivalent carbon content (Acuña et al. 2011). This trait enables medusae to support large feeding structures that can efficiently clear large volumes of water and theoretically enables medusae to survive in lower concentrations of prey than other competing planktivores, such as fish (Acuña et al. 2011). Changes in growth (Olesen et al. 1994) and biomass (Möller 1980; Miglietta et al. 2008) of medusae populations often correlate with zooplankton production after correcting for temporal lags. When prey are plentiful, medusae can grow rapidly (e.g. wet weight-specific growth of 0.88 d^{-1} for *Cotylorhiza tuberculata*; Kikinger 1992), and the biomass of the population has the potential to accumulate until rates of predation by medusae exceed secondary production of zooplankton and the biomass of medusae cannot be sustained (Purcell and Decker 2005). When prey become limited, however, growth of medusae may be inhibited, and individuals may attain smaller sizes than when food is unlimited (e.g. Schneider and Behrends 1994; Lucas et al. 1997). Indeed, food limitation is regularly cited as a major cause of population declines (Table 4.1). However, sometimes medusae have continued to grow (Møller and Riisgård 2007) and accumulate biomass (Olesen et al. 1994) despite the biomass of zooplankton appearing to be too low to support the population. This may be because rates of secondary production are very high despite the low standing biomass or that medusae efficiently exploit patches of zooplankton or may be able to supplement their diet by feeding on picoplankton (e.g. cyanobacteria) and microplankton (e.g. ciliates). Alternatively, the biomass of zooplankton in these studies may have been underestimated because neither study sampled the demersal zooplankton that emerges from the benthos into the water column at night. Emergent zooplankton are an important dietary source for jellyfish because tactile predators such as jellyfish can feed continuously during the day and night (Pitt et al. 2008), which may also allow them to outcompete visual predators for food resources in waters that are dark or contain high humic content (Aksnes et al. 2004). Indeed, in Kertinge Nor, Denmark, densities of epibenthic copepods in the water column can be 20 times greater at night than during the day (Olesen et al. 1994) and could, therefore, provide a significant food source.

If food is limited when medusae first recruit, growth appears to be inhibited, and medusae attain only small sizes. In Horsea Lake, UK, zooplankton productivity is much lower than in the nearby Southampton Water, and *A. aurita* in Horsea Lake are, correspondingly, much smaller than those in Southampton Water (Lucas et al. 1997). Moreover, the bell diameter of *A. aurita* was negatively correlated with population density over 20 years of observations in Kertinge Nor, Denmark (Riisgård et al. 2010) and over 9 years in Kiel Bight, Germany (Schneider and Behrends 1994), suggesting that competition for food may limit growth.

4.3.2 Predation

Until recently, jellyfish were considered a trophic dead end; however, recent studies indicate jellyfish are consumed by a variety of marine predators, including turtles, birds, fish and other gelatinous zooplankton (reviewed by Arai 2005). While a diverse range of predators feed on jellyfish, predation by fish and other gelatinous zooplankton has the largest potential to impact jellyfish populations (Arai 2005). Top-down regulation of jellyfish populations is difficult to demonstrate and quantify; however, several authors have speculated that intense, intra-guild predation by other gelatinous predators can regulate some medusae (Table 4.1). For example, in Nova Scotia, Canada, the hydromedusa *Rathkea octopunctata* comprised 34 % of the diet of the scyphomedusa *Aurelia aurita* indicating that *A. aurita* may regulate natural populations of *R. octopunctata* (Matsakis and Conover 1991). In Norway, *Cyanea capillata* preys heavily on *A. aurita* (Fig. 4.2), and the decline in the *A. aurita* population coincides with an increase in *C. capillata* (Båmstedt et al. 1994). Overlapping temporal succession of several hydrozoans in Norway may similarly indicate intra-guild predation (Hosia and Båmstedt 2007).

A wide range of fish consume jellyfish, including spiny dogfish, chum salmon, ocean sunfish, Atlantic mackerel and Atlantic cod (Arai 1988; Ates 1988; Link and Ford 2006). Although fish probably exert significant predatory pressure,

Fig. 4.2 *Cyanea capillata* capturing *Aurelia aurita* in Kiel Fjord, Germany (Reproduced by permission of Kylie Pitt)

the importance of jellyfish as a dietary component is unknown due to unquantified digestion rates (Purcell and Arai 2001; Cardona et al. 2012). Difficulties with gut content analysis may be circumvented by using stable and enriched isotopes (Pitt et al. 2009b) and molecular techniques. A recent study in the Mediterranean Sea used ^{13}C and ^{15}N stable isotopes as a tool to estimate the relative contribution of gelatinous zooplankton to the diets of several apex predators (Cardona et al. 2012). Although this study provided evidence that loggerhead sea turtles, ocean sunfish and various opportunistic feeders potentially consume large quantities of jellyfish, further research is needed to quantify rates and determine whether these predators can regulate populations of jellyfish.

4.3.3 Parasitism

Parasitism is likely to be an important factor in the decline of many jellyfish blooms and in the regulation of medusae populations. Medusae are infected by many types of parasites, including hyperiid amphipods (Laval 1980; Dittrich 1988); digenean trematodes, or flukes (Martorelli and Cremonte 1998); cestodes (Vannucci-Mendes 1944); isopods (Barham and Pickwell 1969); nematodes (Svendsen 1990); barnacles (Pagès 2000); sea anemones (McDermott et al. 1982) and, potentially, microbes (Doores and Cook 1976). Parasites that infect non-gelatinous hosts can cause the host populations to crash (e.g. krill: Gómez-Gutiérrez et al. 2003;

fish: Heins et al. 2010), and there is strong circumstantial evidence to suggest that hyperiid amphipods may contribute to declines in medusa populations (Mills 1993), and ctenophore populations have also been adversely affected by platyhelminth worms (Yip 1984) and parasitic anemones (Reitzel et al. 2007). Blooms of jellyfish are likely to be particularly susceptible to parasitism because abundances of parasites are positively correlated to densities of hosts (Arneberg et al. 1998) and the population size of hosts is a determinant of parasite infection (Bagge et al. 2004).

4.3.3.1 Hyperiid Amphipods

Hyperiid amphipods are a paraphyletic group of marine amphipods whose features (e.g. large eyes, maxillipeds with no palps) are believed to have arisen through their association with planktonic hosts (Lützen 2005). While some hyperiid amphipods are primarily free-living, most appear to depend on gelatinous hosts for at least some stage of their life cycle (Arai 2005). These hosts include medusae (Fig. 4.3a), siphonophores, planktonic molluscs and salps (Gasca and Haddock 2004). In many hyperiid species, females brood eggs and then deposit juveniles onto the host. The juveniles then feed on their host until they reach a more independent stage (Laval 1980). Some hyperiid adults continue to feed on their host's tissues (Towanda and Thuesen 2006), while others become free-living. *Parathemisto gaudichaudi* is generally regarded as free-living; however, juveniles have been found associated with salps (Madin and Harbison 1977). Other hyperiids attach to the outside of their host and feed on plankton, entrained (Condon and Norman 1999) or caught by the host (Laval 1972).

Hyperiid amphipods can be prevalent in populations of medusae. At times, 100 % of the population may be infected (Towanda and Thuesen 2006), and individual medusae may host hundreds of hyperiids (Dittrich 1988; Towanda and Thuesen 2006). Medusae have a remarkable ability to regenerate damaged tissues when food is abundant (Mills 1993), but if dense infestations of parasites occur during times when food is scarce, mortality may occur. For example, prior to the disappearance of the hydromedusae *Aequorea victoria* and *Mitrocoma cellularia* from Puget Sound, USA, individuals exhibited high proportions of grazing damage (>75 % and 67–100 %, respectively) which was attributed primarily to the hyperiid amphipods *Parathemisto pacifica* and *Hyperia medusarum*. Low proportions of hydromedusae had food in their guts (44 % and 66 %, respectively) and were seemingly unable to regenerate lost tissue. The hyperiid *Hyperia galba* had a similar effect on populations of the scyphomedusae *Chrysaora hysoscella*, *Aurelia aurita*, *Rhizostoma pulmo*, *Cyanea capillata* and *C. lamarckii* over two consecutive years in waters around Helgoland in the North Sea (Dittrich 1988). By autumn almost all medusae were parasitised, and the number of amphipods per medusa reached 486 on *C. hysoscella*. The increasing rates of infection coincided with the medusae shrinking, as the hyperiids consumed the gonads and then the mesoglea. Regeneration by medusae appeared unable to offset rates of tissue loss, and by the end of autumn, all the medusae had disappeared (Dittrich 1988). While there have been many

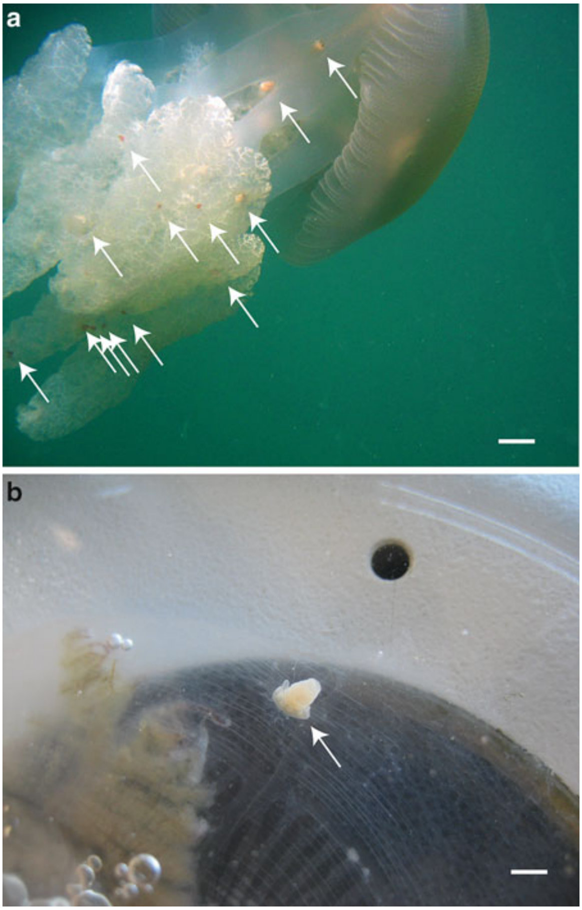


Fig. 4.3 (**a**–**b**) Ectoparasites in Port Phillip Bay, Australia; (**a**) hyperiid amphipods *Hyperia gaudichaudi* (indicated with *arrows*) on the oral arms of the scyphozoan *Catostylus mosaicus* (scale bar is 2 cm) and (**b**) anemone *Peachia hilli* (indicated by *arrow*) attached to the scyphozoan *Pseudorhiza haeckeli* (scale bar is 0.5 cm) (Reproduced by permission of Joanna Browne)

studies on hyperiid amphipods and their hosts (see reviews of Harbison et al. 1977; Madin and Harbison 1977; Laval 1980), only Mills (1993) and Dittrich (1988) attempted to determine their effect on medusae populations. Other species of medusae for which hyperiids may have caused or contributed to the disappearance of populations include *Aurelia aurita* (Möller 1980; Møller and Riisgård 2007) and *Cyanea capillata* (Metz 1967).

4.3.3.2 Digenean Trematodes

Digenean trematodes, which are parasitic flatworms (flukes), infect at least 62 species of medusae (Browne unpubl.). Although there are approximately 18,000 species of digeneans, only 13 infect medusae (Browne unpubl.). Digeneans have a complex life cycle, mostly involving three hosts. The first host is normally a mollusc, the intermediate host is normally another invertebrate and the final host is almost always a vertebrate. Different life history stages of the parasite occur in each host, and some are capable of reproduction (e.g. sporocysts in the mollusc host and sexual adults in the vertebrate host). Digeneans that use jellyfish as an intermediate host leave their mollusc host and penetrate the jellyfish and develop into metacercariae which is a juvenile resting stage in an intermediate host. When the jellyfish are eaten by suitable fish hosts, the metacercariae develop into sexual adults within the fish. The metacercariae are likely to feed upon the jellyfish tissue, and highly parasitised medusae can have an 'ablandamiento total' (=overall softening) of tissue (Girola et al. 1992).

The proportion of medusae infected by digeneans in a population can be very high (Fraser 1970) and is often higher than that observed in other planktonic intermediate hosts (Marcogliese 1995). Rates of infection by digeneans in studies that sampled >1,400 individuals of one medusa species ranged from 0.1 % to 97.6 % (Diaz Briz et al. 2012) and depended on the species of digenean and host and season. The only study to have examined the direct effect of digenean parasites on a population of gelatinous zooplankton has focused on ctenophores. Yip (1984) sampled populations of the host ctenophore *Pleurobrachia pileus* monthly for 3½ years and observed a sharp decline in abundance of the ctenophore following periods of heavy infection by parasites (predominately *Opechona bacillaris* and didymozoid larvae). She proposed that effects on the host could include competition for food, consumption of body tissue and increasing body weight of the host interfering with normal movement.

4.3.3.3 Parasitic Anemones

Larval anemones of the genera *Edwardsiella* and *Peachia* (Fig. 4.3b) parasitise jellyfish and feed on their intestinal fluids, gonads and mouth tissues (Badham 1917; Spaulding 1972; Mills 1993). As adults, the anemones are benthic and free-living (McDermott et al. 1982; Reitzel et al. 2006). While many medusae are infected by larval anemones (Lauckner 1980), the only ecological studies about their effects on host populations have been done on ctenophores. In the laboratory, larval *E. lineata* decreased the growth rates of their host ctenophore *M. leidyi* and indirectly decreased fecundity through their influence on host size (Bumann and Puls 1996). These parasite-induced effects led the anemone to be proposed as a biological control on its invasive host *M. leidyi* (Bumann and Puls 1996). However, using the anemone as a biological control would be risky because the anemone is linked to the skin irritation 'sea bathers eruption' (Freudenthal and Joseph 1993) and may alter benthic communities (Bumann and Puls 1996). Recently, *E. lineata* is believed to have followed its invasive host to the northeast Atlantic (although there is some difficulty in differentiating *E. lineata* and the similar *E. carnea*) (Selander et al. 2010).

4.3.3.4 Importance of Medusae Parasites and Relevance to Blooms

While there have been many studies of some medusae parasites, particularly hyperiids, those above are examples of the few that have examined the effects of parasites on medusae populations through time. Many medusa parasites (e.g. microbes) that have the potential to have detrimental effects on their hosts are poorly understood (Ohtsuka et al. 2009), but further research will enable perspective of their importance and relevance to medusae mortality and decline of blooms.

Recently the ability of parasites to affect entire communities has been highlighted (Lafferty 2008; Hatcher et al. 2012). Medusae parasites may influence other organisms through predation, transference and regulation of host populations. Parasites which use medusae as intermediate hosts may be transferred to commercially important species. For example, the mackerels *Scomber scombrus*, *S. japonicus* and *S. australasicus* are infected by numerous digeneans that use jellyfish as hosts (Bray and Gibson 1990; Bartoli and Bray 2004). The transmission of parasites depends on the density of the hosts (e.g. farmed salmonids and sea lice: Jansen et al. 2012), and when jellyfish form blooms, parasites such as larval anemones and hyperiids may spread more easily between medusae hosts (Spaulding 1972; Laval 1980). There may also be increased transfer of parasites to predators; the parasitic anemone, *Edwardsiella lineata*, is transferred when its host *Mnemiopsis leidyi* is eaten by *Beroë ovata* (Reitzel et al. 2007). Peaks in medusa populations offer an increased abundance of hosts and therefore appear to be linked to peaks in parasite abundance (Williams and Robins 1981; Dittrich 1988). Medusae parasites may have positive effects on other animals by relieving predation pressure by the medusae hosts, or they may be a food source. For example, hyperiid amphipods are picked directly from their hosts by pile perch *Rhacochilus vacca*, the symbiont crab *Cancer gracilis* (Towanda and Thuesen 2006) and sea birds (Harrison 1984).

4.3.4 Disease

While disease is often considered to be a potential cause of mortality in medusae, few studies have confirmed infections as a cause of death. Hydromedusae with bacterial infections are able to recover if sufficient food is available (Mills 1993). However, at the end of the hydromedusae's seasonal occurrence, the reduced availability of prey may render them more susceptible to these infections (Mills 1993). Late in the season, for example, over 80 % of the hydromedusa *Clytia gregaria* had bacterial infections on their bells, which was thought to contribute to mortality when coupled with limited food availability (Mills 1993). Similarly, mortality of *Gonionemus vertens* was thought to be primarily due to infection characteristically associated with senescence (Mills 1993). Bacteria also infected wounds generated by bites of argonauts in the rhizostome *Phyllorhiza punctata* which may have exacerbated the physical injuries incurred (Heeger et al. 1992). Although pathogens other than bacteria (e.g. viruses and fungi) probably infect medusae, no studies of such pathogens exist.

4.3.5 Death Post-Spawning

Scyphozoan jellyfish have, on several occasions, been observed to die shortly after spawning (Table 4.1). Mortality post-spawning has been examined particularly in *Aurelia aurita*. In the Baltic Sea mortality rates prior to maturation were low, but after spawning the medusae degraded and died (Möller 1980). Starvation and increased parasitism were suggested to be the major cause of degradation rather than spawning itself. However, Spangenberg (1965) observed that sexual products and gastric filaments of *Aurelia aurita* were released simultaneously during spawning. Because gastric filaments (or gastric cirri) are necessary for digestion within the stomach, their loss during spawning suggests starvation as the most likely explanation for deterioration in this case (Spangenberg 1965; Arai 1997). Contrary to these studies, however, Hamner and Jenssen (1974) found that after spawning medusae were able to 'ripen' gonads within a couple of weeks. Therefore, their observations in the laboratory did not support simultaneous deterioration of somatic and reproductive tissue, although they did observe deterioration and mortality post-spawning in the field.

Cyanea is another genus that reportedly spawns and then deteriorates (Fancett 1986). However, in the Niantic River estuary, USA, *Cyanea* sp. lose their tentacles prior to losing their oral folds (which contain the planulae) and gonads, and so the major cause of death may be starvation due to loss of tentacles rather than spawning (Brewer 1989).

4.3.6 Metabolic Intolerances to Physical Conditions

Patterns of occurrence of many medusae are often correlated with seasonal changes in physical parameters such as temperature or salinity (e.g. Fancett 1986; Lo and Chen 2008; Primo et al. 2012) which, in turn, are correlated with a variety of other changes, such as decreased zooplankton production. Only in regions where seasonal changes in the physical environment exceed the physiological tolerances of species, however, are physical factors likely to be the main driver of mortality. To rigorously identify physical conditions as the main cause of mortality requires experiments on tolerance limits to be undertaken, preferably at the location of interest to account for local adaptation, and then related to field observations.

4.3.6.1 Temperature

Although populations of medusae often disappear when water temperatures decrease during autumn, only in Chesapeake Bay is there robust evidence that death of medusae is caused by cooling water temperatures. In laboratory experiments, the pulsation rate of *Chrysaora quinquecirrha* slows with declining water temperature, and at 10 °C medusae cease to pulse and die (Gatz et al. 1973). These results are consistent with observations in the field and laboratory, whereby medusae sink deeper into the water column when the temperature decreases to 15 °C and then disappear entirely from the water column at 10 °C (Sexton et al. 2010), suggesting that the cold water may have been the dominant cause of death. Warm temperatures can also invoke mortality. For example, following an ENSO event in 1997–1998 which elevated temperatures 1–2 °C above their long-term seasonal average, the normally perennial population of the zooxanthellate rhizostome *Mastigias papua* disappeared from Ongeim'l Tketau lake in Palau (Dawson et al. 2001; Martin et al. 2006). Concurrent laboratory experiments showed that mortality of medusae increased greatly at temperatures similar to those measured in the lake; therefore, warm water was considered the major cause of mass mortality (Dawson et al. 2001).

4.3.6.2 Salinity

Evidence linking changes in salinity to mortality events of medusae is relatively weak and constrained to correlative observations. For example, *Aurelia aurita* disappears from the surface waters of a coastal lagoon in Taiwan following heavy rain during summer, but it is unclear whether the population dies, is advected from the lagoon or simply remains below the halocline (Lo and Chen 2008). In Western Australia, the distribution and persistence of *Phyllorhiza punctata* appears to be correlated to rainfall, with periods of heavy rain preceding the disappearance of the population (Rippingale and Kelly 1995). Populations of *Chrysaora quinquecirrha* in the mesohaline region of Chesapeake Bay are similarly correlated with streamflow and salinity (Cargo and King 1990; Purcell et al. 1999), but research has focused mainly on the effects of salinity on production of medusae rather than as a cause of mortality.

4.3.6.3 UV Radiation

Ultraviolet (UV) radiation damages tissues and induces vertical migration in zooplankton (Rhode et al. 2001). Consequently UV radiation could be detrimental to medusae. In Lake Tanganyika, the freshwater hydrozoan, *Limnocnida tanganjicae*, died within 1 h when exposed to UV radiation equivalent to that found close to the surface waters (Salonen et al. 2012). However, *L. tanganjicae* undertakes diel vertical migration, and this, presumably, prevents mortality in situ. The upside-down jellyfish *Cassiopea* sp. is restricted to occurring in shallow waters due to its need to photosynthesise and, therefore, may be susceptible to exposure to UV radiation. The zooxanthellae within this species synthesise mycosporine-like amino acids that have a photoprotective function and that can be translocated to the host to provide protection against UV radiation (Banaszak and Trench 1995). Pigments may also be formed through uptake of glycoproteins, which may serve to protect cells in zooxanthellate medusae from UV radiation (Blanquet and Phelan 1987).

Fig. 4.4 Mass stranding of *Crambione mastigophora* at Cable Beach, Broome, Western Australia (Reproduced by permission of James Browne, Kimberley Marine Research Station, Cygnet Bay)

Whilst no studies have attributed large-scale mortality of medusae to UV radiation, increasing levels of radiation could, potentially, induce mortality in shallow systems where vertical migration is not possible.

4.3.7 Stranding

Mass strandings of jellyfish are common on beaches (e.g. Houghton et al. 2007; Fuentes et al. 2010; Fig. 4.4) and, because of their conspicuous nature, often attract the attention of media (Lilley et al. 2009; Condon et al. 2012). Strandings, however, are more likely to be a consequence, rather than a cause of mortality for medusae, and the timing of events may relate to oceanographic and weather conditions. For example, large numbers of the rhizostome *Cotylorhiza tuberculata* strand on beaches in Vlyho Bay, Greece, during autumn, associated with strengthening winds (Kikinger 1992). These strandings may be facilitated by reduced swimming ability associated with sloughing of the subumbrella muscles as the medusae senesce (Kikinger 1992). Moreover, *Chrysaora hysoscella* that wash ashore on beaches in the Irish Sea often lack peripheral tentacles and oral arms, indicating that these medusae may have senesced prior to stranding (Houghton et al. 2007). Mass strandings of decaying medusae on beaches may represent a substantial input of carbon to beach environments, which are typically poorly productive and rely on allochthonous inputs of organic matter.

4.4 Factors That Promote Survival of Jellyfish

The persistence of medusae populations may relate to their variable abilities to either withstand the drivers of mortality or to recover from them (see also Lucas and Dawson, Chap. 2). The ability of medusae to catabolise their own tissues when starving and to heal wounds and regenerate lost body parts is likely to provide medusae with the ability to potentially survive stressors.

4.4.1 Ability to Shrink When Starved

When food is scarce, most organisms can utilise stores of lipids to sustain themselves. Medusae, however, contain approximately half the lipid content (as % ash-free dry weight, AFDW) of non-gelatinous pelagic taxa (Clarke et al. 1992; Donnelly et al. 1994), and the majority of lipids are phospholipids which constitute components of cell membranes (Arai et al. 1989, Costello 1992). Due to the lack of storage lipids, the ubiquitous responses of medusae to starvation are to catabolise their own tissues and rapidly lose mass (Hatai 1917; Hamner and Jenssen 1974; Arai et al. 1989). The degree of degrowth can be remarkable. For example, *Cassiopea* can lose up to 99 % of its mass (Mayer 1914), and *A. aurita* can shrink to a quarter of its original diameter and remain viable; however, once the diameter is less than 2 cm, the medusae usually become deformed and deteriorate (Hamner and Jenssen 1974). In the hydromedusa *Aequorea victoria*, proteins, lipids and carbohydrates are catabolised at similar rates (Arai et al. 1989). However, while *A. aurita* and *A. victoria* shrink rapidly when starved (Hamner and Jensen 1974; Arai et al. 1989), the hydromedusa *Cladonema californicum* actually increases diameter and maintains an enlarged diameter for up to 28 days following the onset of starvation, despite losing 69–77 % of its dry mass (Costello 1998). Maintaining their diameter whilst losing mass, however, compromises their ability to swim (Costello 1998). The difference in response of the few taxa for which starvation has been studied may reflect differences in their feeding ecologies. Specifically, *C. californicum* is an ambush ‘sit and wait’ predator that relies on maximising encounter rates to capture prey, whereas *A. aurita* and *A. victoria* are cruising predators that use vortices generated by active swimming to entrain their prey (Costello 1998). Consequently, *A. aurita* and *A. victoria* depend much more heavily on swimming to capture prey and regrow. Maximising bell diameter, potentially at the expense of maintaining other structures, such as muscles, may optimise survival of ambush predators and maximise their chance for recovery once prey become more numerous (Costello 1998).

Aurelia aurita and *Cladonema californicum* can both regrow following more than 6 weeks of starvation (Hamner and Jenssen 1974; Costello 1998). In both species the pattern of growth following starvation is normal, and individuals can reinstate normal feeding and reproductive processes. However, whilst in the laboratory medusae exhibit an extraordinary ability to degrow and regrow, we could find no examples of cohorts of medusae recovering after shrinking in the field. In the field, degrowth is usually determined from a decrease in the average size of medusae (Möller 1980); however, decreases in average size can also be explained by selective mortality or advection of the larger size classes in the population (Brewer 1989; Olesen et al. 1994) and, therefore, need to be interpreted cautiously. Degrowth (where it has been claimed) is usually observed during autumn (e.g. Möller 1980; Ishii and Båmstedt 1998; Møller and Riisgård 2007) which coincides with cooling water temperatures and reduced rates of zooplankton production, conditions that typically persist for several months. Whilst medusae can sustain at least three months starvation in the laboratory (Hamner and Jensen 1974), the two studies of regrowth by medusae have been undertaken at relatively warm and constant temperatures (16–18 °C, Hamner and Jensen 1974; 18 °C, Costello 1998 – both studies done in California). Indeed, interactive effects between regrowth and temperature are yet to be tested but may demonstrate that regrowth is not viable when water temperatures approach the thermal minimum for a species.

4.4.2 *Ability to Heal Injuries and Regenerate Lost Body Parts*

Medusae have remarkable abilities to heal injuries and regrow damaged body parts (Zeleney 1907; Mills 1993). For example, parasitic hyperiid amphipods often consume the manubria of the hydromedusa *Aequorea victoria* (Mills 1993). However, if the damaged individual is transferred to an aquarium and fed well, it can regenerate a new manubrium within 6 days (Mills 1993). Similarly, a hole penetrating the centre of the umbrella of *Mitrocoma* can heal within 7 days (Mills 1993). Whilst injuries can heal under laboratory conditions, recovery from injury also appears to occur in the field. For example, it is common to see substantial scars created by the healing of injuries derived from the blades of boat propellers in large medusae (Pitt pers. obs.). Rates of regeneration increase with severity of the injury, up until a threshold. For example, regeneration of the oral arms of *Cassiopea xamachana* increased as additional oral arms were removed, with the maximum rate of regeneration associated with the removal of 6 of the 8 oral arms (Zeleney 1907). Moreover, jellyfish can also regenerate the same body parts multiple times (Zeleney 1907). Mechanisms of wound healing are, however, very poorly studied. Very small wounds (1.2 mm diameter) in the myoepithelial cells of the swimming muscle are closed by the muscle cells differentiating into epithelial cells and migrating to the centre of the wound before dedifferentiating into contractile muscle cells again (Lin et al. 2000).

4.5 Conclusions

Rarely have the causes of mortality of medusae been reliably identified. Extreme variability in persistence of populations of the same species among locations and between years indicates that medusae may only rarely attain their maximum physiological longevity in the field, with environmental parameters that vary both temporally and spatially the main drivers of mortality. Mortality is likely due to multiple stressors interacting rather than individual events. Small variations in the timing or magnitude of the stressors may invoke changes in the rate or timing of mortality. Mass mortality, particularly in shallow or enclosed water bodies, such as coastal lagoons and fjords, can have major implications for the ecology and biogeochemical cycling of the systems. Being able to predict the duration of blooms and when they are likely to decline could benefit coastal industries, such as tourism, fisheries and power generation, which are often negatively impacted by jellyfish (see Lucas et al., Chap. 6). Reliable identification of the factors leading to the collapse of blooms should, therefore, be a priority for research.

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Chapter 5
Ecological and Societal Benefits of Jellyfish

Thomas K. Doyle, Graeme C. Hays, Chris Harrod, and Jonathan D.R. Houghton

Abstract Jellyfish are often considered as stressors on marine ecosystems or as indicators of highly perturbed systems. Far less attention is given to the potential of such species to provide beneficial ecosystem services in their own right. In an attempt to redress this imbalance, we take the liberty of portraying jellyfish in a positive light and suggest that the story is not entirely one of doom and gloom. More specifically, we outline how gelatinous marine species contribute to the four categories of ecosystem services (regulating, supporting, provisioning and cultural) defined by the Millennium Ecosystem Assessment. This discussion ranges from the role of jellyfish in carbon capture and advection to the deep ocean through to the creation of microhabitat for developing fishes and the advancement of citizen science programmes. Attention is paid also to incorporation of gelatinous species

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into fisheries or ecosystem-level models and the mechanisms by which we can improve the transfer of information between jellyfish researchers and the wider non-specialist community.

Keywords Jellyfish blooms • Ecosystem services • Jelly-falls • Carbon sequestration • Jellyfish fisheries • Green fluorescent proteins • Nutrient cycling • Predator-prey interactions • Pelagic refugia • Eco-tourism

5.1 Introduction

In the public eye, jellyfish are largely synonymous with one thing – stinging. Of course, many jellyfish do give very nasty stings (particularly cubozoans, *Cyanea capillata* and *Physalia physalis*) and some species can cause fatalities (many cubozoans), but the reality is that in the majority of cases (and for most people), jellyfish produce a sting that is very mild and forgotten about in 20 min. Many of the jellyfish names conjure up images of something deadly or dangerous: the Portuguese man o'war (*Physalia physalis*), the sea nettle (*Chrysaora* sp.) and the lion's mane (*Cyanea capillata*). The latter species was made infamous by Sir Author Conon Doyle's story where an unidentified creature caused the death of a victim. The killer is found to be a lion's mane, '…with poor Mr Fitzroy McPherson suffering an agonising death after being brutally scourged with a most vicious lashing weapon' (Curtis 2001). Such vivid storytelling typical of a classic detective story of Sherlock Holmes certainly contributed to the branding of jellyfish.

Too often, this is the only story told about jellyfish. As a group of over 1,200 species (Fenaux 1998; Godeaux 1998; Costello et al. 2008), surely there must be a positive side as well? Typical questions that are often posed by the media and general public include 'what are jellyfish?', 'what do they do?' and 'if there were no jellyfish would it really matter?' Conversely, fish provide sustenance, jobs and recreation, all of which come under the umbrella of human demand for ecosystem services (Costanza et al. 1997; Holmlund and Hammer 1999). This anthropocentric line of argument is innate in human society, and all of the Earth's natural resources are constantly redefined according to it. However, the benefits of particular species for society are often more cryptic and emerge from research rather than commerce. For example, until the isolation of penicillin from microorganisms, or quinine from *Cinchona* spp., one might easily have asked questions as to the importance of mould or bark.

An interesting question is whether other harmful species receive as bad a press as jellyfish? Perhaps the most comparable taxa are spiders and snakes: both are venomous and conjure up images of being bitten (stung). Yet arguably more people value or accept spiders and snakes as having a positive role in ecosystems, e.g. spiders control pest species (Marc et al. 1999), so are good, and snakes too can control rodent populations (Kotler et al. 1993) but also are wonderfully diverse/colourful/

large/terrestrial and are thus conspicuous and intriguing. Conversely, jellyfish are largely hidden from sight, transparent and appear somewhat sinister without recognisable body parts such as eyes. In this context, it is not surprising that jellyfish are misunderstood and receive a lot of bad press. However, as a scientific community we cannot simply shirk all blame onto the media, as we are equally adept at highlighting the negative aspects of jellyfish blooms. To add some numbers to this claim, we analysed a range of jellyfish papers published in 2010 following the methods of Bonnet et al. (2002). Of the 48 articles considered (Web of Science, search term ‘jellyfish’), 35.4 % had a predominantly negative interpretation (mentioning negative impacts within the first 10 % of lines), and 20.8 % had distinctly negative content (> 10 % of lines had negative meaning with respect to jellyfish). Naturally, jellyfish blooms can bring about disastrous socio-economic impacts (Purcell et al. 2007), and we are certainly not challenging this fact. Yet, the corollary of a negative spin is the overwhelming perception of jellyfish by the non-jellyfish scientific community, funding organisations and general public that such species are unnatural and unwanted constituents of our oceans. From an ecological viewpoint, this is dangerous ground, as the commercial viability of jellyfish fisheries is an extremely hot topic. Of great concern is the flippant manner in which wholesale removal of jellyfish from marine systems is discussed (i.e. ‘no one likes them, they do not serve any real purpose and so no one will miss them’). Certainly, it is hard to envisage thorough environmental impact assessments underpinning future commercial jellyfish operations, yet the consequences of removing what Pauly et al. (2009) described as ‘arguably the most important predators of the sea’ are unlikely to be negligible.

This trend towards negativity is understandable nonetheless among academics where publically funded science must be increasingly justified in a broader economic context (Smith et al. 2011). Indeed, given that jellyfish have long been considered by many as transient or peripheral components within marine food webs, it is difficult to secure resources on ecosystem functioning grounds alone. Within this conundrum lies what Fanelli (2010) referred to as ‘the publication bias’ where the pressure to publish can conflict with the objectivity and integrity of research given that scientists are required to generate publishable results at all costs. Within the media, ‘bad news’ is generally ‘good news’, and scientists looking for funding for research often aim to be solving large problems that are relevant to wider society. Here, we take the liberty of portraying jellyfish in a more positive light. From trophic complexity through to enhanced biodiversity and ecosystem services, we put forward the argument that there is far more to jellyfish than bad news.

In the context of this chapter, the word ‘jellyfish’ refers to all cnidarian scyphomedusae, hydromedusae, siphonophores and cubozoans, as well as the ctenophores. In some sections we also briefly mention other gelatinous zooplankton from the phylum Chordata, namely, the salps, doliolids, pyrosomes and appendicularians. While we acknowledge they are non-related, as Haddock (2004) stated, many of these groups share convergent features of transparency, fragility and planktonic existence.

5.2 Ecosystem Services of Jellyfish

Ecosystem services are generally described as the ‘benefits people obtain from ecosystems’ (Anonymous 2005). Considering the overwhelmingly negative perception of jellyfish, it is not surprising that such species are considered almost exclusively as stressors that impinge on the viability of ecosystem services (e.g. competition with commercial fish stock or reduction in bathing water quality). These are valid arguments but there is more to the story. Here, we revisit their role as service ‘providers’ under the umbrella of regulating, supporting, provisioning and cultural services (see Fig. 5.1).

5.2.1 Regulating Services

Perhaps one of the most important services provided by jellyfish is climate regulation through the process of carbon sequestration (becoming a source or sink for greenhouse gases) and transport through the water column. Jellyfish-falls or the accumulation of jellyfish carcasses at the seabed can also play an important role in the transfer of carbon from surface waters to the seabed (Lebrato et al. 2012) through an exaggerated process of pelagic-benthic coupling. For example, mass deposition events of dead jellyfish have now been documented globally (Billett et al. 2006; Lebrato et al. 2012). At times the amount of carbon that can be deposited from a single jellyfish-fall event may be ca. four times the annual carbon input to the seabed (Lebrato and Jones 2009). Indeed, it is possible that jellyfish-falls could mitigate some of the losses of carbon from the classic phytoplanktonic carbon flux, which may decrease in the future (Lebrato et al. 2012). For example, Buesseler et al. (2007) suggested that smaller phytoplankton communities (which have lower export efficiency) may be favoured instead of large diatom dominate communities.

It is not just jellyfish-falls that are important for carbon sequestration. Mass occurrences of salps that feed primarily on small phytoplankton can serve as vectors of carbon from the surface waters to the ocean depths through the production of faecal pellets, which have high organic content and fast sinking rates (Madin 1982; Turner 2002; Madin and Deibel 1998). Indeed, the sinking rates of salp faecal pellets (43–2,700 m d^{-1}) can be considerably faster than the sinking rates for euphausiid pellets (126–862 m d^{-1}) and an order of magnitude faster than copepod pellets (12–225 m d^{-1}) (Andersen 1998). As such, their faecal pellets can form a large proportion of the matter in sediment traps (Andersen 1998). Doliolids also produce pellets, and appendicularians produce both faecal pellets and discarded houses, which also contribute to the downward flux of particles (Turner 2002), albeit with the loss of some carbon through recycling, predation and release of dissolved organic carbon (DOC).

Disease and pest regulation might not immediately seem an obvious benefit from animals that themselves are often classified as pests. Yet, some jellyfish species have played a clear role in pest regulation. The introduction (by ballast water) of

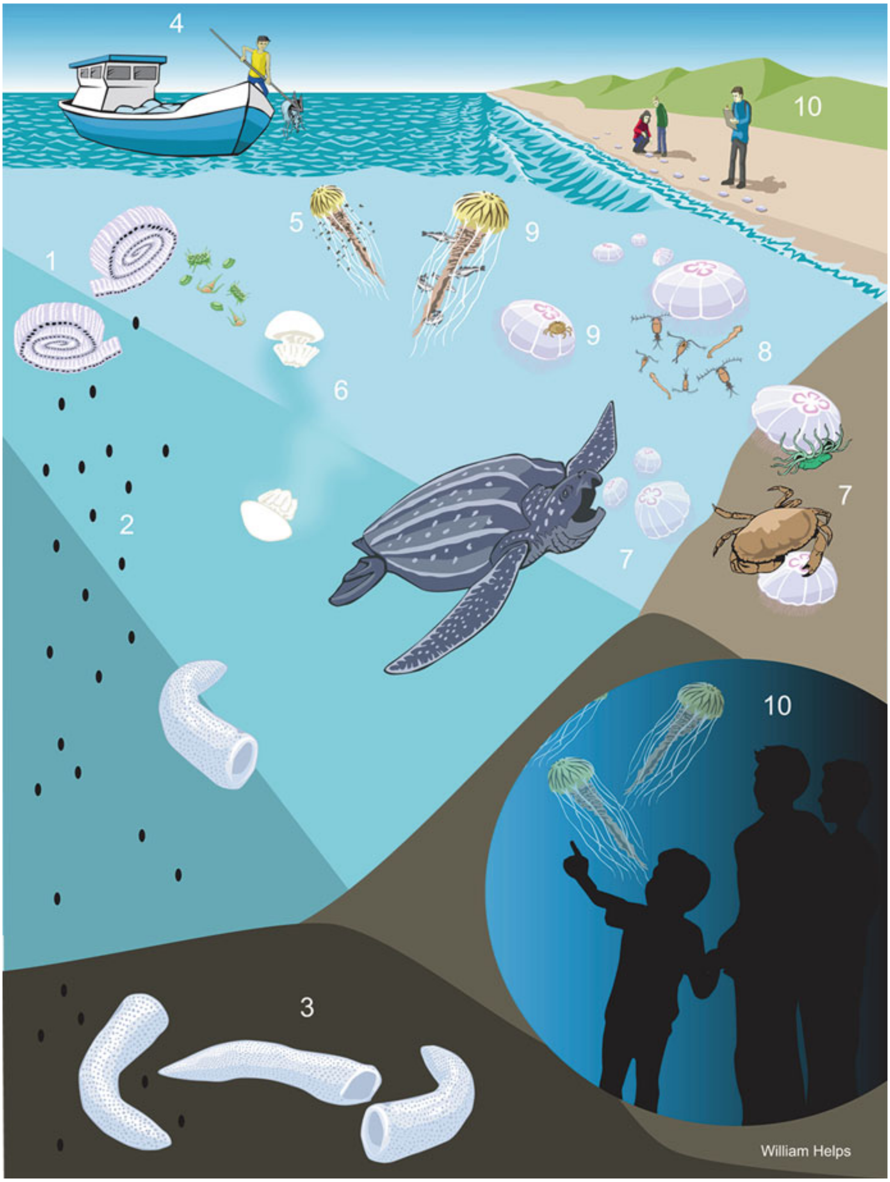

Fig. 5.1 The ecosystem services provided by jellyfish. Regulating services: (*1*) salps consume phytoplankton and transport carbon to the benthos via faecal pellets (*2*). (*3*) Accumulation of jellyfish carcasses (pyrosomes) on the seabed plays an important role in the transfer of carbon from surface waters to the benthos. Provisioning services: (*4*) jellyfish harvested for food and other uses. Supporting services: (*5*) sloppy feeding provide nutrients to support primary production, (*6*) swimming jellyfish contribute to oceanic mixing due to displacement of water as they move through it, (*7*) jellyfish provide a prey source for hundreds of different animals, (*8*) jellyfish are important predators in pelagic marine systems, and (*9*) jellyfish provide habitats and refugia for a large variety of taxa. Cultural services: (*10*) citizen science programmes encourage the public to count and identify jellyfish stranded on beaches, and jellyfish in aquaria capture the imagination of children (Scientific illustration by William Helps)

Mnemiopsis sp. into the Black Sea in 1980s had catastrophic consequences for the pelagic fish populations which led to large economic losses to the Turkish fishing industry (Kideys 2002). The introduction of another invasive species *Beroe* sp. in 1997, a predator of *Mnemiopsis*, has helped the ecosystem to recover further. It is thought that *Beroe* controlled the *Mnemiopsis* population as its abundance declined precipitously once *Beroe* sp. arrived (Kideys 2002). Given that *Beroe* feeds almost exclusively on *Mnemiopsis* (which almost disappeared entirely from water column itself after the *Mnemiopsis* decline), this jellyfish did not replace one problem with another (Kideys 2002). In a similar vein, jellyfish also have a role in biodiversity regulation, which may strongly influence the provision of ecosystem services (Díaz et al. 2005). For example, at low densities jellyfish may act as keystone species (Piraino et al. 2002; Pauly et al. 2009) that act as the main predator of commercially important or numerically abundant fish populations (Purcell 1989; Purcell and Grover 1990). By controlling such fish populations (by predation of fish eggs and larvae), jellyfish indirectly free up resources for less well-established fish species and thus may enhance local biodiversity (Boero et al. 2008).

5.2.2 Provisioning Services

Provisioning services include those ecosystem resources that provide food, fibre and fuel (Anonymous 2005). Historically, jellyfish have been consumed in China for over 1,700 years (Omori and Nakano 2001), but they are also a traditional food in many other Asian countries. In China, it is a tradition to have a jellyfish salad during a wedding or formal banquet; in Japan, jellyfish are served as an appetiser (Hsieh et al. 2001; Omori and Nakano 2001). With the burgeoning Chinese population, the demand for jellyfish is now rising. Indeed, some jellyfish fisheries in China are now fully exploited with stock enhancement being carried out in some areas (Dong et al. 2009). At least 10 species of jellyfish (all Rhizostomeae) are commercially harvested mainly from China, Japan and other parts of South East Asia (e.g. Indonesia, Malaysia, the Philippines, Thailand, Singapore), with one species *Rhopilema esculentum* being the most important species. Emerging fisheries are also developing in the Gulf of Mexico (the USA and Mexico) using *Stomolophus meleagris*, Australia (*Catostylus mosaicus*), India (*Crambionella orsini*) and Turkey (*Rhizostoma pulmo*). Although jellyfish have a low nutritional value (Doyle et al. 2007), their consumption is thought to have health benefits. For example, jellyfish are considered a cure for arthritis, hypertension, indigestion, fatigue and back pain (You et al. 2007) but are also consumed as a natural diet food or beauty enhancement drink (Hsieh et al. 2001). Indeed, jellyfish collagen has been used experimentally to treat patients with rheumatoid arthritis and may also have a significant medicinal potential for rebuilding muscle, cartilage and bone (collagen scaffolds used in tissue engineering) (Addad et al. 2011) as bovine and other animal sources of collagen become less available and more regulated.

The first records of harvested edible jellyfish date from 1950. Annual catches remained <5,000 Mt until 1970, but with increasing demand from the Japanese market, the jellyfish industry became more commercial in the 1970s with young medusae bred artificially in ponds or released into the sea to enhance the natural stock (You et al. 2007). Since 1992, catches of between 200,000 and 500,000 Mt year^{-1} have been consistently taken (Kingsford et al. 2000). While the wet tonnage of jellyfish harvested is broadly similar to other commercial fisheries, in monetary terms it is relatively minor compared with bony fish and cephalopods. Japan is the main consumer of jellyfish, importing 5,400–10,000 tonnes year^{-1} of semi-dried jellyfish products between 1988 and 1999, at a value of ~ US$25.5 million (Omori and Nakano 2001, Tables 3 and 4). Other consumers include South Korea (US$17 million), Singapore, Taiwan (US$20 million), Hong Kong and the USA (US$6 million) (values for 1995, see Kingsford et al. 2000).

Processing jellyfish is a low-cost but labour-intensive operation in Asia, involving Jellyfish Masters who oversee the whole process. The umbrella ('head') and oral arms ('legs') are separated and cleaned immediately after capture. There follows a stepwise reduction of the water content of both parts using a salt and alum mixture, a 3–4-day period of soaking in brine, followed by several transfers to another container of salt with a lower alum concentration. The salted jellyfish are dried on draining racks at room temperature. The whole process takes 20–40 days, resulting in a cured jellyfish containing 60–70 % water and 16–25 % salt that has a shelf life of 1 year at room temperature. The colour should be creamy white and have a crispy but tender texture (Hsieh et al. 2001). Prior to consumption, the jellyfish need to be desalted and rehydrated overnight. The jellyfish can be made into a number of dishes, either cooked or uncooked. To cater for the busy modern lifestyle, shredded, desalted ready-to-use products are now becoming available, packaged with a variety of condiments and sauces.

Jellyfish are also the source of novel compounds; indeed, one of the greatest benefits that jellyfish have had to society has been the discovery and subsequent development of the green fluorescent protein (GFP) (reviewed by Tsien 1998; Chalfie and Kain 2006; Zimmer 2009). Following the initial discovery of fluorescent proteins (FP) in jellyfish and other marine fauna, cloning techniques have produced FPs that are available across almost the whole visible colour spectrum, ranging from violet (emission peak 424 nm) through to far red (emission peak 650 nm) (Chudakov et al. 2010). Because of their range of colours and non-invasive characteristics, GFP and GF-like proteins have been described as 'living light microscopes' that have revolutionised studies of cell biology and physiology by allowing scientists and doctors to image and monitor cellular and molecular events taking place inside living cells and organisms. Applications can be broadly divided into structural (e.g. labelling and imaging of whole organisms, cells, organelles, nucleic acids and proteins) and functional (e.g. protein interactions, promoter activity, sensory activities, drug screening) (reviewed by Chudakov et al. 2010). Protein labelling is one of the most popular and widespread applications of FPs, as it allows us to observe protein expression localisation, translocation, interactions and degradation in living systems in real time. FPs also can help visualise particular cell types in whole animals, organs, tissues and cell cultures, which is particularly important in such fields as immunology, neurobiology and carcinogenesis, as it is helping us to understand how diseases such as cancer, Alzheimer's and Parkinson's develop. Multiple FPs can also be combined to visualise locations of different cell types in living systems, most notably demonstrated by the Brainbow application whereby many individual neurons can be visualised by more than 100 colours of FP. Whole animals can now be labelled with FPs to discriminate between transgenic and wild-type forms and for human entertainment, the creation of unusually coloured aquarium fish and other pets.

More recently there has been much research effort in extracting other compounds. A mucin (a glycoprotein that has lubrication and protective functions) called 'qniumucin' was found in all six jellyfish species examined. This mucin has significant potential as there are no methods to produce large quantities of mucins artificially for therapeutic use (Ohta et al. 2009) whereas jellyfish could be harvested in sufficient quantities to meet this demand. Applications include 'carriers for drug delivery, components of artificial extracellular matrices, antibiotic reagents, moisture retainers for cosmetic materials, and food additives' (Masuda et al. 2007). Venoms from different jellyfish species also have biological functions including profound cardiovascular activity, but research into the medical utility of these venoms is still its infancy, especially compared with terrestrial venoms (Hodgson and Isbister 2009).

5.2.3 Supporting Services

5.2.3.1 Nutrient Cycling

All ecosystem services are underpinned by supporting services, such as nutrient cycling and provisioning of habitats, to which jellyfish and other gelatinous zooplankton contribute significantly. For example, the remarkable filtration houses of the appendicularians play a hugely important and often underestimated role in nutrient cycling. The appendicularian filter house sieves and concentrates a wide range of particle sizes from 0.2 to 30 μm, thus capturing organisms from bacteria to microplankton (Gorsky and Fenaux 1998; Berline et al. 2011), much of which is unavailable to competing zooplankton (e.g. copepods). As they can directly obtain energy from the microbial loop, rather than the classic 'diatom-copepod-fish' food chain (Gorsky and Fenaux 1998), appendicularians play an important role in the nutrient cycling of plankton by providing an alternative energy pathway. Indeed, many adult and larval fish prey directly on appendicularians, especially the pleuronectids (Last 1978).

Jellyfish may also contribute significant but small amounts of nutrients to support primary production (Pitt et al. 2009). The products (inorganic nutrients C, N and P) regenerated by jellyfish excretion, mucus production and 'sloppy feeding' can be significant. For example, Pitt et al. (2005) showed that jellyfish blooms in

Lake Illawarra, Australia, produced up to 8 % of the phytoplankton N requirements. An elegant mesocosm study in a similar lake using two different species of jellyfish (one zooxanthellate jellyfish and one non-zooxanthellate jellyfish) revealed that excretion of nutrients (phosphate in this study) by non-zooxanthellate jellyfish can greatly increase phytoplankton production (West et al. 2009). In the same way, jellyfish-regenerated products released to the water are available to bacteria, i.e. for respiration rather than for production, and can create a 'jelly loop' involving the cycling of carbon between jellyfish, bacteria, heterotrophic nanoflagellates and ciliates (Condon et al. 2011).

Similar recycling and movements of nutrients occur for other jellyfish taxa, most notably salps, doliolids and appendicularians which produce faecal pellets and appendicularian houses (as discussed above in terms of carbon sequestration). For example, the discarded houses of appendicularians (often many a day) are used as a source of food by many organisms including copepods and leptocephali larvae (Alldredge 1976; Steinberg et al. 1994; Mochioka and Iwamizu 1996; Sato et al. 2001).

Jellyfish may also contribute indirectly to nutrient recycling by a process known as biogenic mixing: here, swimming animals contribute to oceanic mixing due to the displacement of water as they move through it (Katija and Dabiri 2009). As jellyfish swim between different layers in the water column, they facilitate the transport of nutrients and other dissolved matter across physiochemical boundaries. Considering the abundance of jellyfish and the scale of the diel vertical migrations that many oceanic jellyfish (e.g. pyrosomes, salps and siphonophores) undergo each day – up to 800 m (Wiebe et al. 1979) – such mixing can be significant and can have impacts on ecosystem function, e.g. via the resupply of nutrients to depleted surface waters which may enhance surface primary productivity.

The presence of jellyfish within marine systems can also enhance the delivery of carbon from phytoplankton to higher trophic levels. For example, there is an inherent inefficiency in the transfer of energy from phytoplankton through to herbivorous zooplankton through poor trophic phasing (Boero et al. 2008). However, because some jellyfish taxa (e.g. appendicularians and salps) can exploit this available resource, they can limit the amount of energy that would ordinarily enter the benthos as phytoplankton detritus (Boero et al. 2008).

5.2.3.2 Jellyfish as Prey

Predation upon jellyfish has been thoroughly summarised by Arai (1988, 2005), Ates (1988), Purcell (1997) and Pauly et al. (2009) and as such, does not require detailed replication here. However, in brief, it is well documented that a wide range of taxa including other jellyfish, molluscs, arthropods, fish, reptiles and birds routinely or episodically prey upon gelatinous organisms. Some examples of intraguild predation include the scyphomedusae *Cyanea capillata* feeding on *Aurelia aurita* (Purcell 1991), the siphonophore *Apolemia uvaria* consuming salps (11.3 % of diet) (Purcell 1981) and the hydromedusae *Aequorea victoria* having up to ten jellyfish species in its diet (mostly hydromedusae), totalling 10.5 % of the total number of prey items (Purcell 1991). There are very few examples of jellyfish that feed exclusively on other jellyfish; however, the ctenophore *Beroe cucumis* is known to feed heavily upon the ctenophore *Bolinopsis infundibulum*. In terms of other taxa that feed on jellyfish, fish are well represented. Arai (1988, 2005) compiled a detailed list of fish species that are known to have jellyfish in their stomach contents (at least 10 % of stomachs examined or to consume at least 5 % of the volume, weight or prey items eaten). The list now includes 69 species of fish in 34 families and is certain to expand with time (Arai 2005). Indeed, Pauly et al. (2009) using information extracted from FishBase (www.fishbase.org), data published by Arai (1988, 2005) and other sources found a total of 124 species of fish which are reported as feeding occasionally or predominately on jellyfish. Importantly, many species that feed on jellyfish are common and commercially valuable. For example, chum salmon (*Oncorhynchus keta*) can have a diet composed mostly of jellyfish (*Pleurobrachia* spp.) depending on location and time of year (Arai et al. 2003). Link and Ford (2006) examined the gut content of ca. 45,000 spiny dogfish (*Squalus acanthias*) between 1981 and 2000 and found that ctenophores constituted between 5 % and 15 % of total prey ingested, with the overall inference of an increase in abundance over the study period. Laboratory studies have shown that mackerel (*Scomber scombrus*) will feed on the hydromedusae (*Aglantha digitale*) when offered alone or with a mixture of copepod prey (Runge et al. 1987). Appendicularians, which are often one of the most abundant groups in the plankton, are a particularly important prey item for many larval fish (Gorsky and Fenaux 1998). Indeed, the appendicularians *Oikopleura dioica* and *Fritillaria borealis* can form between 40 % and 75 % of the prey of pleuronectiform (flatfish) larvae highlighting how some fish species may be almost dependent upon jellyfish during this early life history stage (Gorsky and Fenaux 1998). Clearly, jellyfish are important components of the diet of many fish species.

The most recognisable and observed predator of jellyfish is without doubt the leatherback sea turtle *Dermochelys coriacea*. However, it was only recently that our understanding of how such large animals (~ 450 kg) can survive on a diet of jellyfish has been considerably advanced. For example, Houghton et al. (2006) demonstrated how the distribution of the large jellyfish *Rhizostoma octopus* (in the Irish Sea) explained almost a quarter of the variance in leatherback sightings over a period of >50 years. By attaching a video camera system to the carapace of leatherbacks ($n = 19$), Heaslip et al. (2012) demonstrated that an adult leatherback can consume on average 261 jellyfish d^{-1}, (or 330 kg jellyfish wet mass d^{-1}), which is equivalent to 73 % of its body mass d^{-1}. Even though jellyfish have a low calorific value compared to other prey items (Doyle et al. 2007), consumption of sufficient quantities can sustain large predators such as leatherbacks. This is made possible by the high digestion rates of jellyfish which can be considerably faster than other prey items (e.g. 20 × faster than shrimp; Arai et al. 2003). From the above, it is clear that jellyfish offer a potential prey source for many different animals, with leatherback sea turtles at one end of the spectrum (specialised jellyvore) and a large number (hundreds) of other animals that opportunistically or regularly include jellyfish in their diets (Arai 2005).

5.2.3.3 Jellyfish as Predators

As a group, jellyfish are hugely important predators in pelagic marine systems (Pauly et al. 2009). Considering their longevity and evolutionary head start on other taxa (evolved 500 to 540 MYA, Richardson et al. 2009), they have arguably shaped pelagic marine ecosystems with their diverse array of armature and prey-capture mechanisms. Such feeding mechanisms will be discussed in more detail below under the ecological role of jellyfish, but briefly, the diversity of feeding mechanisms and body sizes ensures that jellyfish are capable of feeding on a large range of prey types and sizes (from microheterotrophs, zooplankton, other jellyfish and fish). Furthermore, most jellyfish are characterised by some sort of selectivity (Purcell 1997). The variety of feeding mechanisms, nematocyst and colloblast structures, toxicity of nematocysts, life cycle and life history, prey behaviour and escape ability (Purcell 1997; Boero et al. 2008) are all thought to contribute to different diets observed. Most scyphomedusae, hydromedusae and siphonophores are carnivorous and feed on a variety of zooplankton taxa from copepods, veliger larvae, fish eggs/larvae and other jellyfish. Most have broad diets; however, there are some specialists such as the siphonophore *Hippopodius hippopus* feeding only on ostracods (Purcell 1981).

Understandably, consideration of jellyfish as predators centres typically on their capacity to deplete resources available to commercially valuable fish stocks (Brodeur et al. 2002; Lynam et al. 2005; Hong et al. 2008). Indeed, when jellyfish occur in high numbers, their collective prey-consumption rate can be so high that this predation directly or indirectly controls the population size of other zooplankton organisms including larval fish (Purcell 1989). More specifically, intense predation by jellyfish on certain prey can cause a shift in the trophic structure of marine communities as a result of trophic cascades. There is some evidence that in many systems in the world jellyfish biomass can exceed that of finfish stocks (e.g. Lynam et al. 2006), although consideration must be given to the ratio of wet to dry body mass in these different faunal assemblages. This is certainly an issue of grave concern, but care should be taken not to consider jellyfish as the sole causative factor, as the dramatic depletion of global finfish stocks is more closely linked to human demand and the impacts of climatic variation (Graham and Harrod 2009). Nonetheless, there is genuine concern that jellyfish may capitalise on the niche left by the removal of fish preventing the re-establishment of stocks over time leading to an ecological phase shift (Knowlton 2004). This issue warrants closer attention however, as this scenario requires prey (i.e. crustacean zooplankton) to be a limiting factor as predation on the same food source does not necessarily lead to competitive exclusion. Put another way, the co-occurrence of jellyfish and fish within a particular system is not a recent phenomenon, yet until human intervention fish stocks did not face imminent collapse. As before, we are not challenging the assertion that jellyfish pose a threat to the sustainability of remaining fisheries; rather that their negative portrayal can mask the need to consider them as natural components of marine systems, rather than a mere threat to human enterprise.

5.2.3.4 Provision of Space: Jellyfish as Habitats and Nurseries

Jellyfish are relatively large compared to other planktonic organisms but are comparatively slow swimmers when compared with nektonic animals of a similar size or mass. In an environment that is remarkably devoid of physical habitat, these attributes combined with the intricate morphology of jellyfish create a structurally complex mosaic of surfaces and constantly changing ‘nooks and crannies’ for other marine organisms to exploit. In much the same way as coral reefs and oyster beds create a three-dimensional habitat for a great diversity of benthic organisms, jellyfish provide this three-dimensional structure in pelagic habitats (biological engineers) (Breitburg et al. 2010). For many taxa, clearly their relationship with jellyfish has laid the ‘foundation’ for the successful invasion of the pelagic zone (e.g. amphipods and pycnogonids) (Laval 1980 in Bishop and Geiger 2006) and subsequently for the evolutionary diversification and evolution of new taxa (Pagès 2000). The relationships and use of jellyfish are so varied and often so bizarre and intricate that the symbiotic relationship between jellyfish and other marine organisms is at times more akin to those typically described for tropical rainforests. For simplification here we describe three types of relationships between jellyfish and symbionts based on how they use and exploit this largely transparent but solid substrate. Jellyfish can provide (1) pelagic refugia or shelter, (2) pelagic substratum and (3) a host for algal symbiotic associations.

Pelagic refugia: One of the best documented biological interactions between jellyfish and a marine organism is the interactions between jellyfish and juvenile fish. The association is generally considered to be a facultative symbiotic relationship, whereby a jellyfish may be the only available refuge in a pelagic environment for juvenile fish. Indeed, fish from over 333 families are known to show aggregative behaviour beneath floating objects, 9 of which are known to associate with jellyfish (Castro et al. 2001). Four of these families are pelagic, three are demersal and two are deep-sea inhabitants (Mansueti 1963). For demersal species, jellyfish may act as a substitute for their eventual benthic habitat until they are of sufficient size to recruit into these benthic habitats (Kingsford and Choat 1989). It is also possible that the juvenile fish obtain food from the association via a range of different pathways, i.e. by feeding directly on (i) the jellyfish itself, (ii) zooplankton taken from the host, (iii) prey encountered by the fish as the jellyfish moves through the water column and (iv) predation upon amphipod parasites present on the jellyfish host (Mansueti 1963; Purcell and Arai 2001). Together, the provision of shelter and food may increase the survival of juveniles to adulthood (Brodeur 1998; Lynam and Brierley 2007). These beneficial interactions are vastly overshadowed in the literature by introductory paragraphs (often on subjects completely unrelated to fisheries) that make reference to negative interactions such as predation or competition for resources between juvenile fish and jellyfish. We are not claiming that competition or predation are negligible, rather that jellyfish-fish interactions are complex and not always detrimental to fish.

A pelagic substratum: While jellyfish provide shelter for developing fish, they provide a substratum (habitat) for a range of taxa from microbes through to invertebrates including crustaceans (including barnacles, copepods, amphipods, brachyuran crabs, shrimp) (Perissinotto and Pakhomov 1997; Pagès 2000), pycnogonids (Pagès et al. 2007), digeneans (Martorelli 2001) and protists (Moss et al. 2001). For the majority of these 'hitch-hikers', the exact relationship between the jellyfish host and symbiont (whether facultative, commensal or parasitic) may be unknown (Gasca and Haddock 2004; Towanda and Thuesen 2006). The most well-known ectosymbiont is the amphipod *Hyperia medusarum*. In a recent study Towanda and Thuesen (2006) demonstrated clearly that *H. medusarum* parasitises *Phacellophora camtschatica* by directly consuming tentacles and other tissues, with 100 % infestation rates at times and as high as 446 individuals on a single jellyfish. This amphipod probably overwinters as juveniles on holoplanktonic jellyfish (Towanda and Thuesen 2006). These overwintering jellyfish therefore act as intermediate hosts until the definitive host *P. camtschatica* appears in spring and the hyperiids jump ship (Towanda and Thuesen 2006). This same study also highlighted the symbiosis between brachyuran crabs and jellyfish. At least eight species of brachyuran crabs have now been found on jellyfish (Towanda and Thuesen 2006). On the Pacific coast of North America, megalopae and instars of *Cancer gracilis* can be found 'riding' *P. camtschatica* jellyfish from early May until October and are never found in the plankton. This symbiotic relationship is unusual as initially the megalopae feed on the jellyfish, but as they develop and grow as instars, they feed more on the parasitic *H. medusarum* and therefore have a beneficial relationship with the host (Towanda and Thuesen 2006). Some parasites use jellyfish as intermediate hosts en route to their definitive host that is normally a fish. For example, the prevalence of metacercaria (resting) stage of digeneans in three jellyfish species off Argentina varied between 1.4 % and 30 %, highlighting the importance of jellyfish in the distribution of metacercaria (Martorelli 2001).

5.2.3.5 Jellyfish as Hosts for Algal Symbiotic Associations

Normally reserved for discussions on reef building corals, many jellyfish taxa also have algal symbiotic zooxanthellae (photosynthetic dinoflagellates). The golden jellyfish (*Mastigias papua*) conduct daily horizontal migrations and avoid shadows in landlocked marine lakes in Palau in order to maintain their zooxanthellae in direct sunlight (Dawson and Hamner 2003). Even more unusual is the behaviour of the upside-down jellyfish *Cassiopea* sp., which spends the majority of their time upside down resting on the seabed. They do so to maximise photosynthesis as they contain zooxanthellae in their oral arms, and their activities can increase benthic oxygen production almost 100-fold (Welsh et al. 2009). Another algal host is the pleustonic jellyfish *Velella velella*. This species is found in surface waters circumglobally in tropical and temperate open ocean waters (Purcell et al. 2012), where its symbiotic zooxanthellae are able to photosynthesise and subsidise the host's energy budget.

5.2.4 Cultural Services

There is no doubt that marine organisms contribute to widespread human curiosity (Greene 2005), particularly as most are never seen, only sparingly at the surface or rarely stranded on our shores. Indeed, Hardy (1956) eloquently wrote that 'how much more curious many of us might be if the sea were in fact separated from us by a vertical screen instead of lying beneath us under a watery floor'. With the explosion of jellyfish aquaria throughout the world, jellyfish are now at the fore of Hardy's proverbial sea wall, as ambassadors of the marine environment, enthralling people with their 'unfamiliar forms, like floating parachutes with trailing tentacles' (Hardy 1956).

For 20 years, the Monterey Bay Aquarium in California has been associated with stunning displays of jellyfish, most notably the Pacific Sea Nettle (*Chrysaora fuscescens*). Between 2002 and 2008, the aquarium ran the award-winning 'Jellies: Living Art' special exhibition, which combined displays of 25 species of jellyfish with works of art depicting jellyfish. While many of the jellyfish species were local to the area, several were rare and had never been maintained in captivity or seen in the USA before. The concept of this innovative exhibition was to celebrate the beauty of these gelatinous organisms and show how contemporary and classical artwork draws inspiration from the sea. The galleries of art and jellyfish exhibited together highlighted visual themes from nature and art: shape and size, rhythm and movement and colour and pattern. To date, this has been the most popular display in the aquarium's history attracting over 10 million visitors. Many people have enjoyed the aesthetic aspects of the display and used words like relaxing, peaceful, colourful and beautiful to describe many of the experiences (Monterey Bay Aquarium 2004). The display won several awards including the prestigious Curator's Choice Award from the American Association of Museums and the Exhibit Award from the Association of Zoos and Aquariums. The Monterey Bay Aquarium is not unique in displaying jellyfish as a visitor attraction. Many public aquaria around the world now maintain their own jellyfish for year-round displays, with more than 50 in the USA alone.

Several ecosystems are able to utilise jellyfish populations as ecotourist attractions. The most famous is Jellyfish Lake (formerly Ongeim'l Tketau) in Palau, a landlocked marine lake on Eil Malk Island, home to year-round populations of several million golden jellyfish, *Mastigias* sp., and common jellyfish, *Aurelia* sp. Since the marine lakes of Palau were brought to the attention of the general public in the early 1980s, many articles have appeared in print, radio and film media, and Jellyfish Lake has become one of the most popular snorkelling sites in the tropical Pacific (Dawson et al. 2001). Palau's main industry is adventure and ecotourism (accounting for >40 % of gross domestic product) as visitors are attracted to the coral reefs and tropical rainforests of this highly biodiverse region. Between 1986 (when Jellyfish Lake was first incorporated into dive tours) and 1997, tourism in Palau increased by 500 % (Dawson et al. 2001). It is estimated that, on average, 30,000 tourists visit Jellyfish Lake each year, providing a valuable source of revenue for the country.

Many jellyfish have attributes that can astonish, none more so that the 'immortal jellyfish' *Turritopsis nutricula* that can escape death by transferring back from a fully mature adult individual medusae into a polyp (Piraino et al. 1996). Such attributes also make jellyfish conceptually interesting animals for experimental biology (Boero 2002; Mackie 2002). Within this context it is important that we re-shift our focus so that jellyfish do not become the Trojan horse for 'doom and gloom'. Recruiting volunteers to count jellyfish beach strandings is an excellent means of encouraging public participation in science, known as citizen science, and enhancing the cultural appreciation of the marine environment. Indeed, as Silvertown (2009) stated 'the best way for the public to understand and appreciate science is to participate in it'.

5.3 Spreading the Word: Highlighting the Ecological Role of Jellyfish to the Non-specialist Community

In most cases where jellyfish have been included in marine fisheries or ecosystem models, all species are considered either a single functional group or an 'average' group of gelata (see Haddock 2004) feeding on the same prey throughout their life history (Boero et al. 2008; Pauly et al. 2009). Indeed, the trophodynamics of multiple gelatinous species within a 'jellyweb' (Robison 2004) or changes in trophic position in space and time are rarely taken into account (Boero et al. 2008). The view that jellyfish are an amorphous component in ecosystem models can now be challenged with further evidence emerging that jellyfish might be as varied in their trophodynamics as other marine organisms (Fleming et al. 2011). For example, concomitant with studies showing distinct size-based shifts in prey in fishes (Olson 1996; Harrod et al. 2005), dietary and sized-based trophic shifts in the moon jellyfish *Aurelia aurita* (Graham and Kroutil 2001; Fleming et al. 2011) suggest jellyfish could exhibit similar trophic complexities to fish.

As is often the case, jellyfish researchers and fisheries scientists often operate in different academic spheres. Pauly et al. (2009) highlighted this problem and provided clear guidance to jellyfish researchers on how to generate data that might help bridge this gap. An important point is that we cannot expect the ecological modelling community to fully take account of the trophic complexity of jellyfish if we are providing them with little evidence to go on. For example, given that jellyfish constitute a polyphyletic assemblage that exceeds 1,200 species, the classification of clear functional groups would greatly simplify and improve how the non-specialist community engages with jellyfish research. Indeed, as an example of how this might be achieved, Haddock (2007) classified ctenophores in terms of feeding mechanisms, e.g. tentacles for feeding, lobes for feeding, engulfers and trophic specialists. Riisgård and Larsen (2010) also wrote an excellent review of suspension-feeding invertebrates, which included several jellyfish taxa listing them as mucus-net filter feeding (salps), cnidae prey-capture mechanisms and colloblast prey-capture mechanisms. If we take one of these groups – tentaculate feeders (Fig. 5.2) – as an

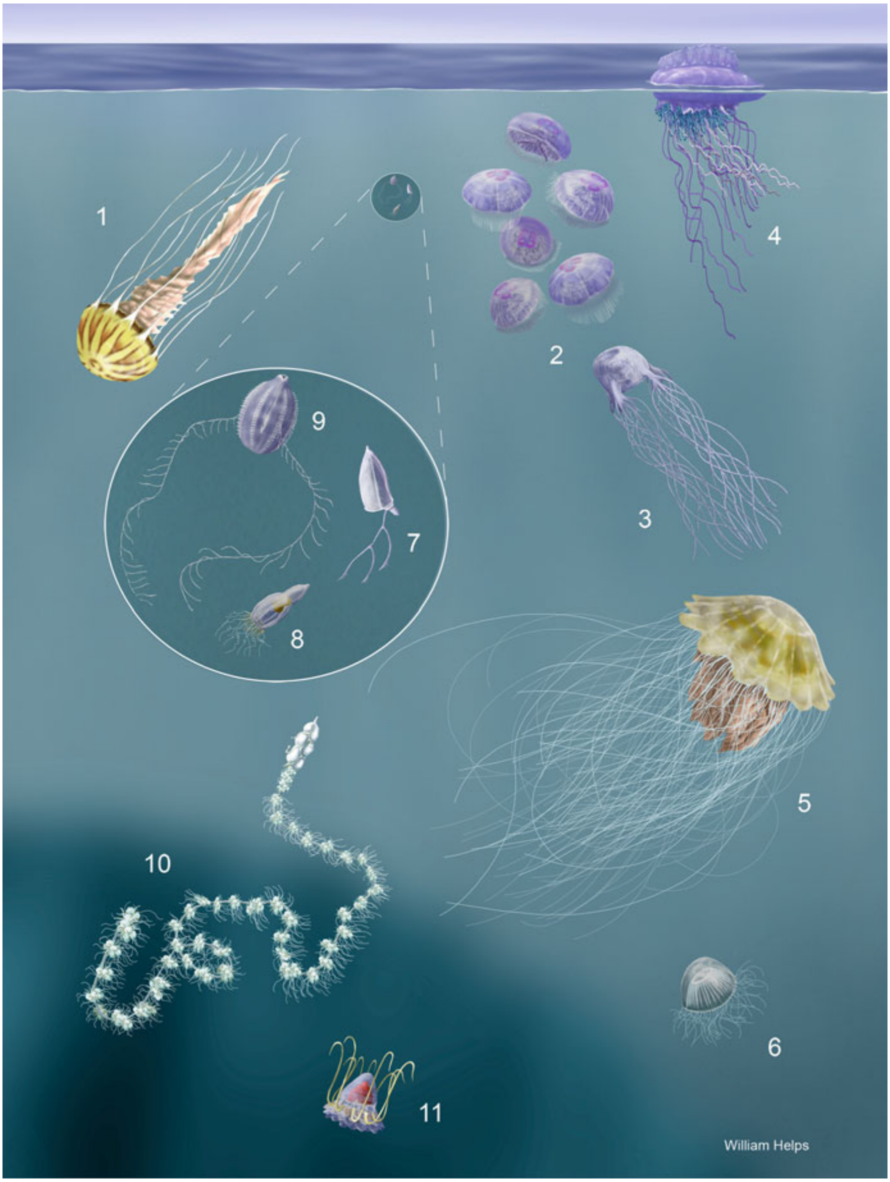

Fig. 5.2 The diversity and relative size of jellyfish within one functional group – the tentaculate predators. Figure illustrates the great variation in jellyfish morphology (e.g. bell shape, colonial structure) and tentacle length, number and type (i.e. nematocyst or colloblast bearing). (1) *Chrysaora hysoscella* has 24 tentacles (up to 4 m in length when fully extended) and well-developed oral arms. It swims continuously and fluid motion is responsible for prey entrainment and capture along tentacles and oral arms. (2) *Aurelia aurita* (aggregation). Each *A. aurita* has hundreds of very short tentacles typically not longer than one bell diameter. *A. aurita* uses the flow of water during bell pulsation and especially contraction (i.e. recovery stroke) to capture prey

example to illustrate the diversity of jellyfish morphology and trophodynamics within one 'functional group', we find gelatinous species capable of feeding on the smallest of particles including protistan prey (e.g. hydromedusae; Colin et al. 2005) through to those that are capable of feeding on fish (e.g. *P. physalis* and *Cyanea* spp.). Saliently, within most jellyfish taxa (especially scyphomedusae and hydromedusae), much of the foraging activity is related to bell size and shape and ultimately how they use their bell and its tentacles to capture prey (Costello et al. 2008). For example, in a seminal study, Costello et al. (2008) described two basic propulsion/foraging modes for scyphomedusae and hydromedusae: typically small 'ambush predators' and larger 'cruising predators' (>200 mm) (with some exceptions; e.g. see Sørnes et al. 2008). This difference in strategy emerges from an architectural constraint imposed by having weak subumbrellar muscles (one cell thick) and therefore limited bell shape for large jellyfish. For example, large medusae (>200 mm) are typically flattened (oblate) and therefore not capable of jet propulsion, whereas small medusae can have a spectrum of bell shapes from flattened to prolate. Such foraging modes have profound consequences for prey selection, as the large jellyfish are dependent on 'rowing' through the water to create vortices to entrain prey (Costello and Colin 2002). Smaller prolate jellyfish typically swim via jet propulsion (to exploit new areas quickly) but feed by drifting with outstretched tentacles. These two modes result in interspecific dietary differences with cruising predators feeding mostly on soft-bodied prey (other jellies, and fish eggs and larvae), whereas ambush predators can impact on crustacean zooplankton (Costello and Colin 2002). Central to this variation in tentaculate foraging strategy and morphology is the

Fig. 5.2 (continued) (Costello and Colin 1994) during continuous swimming. (3) *Chironex fleckeri* has a box-like appearance with groups of tentacles located at each corner. They are unusual among tentaculate predators as they have well-developed eyes (including image forming optics) that enable it to use terrestrial visual cues for navigation and ultimately increase chances of prey capture (Garm et al. 2011). (4) *Physalia physalis* has a gas-filled float that keeps it at the surface with tentacles trailing below. Unwary prey, especially fish larvae (Purcell 1984) simply drift into the tentacles. (5) *Cyanea capillata* is a large and highly venomous jellyfish with hundreds of long tentacles. *C. capillata* can capture prey by dragging its long tentacles through both the power (contraction) and recovery (relaxation) stroke vortices. It may also ambush cruising prey as many long tentacles lie outside the vortices (Costello and Colin 1995). (6) *Aequorea victoria* has a flattened bell (oblate) and has a flow-based feeding mechanism, i.e. continuously swims and entrains soft-bodied prey in its hundreds of tentacles (Costello and Colin 2002). (7) *Muggiaea atlantica* swims in an arc to spread out its tentacles and remains virtually motionless for several minutes (Mackie et al. 1987). (8) *Leuckartiara octona* is a streamlined or prolate jellyfish that swims by jet propulsion. It is an ambush predator that feeds by drifting and waiting for prey to encounter its outstretched tentacles. (9) *Pleurobrachia pileus* has two tentacles armoured with colloblast cells (special adhesive cells rather than nematocyst bearing). It swims in a semicircle, and once its tentacles are fully extended, it stops and waits for a prey item to become ensnared in the sticky tentacles (Haddock 2007). (10) *Apolemia uvaria* can be 20 m in length and has repeating units called cormidium which has numerous highly extensible tentacles (Mackie et al. 1987; Mapstone 2003). (11) *Periphylla periphylla* is a mesopelagic jellyfish that swims with its tentacles in aboral position (forward, unlike most other jellyfish) forcing (ramming) water and entrained prey past the tentacles (Sørnes et al. 2008). For scale, *Cyanea capillata* is typically 0.6 m in diameter (Scientific illustration by William Helps) concomitant evolution of nematocysts, one of the most complex secretion products of any cells found in the animal world (Mackie 2002). They have been described as a 'secret weapon' (Mackie 2002; Fautin 2009) that has 'enabled the group to achieve enormous success as predators with little of the investment in elaborate sensory and morphological specialization that characterizes most predators' (Mackie 2002). Indeed, tentaculate jellyfish are tactile rather than visual predators feeding efficiently in turbid water and during the hours of darkness (Hays et al. 2012). The remarkable exception to this rule is the cubozoans which have well-developed eyes and actively hunt their prey (Garm et al. 2011).

Returning to our original goal of showcasing jellyfish in a more positive light, we propose that functional groups can improve the transfer of information between jellyfish researchers and the wider non-specialist community. By using an existing ecological framework, we may encourage jellyfish researchers to view the group more as a collective rather than individual species. As studies on the trophic complexity of jellyfish continue to emerge, the conceptual approach detailed here may help with the broader dissemination of key findings.

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Chapter 6
Living with Jellyfish: Management and Adaptation Strategies

Cathy H. Lucas, Stefan Gelcich, and Shin-Ichi Uye

Abstract While jellyfish are some of the most ancient multicellular organisms on Earth, man only started to take notice of their impact on human activity and enterprise from about the 1960s. In some regions of the world, jellyfish blooms impose considerable socio-economic hardship to net-based fisheries, aquaculture, power generation and tourism. Blooms are likely to be difficult if not impossible to eradicate, but these industries are striving to develop management strategies that will enable them to successfully coexist with blooms. This chapter reviews the detrimental effects that jellyfish have on society and human wellbeing. We also summarise adaptation and management strategies that are currently being developed and utilised by fishing, power generation and tourism industries to educate and inform the public and manage the actual jellyfish blooms and help ensure the financial viability of these industries in regions that experience blooms.

Keywords Jellyfish blooms • Socio-economic impacts • Net-based fisheries • Giant jellyfish • Salmon aquaculture • Power station water intakes • Mediterranean tourism • Box jellyfish • Irukandji • Citizen science • Jellyfish forecasting

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6.1 Introduction

While cnidarian medusae and ctenophores (hereafter termed ‘jellyfish’) are some of the most ancient multicellular organisms on Earth, humans only started to pay attention to them from the middle of the last century, and we have now come to realise that jellyfish impact society and human health in a number of ways. They frequently make the headlines around the world with well-known examples such as the dangers of swimming in the sea off northern Australia during the ‘stinger season’ when the potentially deadly box jellyfish, *Chironex fleckeri*, are present; reports of mass stranding of the mauve stinger, *Pelagia noctiluca*, on Mediterranean beaches; and the impact that giant jellyfish, *Nemopilema nomurai*, have had on the Japanese and Korean set-net fishing industry in recent years. Much of what people perceive about jellyfish and jellyfish blooms in particular is based on somewhat sensationalist headlines, for example, ‘Monster jellyfish hit coast’ (thesatellite.com.au, 16 Feb 2010), ‘Attack of the blobs’ (nature.com, 1 Feb 2012), ‘Invasion of the killer jellyfish’ (mirror.co.uk, 13 Aug 2008) and ‘Climate change and the scary jellyfish scourge’ (washingtonpost.com, 3 Aug 2009).

Given the predominance of negative headlines about jellyfish, it may be rather easy to assume that jellyfish serve no purpose to man, other than be a nuisance. However, jellyfish have had a surprisingly long and fruitful relationship with man. The Chinese have been eating jellyfish for well over a thousand years and value them for their medicinal properties (Hsieh et al. 2001; Omori and Nakano 2001). The chemical properties of jellyfish are stimulating major advances in biomedical research and providing a host of opportunities for medical and biotechnological applications. Jellyfish toxins are being analysed for their potential anticancer or antioxidant properties (reviewed by Mariottini and Payne 2010), while jellyfish collagen is being considered as a candidate for replacing bovine or human collagens in selected biomedical applications (Addad et al. 2011). In 1991, nearly 2,500 polyps and ephyrae of *Aurelia aurita* were sent up into space in the space shuttle *Columbia*, in an experiment to test the effects of microgravity on development (Spangenberg 1992). Research on jellyfish species has resulted in two Nobel Awards. The first, a Nobel Prize in Medicine, was awarded to Charles R. Richet in 1913 for his discovery of anaphylaxis following experiments on the Portuguese man o’ war, *Physalia physalis*. The second, a Nobel Prize in Chemistry, was awarded to Osamu Shimomura, Martin Chalfie and Roger Tsien in 2008 for their discovery and subsequent cloning and development of green fluorescent proteins (GFPs) from the crystal jellyfish, *Aequorea victoria*.

The ecological and societal benefits of jellyfish have been explored in detail by Doyle et al. in Chap. 5. The aim of this chapter is to review the detrimental effects that jellyfish have on society and human wellbeing, from fishing and aquaculture to power provision and tourism. We also discuss the management and adaptation strategies that are being developed to alleviate the impact that jellyfish blooms are having on human activities and enterprise in the sea.

6.2 Detriments of Jellyfish to Society

Predominantly, jellyfish blooms affect the 'provisioning' and 'cultural' ecosystem services (www.maweb.org/en/index.aspx), in particular fishing and aquaculture (Doyle et al. 2008; Nagata et al. 2009), power and desalination (Daryababard and Dawson 2008) and tourism (Fenner et al. 2010) industries (see reviews of Purcell et al. 2007; Dong et al. 2010). These detrimental socio-economic impacts on humankind are widely reported by the media. The scientific community also tends to focus on the negative impacts of jellyfish blooms on human enterprise and health, although in many cases rigorous analysis is hampered by a lack of quantitative evidence.

6.2.1 Net-Based Fisheries

Jellyfish and commercially important fish species interact in a number of complex ways. Jellyfish feed on the eggs and larvae of fish, are competitors with zooplanktivorous fish for the same food resource (i.e. they are at or near the same trophic level) and may transmit parasites and bacterial pathogens to fish (Purcell and Arai 2001; Delannoy et al. 2011). Commercial fisheries are dominated by pelagic fish and shrimp in coastal regions supported by high primary and secondary productivity (Doyle et al. 2008; Purcell 2012), and there is evidence that jellyfish numbers have increased in regions where fish stocks have declined due to overfishing, for example, the Benguela upwelling (Lynam et al. 2006). Similarly, several marine fishery resources in Chinese waters have been heavily exploited in recent decades (Tang et al. 2003). In the major fishing grounds of the northern East China Sea, *Cyanea nozakii* jellyfish accounted for up to 98 % of the total fishery catch in the bloom years of 2003 and 2004 (reviewed by Dong et al. 2010).

Although the economic costs associated with jellyfish feeding on larval fish stocks are very difficult to assess, direct physical interference by jellyfish on net-based fisheries is without question and financially demonstrable. Blooms of jellyfish cause severe nuisance by (1) clogging and bursting fishing nets, (2) decreasing fish catch, (3) killing and spoiling fish, (4) stinging fishermen as they try to remove jellyfish, (5) increasing the time and labour effort during the removal of medusae from the nets and an in some instances, (6) causing fishing boats to capsize (e.g. Kawahara et al. 2006; Purcell et al. 2007; Uye 2008; Dong et al. 2010; Quiñones et al. 2012). This is particularly so for Japanese and Korean fisheries located in the Sea of Japan, Yellow Sea and East China Sea, where over the last 10 years, most net fisheries have been affected by blooms of the ubiquitous moon jellyfish, *Aurelia aurita*, and giant jellyfish, *Nemopilema nomurai* (Uye 2008). The latter species is one of the largest jellyfish in the world capable of growing to a size of 2-m diameter and 200-kg wet weight and is distributed in the East Asian Marginal Seas (see Uye, Chap. 8 for detail).

According to the Japanese Ministry of Agriculture, Forestry and Fisheries, there are over 4,000 set-nets of various scales around the Japanese coast (http://maff.go.jp/e/index.html), 1,900 of which are located in regions where *Nemopilema* are present. A large-scale set-net consists of a 2–5-km-long 'leading net' heading into a large chamber and a series of two progressively smaller 'trapping nets', which work by herding the fish into the second trapping, or 'harvest net'. The set-net fisheries represent a significant investment in Japan. The installation cost of one net is 300–700 million JPY (US$ 3.8–8.9 million) and provides a livelihood for between 10 and 30 fishermen. The annual revenue from a large net can be up to 100–300 million JPY (up to US$ 3.8 million); thus, it requires a long-term investment in order to make a profit. This type of fishery has been severely affected, in some years by *N. nomurai*. Following the 2005 bloom in Japan, there were >100,000 *Nemopilema*-related complaints registered with the Fisheries Agency of Japan. Of these, 60 % were related to reduced catch, value of catch and suspension of operations, 30 % to increased labour time to remove fish and 10 % to net damage. The financial implications of *Nemopilema* blooms can be severe. The cost of fixing a set-net is between 1 and 10 million JPY (US$ 12,600–126,000), while the cost of physically modifying a net (i.e. larger mesh size and bypass nets; see Chap. 8) to mitigate the impact of jellyfish is 5–10 million JPY (US$ 63,000–126,000). During these periods, fishing is suspended and the fishermen may be laid off work. Following the 2005 bloom, Aomori Prefecture (northernmost prefecture on the largest island of Japan, Honshū) estimated the monetary loss to be two billion JPY (US$ 25 million), while the nationwide loss was estimated to be 30 billion JPY (US$ 380 million) (Uye 2008). In 2009, perhaps a largest bloom year ever, the monetary loss was apparently less than 10 billion JPY (US$ 125 million), thanks to early warning of the approaching bloom.

Japanese and Korean fisheries are not alone in being impacted by jellyfish blooms, although many incidents are not reported. The shrimp fishery in the Gulf of Mexico has experienced US$ 10 million in lost revenue as a result of the invasive rhizostome *Phyllorhiza punctata* (Graham et al. 2003). Several fisheries in South America have also been affected. In southeastern Brazil, for example, the rhizostome *Lychnorhiza lucerna* forms year-round blooms which have affected the shrimp fishery by shortening and displacing hauls, as well as clogging nets (Nagata et al. 2009). *Lychnorhiza lucerna* also causes fishing problems in northern Argentina by reducing total fish captures and catch quality, damaging nets and preventing fishermen from operating (Schiariti et al. 2008). The Peruvian anchovy fishery, one of the largest single-species fisheries in the world, is seasonally affected by the semaeostome *Chrysaora plocamia* (see Chap. 10). Summer blooms of this species appear as by-catch in the seine nets. In the summer of 2008–2009, medusae accounted for >10 % of the catch (by weight) in 10 % of the hauls and >30 % of the total catch in 5 % of the hauls. The fishery factories deduct the weight of jellyfish when the by-catch exceeds 13 % (by weight) and refuse to receive the catch if jellyfish account for >40 % of the catch by weight. It is estimated that in 2008–2009 *C. plocamia* caused an economic loss of US$ 200,000 in just over 1 month (Quiñones et al. 2012).

6.2.2 Aquaculture

While it is well established that jellyfish cause problems for some net-based fisheries, rather less well known is the negative impact that large aggregations of jellyfish and ctenophores have on the aquaculture industry (Båmstedt et al. 1998). For example, when mass numbers of jellyfish such as the holoplanktonic *Pelagia noctiluca* develop, they may get transported into coastal waters and become aggregated around the cages of fish farms by tidal currents (Doyle et al. 2008). Damage to fish may be indirect, through hypoxia and subsequent suffocation when there is insufficient water exchange between the cage and surrounding water column, or direct, via stinging of the skin and gills as jellyfish pass through the mesh of the cages, either intact or becoming broken up into smaller pieces (Baxter et al. 2011a; Mitchell et al. 2012). The pieces still possess their nematocysts that can be discharged, therefore injecting toxin into the fish which is particularly problematic if this occurs around the eyes and gills (Rodger et al. 2011). If tissues containing nematocysts are inhaled, severe lesions of the gills occur, which leads to respiratory and osmoregulatory distress, reduced feeding and sometimes subsequent death (Bruno and Ellis 1985; Baxter et al. 2011a, b; Rodger et al. 2011). In addition, damaged gills may become infected by bacterial fish pathogens, such as *Tenacibaculum maritimum*, which has been shown to be carried by the jellyfish themselves (Delannoy et al. 2011).

Several species of jellyfish have been reported to cause both catastrophic large-scale fishkill events and the more chronic problem of gill damage in marine-farmed fish (Table 6.1) (Rodger et al. 2011). Notable examples of mass mortalities include the 250,000 Atlantic salmon killed by a 26-km^2 bloom of the scyphomedusa *Pelagia noctiluca* in the northern Irish Sea in November 2007 (Doyle et al. 2008) and >100,000 salmon killed by the siphonophore *Muggiaea atlantica* in Norwegian coastal waters (Fosså at al. 2003). Between 2003 and 2005, gill disorders were one of the most significant causes of mortality in the Irish salmon farming industry, resulting in an annual average mortality of 12 % (Rodger et al. 2011). Scottish fish farms have also suffered fishkills and poor health associated with the presence of jellyfish such as *Aurelia aurita*, *Cyanea capillata* and *Solmaris corona* (Fig. 6.1, redrawn from Nickell et al. 2010). Of the specific plankton-related incidents reported to Marine Scotland Science between 1999 and 2005 from around Scotland, including Shetland, approximately 60 % of fish deaths by weight (i.e. 5,700 tonnes) and numbers (i.e. 2.8 million) were due to jellyfish. Using recorded data from a subset of farms in the Scottish region of Skye and the Outer Hebrides during 2002–2005, mortalities caused by jellyfish or plankton accounted for >10 % of total recorded losses in terms of fish numbers and 17 % of fish biomass (http://www.scotland.gov.uk/Topics/marine/marine-environment/species/plankton).

Quantitative data charting jellyfish-associated economic losses for fish farmers are scarce, but costs are related to (1) direct losses caused by fish mortalities and disposals; (2) reduced growth during or after exposure to harmful agents such as jellyfish, harmful algae, parasites and bacteria; (3) increased operational costs; (4) production losses during emergency slaughtering and the resulting reduced prices;

Table 6.1 Summary of damage and death of farmed fish caused by gelatinous zooplankton (hydrozoans, siphonophores, scyphozoans, ctenophores)

Species	Country/region	Damage caused
Apolemia uvaria	Sweden, Norway	600 tonnes salmon killed
Aurelia aurita	Norway, Shetland, Ireland	Farmed salmon affected
	Lake Hachirogata, Japan	Mass mortality of fish and bivalves
Bolinopsis infundibulum	Norway	Farmed salmon affected
Catablema vesicarium	Outer Hebrides, Scotland	Salmon killed
Cyanea capillata	Scotland, Ireland	90,000 salmon killed in Ireland in 2004 1,000 salmon killed in Scotland 1996
Moerisia lyonsi	USA	Killed decapods in mesocosms
Muggiaea atlantica	Norway	>100,000 farmed salmon affected by 2,000 siphonophores m^{-3}
Pelagia noctiluca	Brittany, France	Significant mortalities of salmon and trout
	Japan	Mortality of penned fish
	Northern Ireland	250,000 salmon killed
Phialella quadrata	Shetland	1,500 fished killed
Porpita porpita	Japan	Mortality of penned fish
Rhizostome jellyfish	Goa, India	Shrimp
Solmaris corona	Scotland	650,000 farmed salmon mortalities in 2 days in 2002
Velella velella	Ireland	Skin and gill pathology observed in salmon

Source: Båmstedt et al. (1998), Purcell et al. (2007), Nickell et al. (2010), Rodger et al. (2011)

and (5) increased insurance premiums. In 2007, the Irish salmon aquaculture industry produced 10,000 tonnes of salmon with a market value of €50 million (~US$ 62.6 million) (Browne et al. 2008, cited in O'Callaghan et al. 2011). The major Irish Sea salmon fishkill at Glenarm, Northern Ireland (the only commercial salmon farm in Northern Ireland and the Irish Sea), in 2007 resulted in a loss of ~ US$ 1.2 million. Furthermore, it is suggested that aquaculture pontoons and cages may actually benefit the presence of hydrozoans (Guenther et al. 2009, 2010) and certain jellyfish species such as *Aurelia aurita*, by providing a suitable substrate for settlement and subsequent growth of the biofouling polyp phase of the life cycle (Lo et al. 2008; Duarte et al. 2013), thus exacerbating the detrimental effects of hydroids (Guenther et al. 2009, 2010) and jellyfish blooms on aquaculture operations.

6.2.3 Energy Supply from Power Stations

Coastal regions are the preferred location for nuclear- and coal-fired power stations and desalination plants because of the requirement for large amounts of seawater to cool their condensers and a source of water for desalination. Typically, the seawater

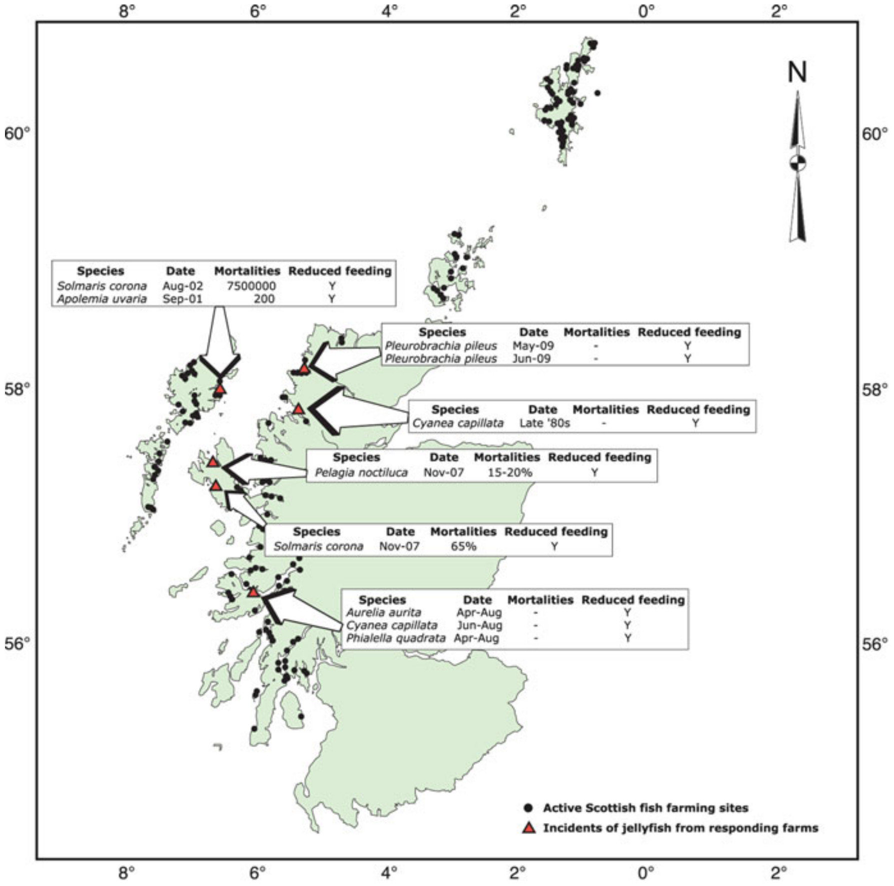

Fig. 6.1 Map showing the location of Scottish fish farms impacted by the jellyfish *Aurelia aurita*, *Cyanea capillata* and *Solmaris corona* (Redrawn from Nickell et al. 2010; base data from Marine Science Scotland; reproduced by permission of The Crown Estate)

intake is located several hundreds of metres from the shore. Large volumes of cooling water extracted by power stations inevitably captures marine flora and fauna, as well as debris (rubbish, sticks, detritus) which then collect on intake screens before entering the cooling system (Purcell et al. 2007). Fish and crustaceans can become impinged on the screens, while smaller, weaker swimmers and plankton can become entrained through the mesh and enter the cooling system. Both impingement and entrainment are detrimental from an environmental health perspective as the organisms are returned to the sea in a physiologically and physically damaged state. When there is a sufficient volume of marine biota and debris, for example, following stormy conditions from a particular wind direction or if there are large blooms or aggregations of marine biota, the screens become blocked, and the flow of cooling intake water significantly reduced (Purcell et al. 2007). Power stations run at reduced efficiency or they may decide to temporarily shut down as a precautionary measure to prevent overheating of the reactors. Provision of power to customers is reduced or even temporarily halted altogether. A 2006 study by the World Association of Nuclear Operators (WANO) reported 44 power outages and load reductions at nuclear plants related to intake blockages since 2004. The most common materials causing blockages were seaweeds and aquatic grasses, mussels, jellyfish, crustaceans (shrimp and crabs) and fish. These materials contributed to 37 of the 44 events.

The clogging of intake screens of power and desalination plants by jellyfish has been a long-standing problem in SE Asia, and in particular Japan, where large seasonal populations of *Aurelia aurita* occur regularly between ~ April and September or November (Yasuda 1998, 2003). The problem is not confined to SE Asia alone, and power stations in India, the Middle East, Europe and North America have been affected by a number of jellyfish species (Rajagopal et al. 1989; Masilamoni et al. 2000; Purcell et al. 2007: Table 4). A study on jellyfish ingress on the Madras Atomic Power (MAP) Station, south-east India, in 1995 and 1996, found that large numbers (up to 17.5 tonnes) of three species, *Crambionella stuhlmanni*, *Crambionella buitendijki* and *Dactylometra quinquecirrha*, appeared on the intake screens between April to July and October, causing reduced flow and head loss (i.e. reduction in vertical drop or pressure). Increased head loss results in increased back pressure on the turbine as well as a reduction in heat transfer efficiency in the heat exchangers. Thus, reduced flow and head produces less electricity. An increase of 10-mm-Hg back pressure in the MAP Station turbine resulted in a loss of ~ INR (Indian Rupees) 0.11 million d^{-1} (~ US$ 2,000 d^{-1}), while damage to the intake screens caused INR 0.4 million per season in revenue loss. Jellyfish that managed to get into the cooling water circuits resulted in the plant shutting down, at a cost of ~ INR 5.5 million d^{-1} (~ US$ 100,000 d^{-1}) (Masilamoni et al. 2000).

In 2011, three power stations were temporarily shut down over the space of 10 days as a result of jellyfish ingress, which was widely reported in the media: Shimane nuclear power station, Japan (25 June); Torness nuclear power station, Scotland (30 June); and Orot Rabin coal-fired power station, Israel (5 July). Most likely these closures in quick succession were coincidental, resulting from regular summer blooms of jellyfish – *Aurelia aurita* in Scotland and Japan and the rhizostome *Rhopilema nomadica* in Israel. Nevertheless, these blooms can be substantial. The magnitude of jellyfish numbers involved in such incidents is illustrated in Fig. 6.2, with media reports indicating that 50 tonnes of *Rhopilema* jellyfish were removed from the Orot Rabin site.

6.2.4 Ship Operations

Similar to coastal power stations, many ships rely on seawater to cool their condensers, and jellyfish can thus impact shipping operations when they clog condensers. In 2006 some capabilities on the US$ 5 billion, 97,000-tonne aircraft carrier

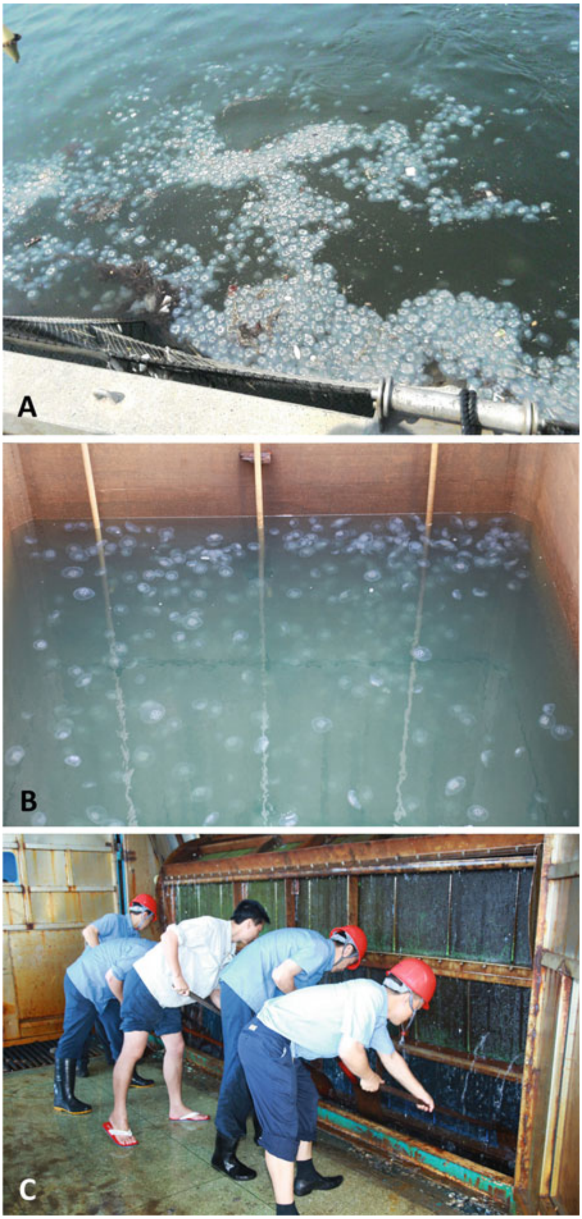

Fig. 6.2 (**a–c**) Blooms of *Aurelia aurita* impacting power stations. (**a**) *Aurelia* medusae near a screen protecting a cooling water intake in Japan; (**b**) Large numbers of *A. aurita* in cooling seawater filters in Qingdao in July, 2009; (**c**) Power station workers cleaning *A. aurita* away from the filter screens in Qingdao in July, 2009 (Photo A reproduced by permission of Shin-Ichi Uye; Photos B, C reproduced by permission of Zhijun Dong)

'USSR Ronald Regan' were disabled when a large number of the rhizostome *Catostylus mosaicus* were sucked into the cooling water condensers in the Port of Brisbane, Australia (Herald Sun, 27th January 2006). Moreover, jellyfish can also clog the bow thrusters of ships which can pose a serious threat when ships are undertaking delicate manoeuvring operations in port (R. Moreton, Port of Brisbane. pers. comm.).

6.2.5 Tourism

Probably the most high-profile example of the impact that jellyfish have on society is the detrimental effect on coastal tourism. Tourism is one of the world's largest economies, with coastal tourism being one of the most common types, and in tropical and subtropical regions, coastal tourism has huge economic importance. The economies of Spain, Portugal, Italy and Greece all depend heavily on tourism, with 130 million visitors, mainly from the wealthy countries of Germany and the UK. However, coastal tourism is very sensitive to public perception. How crowded are the beaches? Is the water clean and safe to swim in? Some of the most popular beach destinations in the world include the northern rim of the Mediterranean, the north and north-east coasts of Australia, the Indo-Pacific and the southern United States, in particular Florida. Several of these regions are adversely affected by the presence of jellyfish, some of which have nasty or even fatal stings (e.g. *Physalia physalis*, *Rhopilema nomadica*, *Cyanea lamarckii*, *Chironex fleckeri*, *Carukia barnesi*) (Purcell et al. 2007). Jellyfish may be present in the shallow waters where people swim and snorkel, or they may get washed up onto the beaches following strong onshore winds. How the public responds to these events depends on their prior knowledge and perception of the potential dangers posed by the species present, their cultural background and whether they feel that their activities and enjoyment will be compromised. For the most part, there is a great deal of negative reporting in the media, and this influences people's perceptions of jellyfish and their own safety and enjoyment.

The most extreme example of jellyfish impacting tourism involves the northern coast of Australia (mainly Queensland, QLD, and the Northern Territory, NT), Thailand, the Philippines and other Pacific nations where cubozoan jellyfish are found (Fenner and Williamson 1996; Fenner et al. 2010). Severe envenomation from the sting of the chirodropid 'box jellyfish' *Chironex fleckeri* causes cardiac and respiratory arrest which may prove to be fatal in only 2–3 min. More recently *Carukia barnesi* and several other unnamed carybdeids have been identified as the cause of Irukandji Syndrome, the symptoms of which include intense lower back and chest pain, abdominal cramps, nausea, vomiting, difficulty breathing, headache, anxiety and severe hypertension that may last for 1–2 days (Gershwin et al. 2010). Several medical studies have summarised reports of stings, hospitalisations, types of treatment and fatalities as a result of *C. fleckeri* and 'Irukandji jellyfish' around the northern coast of Australia between Broome (Western Australia, WA) and Fraser Island (QLD) (e.g. Fenner and Harrison 2000; Macrokanis et al. 2004; Currie and Jacups 2005; Nickson et al. 2009) and other parts of the Indo-West Pacific (Fenner et al. 2010). Based primarily on regional hospital data, the number of reported *Chironex* or Irukandji stings in Australia ranges between <10 and ~ 200 year^{-1} for each region or state, with the majority of casualties being tourists (Sando et al. 2010). Many people require either basic first aid (vinegar, picking off tentacles, cold packs) on site, although for Irukandji stings the majority of victims require transportation to hospital (Table 6.2) for pain management or care for 1–2 days. Fatalities in Australia are remarkably rare. Fenner and Harrison (2000) reported that *Chironex*

Table 6.2 Numbers of people diagnosed with Irukandji Syndrome in tropical Queensland 2001–2007, with methods used to get to hospital (Modified from Sando et al. 2010)

Year	Number of people	Locals %	Tourists %	Self	QAS land	EMQ chopper	RFDS
2001	44	52.3	47.7	23	18	3	0
2002	50	46.0	54.0	22	17	11	0
2003	18[a]	61.1	38.9	6	8	4	0
2004	16	43.8	56.3	3	8	5	0
2005	14	42.9	57.1	3	7	4	0
2006	19	26.3	73.7	3	4	11	1
2007	24	29.2	70.8	4	13	7	0
Total	185	44.1	55.9	64	75	45	1

Self travel to hospital using private transport, *QAS land* Queensland ambulance service land ambulance, *EMQ chopper* emergency management Queensland helicopter, *RFDS* royal flying doctor service

[a] In the original Table 3, Sando et al. 2010, there is one person of unknown origin in 2003, which has been removed from this table

had caused 67 deaths in Australia between 1884 and 1996, while the first reported death from Irukandji Syndrome occurred in 2002 (Fenner and Hadock 2002). Jellyfish-related fatalities are far more common in countries such as Malaysia and the Philippines, where between 20 and 50 people die each year as a result of jellyfish stings (Fenner et al. 2010).

While the potentially fatal box jellyfish may grab the headlines in Australia and the Indo-West Pacific, several other types of jellyfish with nasty stings are prevalent in the region. On the east coast of Australia, ~10,000 stings each summer are attributed to the Portuguese man o'war (known locally as 'blue bottles'), *Physalia physalis*, with *Cyanea* sp. and *Catostylus* sp. stings also reported (Fenner and Williamson 1996). *Nemopilema nomurai*, *Cyanea nozakii*, *P. physalis*, *Aurelia aurita*, *Rhopilema esculentum* and *Pelagia noctiluca* are the most common jellyfish responsible for stings in Chinese coastal waters, where there have been at least 13 known fatalities and several thousand hospitalisations between 1983 and 2007 (Dong et al. 2010: Table 2). In recent years, Mediterranean tourism has been affected by the increased frequency and abundance of the mauve stinger, *P. noctiluca*. While this jellyfish undoubtedly possesses a nasty sting that may require medical treatment (e.g. in July 2008, the French emergency services received >500 calls in one day along a 16-km stretch of coast from Nice to Cannes), it is very rarely life threatening, only proving fatal if the person affected has an underlying medical condition. Nevertheless, the public perception of this jellyfish is highly negative, which combined with the expectation of an uninterrupted beach holiday, results in public reaction that greatly outweighs the actual risk associated with this species. The impact of jellyfish to tourism may be minimal if the beach closures are for only a few hours, but if closures become more persistent year on year or a significant number of people require medical treatment, then the media reports that arise may persuade tourists to seek alternative destinations.

6.3 Management and Adaptation Strategies

6.3.1 Net-Based Fisheries and Aquaculture

At present, year-to-year bloom intensity of *Nemopilema nomurai* has become possible to forecast in early summer based on monitoring of juvenile medusae from ships of opportunity in Chinese waters, the seeding and nursery ground of this species and the transport and timing of appearance of medusae into Japanese waters using hydrodynamic modelling (Uye, unpublished). Thereby, Japanese fishermen can be made aware of impending jellyfish blooms and prepare some countermeasures before medusae outburst in their waters (see Chap. 8). However, a similar bloom forecasting system has not yet been established for *Aurelia aurita*, because the seeding place is often unclear and the seasonal life cycle and physical oceanography differ from one place (or bay) to another. One of the countermeasures used by Japanese fishermen is to slice *Nemopilema* and *Aurelia* with so-called jellyfish cutters using carbon steel wires at the cod-end of trawls to facilitate removal, but the operation is generally confined to small areas compared to the vast geographical range of jellyfish distribution, indicating that slicing is only useful for highly aggregated jellyfish patches. Any net-based fisheries are more or less damaged by entrapped jellyfish, and various types of jellyfish-excluding devices have been invented and deployed. JET (Jellyfish Excluder for Towed fishing gear), a device similar to the TED (Turtle Excluder Device) used in shrimp trawls (Watson et al. 1993; Mitchell et al. 1995), was designed to remove *Nemopilema* from towed fishing nets (Fig. 6.3, redrawn from Matshushita and Honda 2006) and has been used by Japanese fishermen during bloom years. To alleviate the damage by *Nemopilema* blooms, some modified set-nets have already been manufactured (see Chap. 8).

The aquaculture industry is also developing strategies to protect its stock. Options available to fish farmers can be classified as ‘site location’, ‘early warning systems’ and ‘mitigation methods and technologies’ (O’Callaghan et al. 2011). Although not really practicable for established farms, it is suggested that new salmon farms should not be situated in tidal fronts and eddies where jellyfish aggregations tend to develop (Graham et al. 2001) and instead placed in higher energy offshore sites where jellyfish densities are likely to be lower and flushing rates are higher, which improves oxygenation and reduces biofouling. However, technical issues that would need resolving before locating salmon farms further offshore include designing robust and submersible cage structures able to withstand the higher wave energy and managing the increased safety and financial costs associated with access requirements to the offshore site (O’Callaghan et al. 2011). Attempts to develop ‘early warning systems’ of impending blooms using water characteristics (but this requires long-term monitoring datasets), hydrodynamic models such as MIKE 3 (Elzeir et al. 2005), aerial surveys (Houghton et al. 2006; Nickell et al. 2010) and satellite (e.g. MODIS) data (Nickell et al. 2010) are also being undertaken. All have various limitations and investigations are ongoing. For established farms, there is now greater communication between agencies and fishermen; a watch-keeping

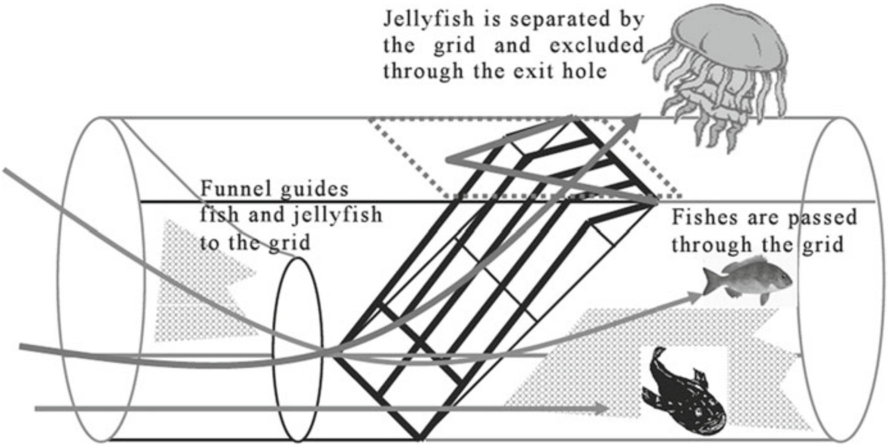

Fig. 6.3 Separation of jellyfish from target fish species by JET, Jellyfish Excluder for Towed fishing gear (Redrawn from Matshushita and Honda 2006)

system is utilised by the Scottish aquaculture industry to inform farmers of approaching blooms (Nickell et al. 2010).

Mitigation strategies that existing fish farms can use to defend their stock include deploying protective covers or booms and mesh or bubble screens to prevent jellyfish from entering the cages. Tank trials show that bubble screens, similar to those used to protect water intakes of power stations, create a horizontal current profile that repels those jellyfish in the upper water column away from the screen and pushes those jellyfish in the lower water column up towards the surface and then away to a collecting boom (Lo 1991, 1996). However, field trials at a Donegal (Ireland) salmon farm indicated that the number of *Muggiaea atlantica* was similar inside and outside the screen (O'Callaghan et al. 2011) and that this method is costly to implement, even for short periods. An alternative to barrier methods is to increase oxygen levels by aeration, which helps to keep the stock healthy (Rodger et al. 2011). Care must be taken to ensure that aeration bubbles do not in fact circulate the jellyfish within the cages. Aeration used in combination with finer meshes and tarpaulins around the cages prior to the arrival of the bloom is more successful in keeping jellyfish away from fish.

The polyp phase of scyphozoan life cycle can also be targeted. Polyps of ubiquitous jellyfish such as *Aurelia* have been found to inhabit man-made structures, including the undersides of marina pontoons, dock walls, marine debris and aquaculture cages (Duarte et al. 2013), and these represent a potential source of medusae recruits close to the target areas. Divers are employed to scrape off fouling epibiota, including hydroids and polyps from the salmon aquaculture cages deployed in Norwegian, Australian, Scottish and Irish waters. Japanese and Norwegian researchers (Guenther et al. 2009, 2010, Nogata et al. unpublished) have found that some antifouling chemicals (copper pyrithione, sea-nine 211) used in ship paints are lethal for hydroids and *Aurelia* polyps and that some chemical compounds isolated from the macroalga *Digenea simplex* inhibit *Aurelia* planula larvae from successful settlement and attachment on to the substrate. Silicone-based paints could also be used to delay or prevent biofouling hydroids and other epibiota (Hodson et al. 2000). If these compounds are painted on the surface of various marine constructions, they could contribute to the reduction of polyp colonisation and population size. However, many such substances (e.g. copper) are banned for use in the organic farms located in Scotland and Ireland. Alternatively, transplant of polyp predators such as nudibranchs (Hernroth and Gröndahl 1985; Hoover et al. 2012) to the polyp colony habitats may be an effective 'biological control' in decreasing polyp population numbers and thus reduce the recruitment success to the medusa population via strobilation (Lucas et al. 2012).

6.3.2 Energy Supplies

To protect water intakes of power stations and desalination plants, screens of various designs are put into place. Scientists working for consultancy companies advise government agencies and power plant operators about which screens, flow velocities and deterrents are most appropriate based on knowledge of fish swim speeds and behaviour. The vast majority of scientific and advisory reports focus on the impacts of fish ingress, with very little information specifically on jellyfish. Screens form either physical barriers (e.g. mesh or wire screens with diverters) or behavioural barriers (e.g. bubble, sound, electrical, acoustic, light, hydrodynamic screens) preventing ingress (Environment Agency 2005). The design, installation and operation of screens and barriers can add significantly to the capital and operating costs of the facilities, but good practice is essential. In addition to the impact of trapped organisms on the safe running of the power station itself, impingement is an important issue to consider from an environmental health perspective. Marine fauna may be removed from the ecosystem or may be returned to the source water body in a weakened condition, injured or dead, which may then represent a health and safety hazard. Alternative screen design (e.g. bubble screens and water jets, suitable mesh sizes, fish diverters) can both reduce the quantity of material captured and ensure maximum survival and subsequent return to the marine environment of organisms impinged (BEEMS, Scientific Advisory Report No 6. 2011). One of the very few reports considering how to mitigate the effects of jellyfish on cooling intakes, Verner (1984) reported on the use of bubble barriers to prevent blockage of cooling water supplies by jellyfish. The method of removal of the 2011 *Rhopilema nomadica* bloom from the Orot Rabin coal-fired station is illustrated in Fig. 6.2. The 50 tonnes of medusae were transferred from the screens into large containers, which were then taken away in trucks for disposal. Following the Torness jellyfish ingress in 2011, a quarterly site report indicated that 'arrangements are being put into place to monitor, and if necessary, to mitigate against any future increased risk of blockages that may be caused by the marine environment'.

6.3.3 Tourism, Including 'Citizen Science'

Cubozoan jellyfish sting incidents represent a major cost to northern Australian communities in terms of public health, leisure and tourism (Bailey et al. 2003; Gershwin et al. 2010). If a person becomes seriously ill following a sting, there are the costs associated with evacuation of the victim to hospital often by helicopter (Table 6.2), duration of stay in hospital (typically 1–2 d for Irukandji victims), lost work days and the development and production of antivenom for *Chironex* (note there is no antivenom for Irukandji as the identity of all the species that cause Irukandji Syndrome is still unknown). On average, northern Queensland records about 50 Irukandji hospitalisations per year, and approximately the same number per year is recorded in northern Western Australia (Macrokanis et al. 2004). It was estimated that the two Irukandji deaths in 2002 resulted in an AU$ 65 million (US$ 66 million) loss in tourist revenue in the region (see Gershwin et al. 2010). As a result, local and regional authorities and report managers in northern Australia and other jellyfish-affected regions of the world have developed a number of mitigating strategies based on medical and scientific advice, aimed at reducing or managing the detrimental effects that jellyfish can have on tourism focusing on (1) education, (2) information, (3) personal protection, (4) removal of jellyfish and (5) medical aid.

As a broad generalisation, the general public is not well informed about which species of jellyfish are dangerous or not, probably with the exception the Portuguese man o'war, *Physalia physalis*, and box jellyfish, *Chironex fleckeri*. For many decades, tourists (mainly the younger 'backpackers') visiting Queensland have known about the risks posed by *C. fleckeri*, and adaptation strategies to minimise the risk of contact are well established. This probably explains why there have been so relatively few deaths from this species in the region (Fenner and Harrison 2000). The situation with the carybdeid cubozoans such as *Carukia barnesi* is rather different. Following the first deaths of two international visitors to Queensland from Irukandji Syndrome in 2002, there was a considerable increase in public and scientific attention as it was clear that far less was known about this group of jellyfish than *Chironex* box jellyfish (Bailey et al. 2003). A survey of ferry passengers between Townsville and Magnetic Island, QLD, to assess local and visitor knowledge, perception and behaviour toward Irukandji Syndrome revealed that international tourists had little knowledge of Irukandji (34 % compared with 88 % locals and 70 % domestic tourists) and mistakenly assumed that it was safe to swim inside stinger nets (which are designed for the larger *C. fleckeri*: 25–30-cm bell diameter cf. 2-cm bell diameter for carybdeids) (Harrison et al. 2004). In addition, only 50 % of visitors had obtained travel health advice before coming to the region (Leggat et al. 2005).

In spite of the obvious dangers, northern Queensland has remained a popular tourist destination, and in fact deaths are remarkably rare given the potential severity of the jellyfish toxin. Education informs people of when it is safe to swim and how to administer basic first aid, while adaptation actions reduce encounters with jellyfish. In the Mediterranean, negative public reaction to the increased frequency of blooms of *Pelagia noctiluca* (Kogovšek et al. 2010) and other jellyfish species tends to outweigh the actual risk. In 2008, the Mediterranean Science Commission set up the CIESM JellyWatch programme to gather baseline data on the frequency and extent of jellyfish outbreaks throughout the jellyfish-affected Mediterranean Sea. The programme includes a citizen science-based system for reporting opportunistic observations, with posters providing information on whether species are 'stingers', 'mild stingers' or 'harmless' written in eight languages (www.ciesm.org/marine/programmes/jellywatch.htm). With the growth of various very successful 'citizen science' programmes around the globe (e.g. beach surveys for jellyfish such as Doyle et al. (2007) and Houghton et al. (2007); Mediterranean Science Commission/CIESM and Monterey Bay Aquarium Research Institute JellyWatch programmes; JelliesZone; UK Marine Conservation Society jellyfish survey), jellyfish now offer a potential looking glass through which to understand and appreciate the marine environment.

At the beaches themselves, several adaptation strategies are used to minimise contact with jellyfish. In Australia information signs warn bathers of the dangers of swimming during the 'stinger season' [Oct–Jun in the Northern Territory, NT], list the symptoms of envenomation by *Physalia*, *Chironex* and Irukandji jellyfish in particular and provide information on how to administer basic first aid or contact the emergency services (Gershwin et al. 2010: Fig. 4). Vinegar is placed in prominent places along the beach or held by lifeguards as the acetic acid inhibits firing of undischarged nematocysts. Stinger nets to protect swimmers are deployed during the box jellyfish season although these are not effective in preventing contact with the Irukandji jellyfish as these are small enough to pass through the 25 × 25-mm mesh (Harrison et al. 2004; Gershwin et al. 2010). Instead all-in-one Lycra stinger suits are more effective at protecting against Irukandji jellyfish. Stinger nets are also deployed in the Mediterranean to protect against *Pelagia noctiluca* blooms. Other mitigating strategies range from short-term beach closures while stranded jellyfish are cleared away to larger-scale removal and disposal of jellyfish from the water using fishing boats (Gili pers. comm., see Canepa et al. Chap. 11).

The Mediterranean coasts of France and Spain are among the most popular tourist destinations in Europe, which brings in significant revenue to the economies of these countries. Because these regions are being more regularly impacted by the increased frequency of *Pelagia noctiluca* outbreaks that have occurred in recent years (Gili and Pagès 2005; Molinero et al. 2005), scientists have turned their attention to developing jellyfish forecasting or 'early warning' systems. On 1 July 2012, the Jellywatch.fr website (http://lseet.univ-tln.fr/JELLYWATCH) was launched. This provides a 'barometer of jellyfish' based on forecasts of stranding and real-time observations for each resort in the region of Provence, Alpes and Cote d'Azur. The barometer provides a 5-point probability rating from 0 (no risk) to 5 (maximum jellyfish alert) based on modelling of particles (jellyfish) using current strength and wind direction and taking into account their diel vertical migration (Fig. 6.4). Other large-scale remote-sensing and modelling programmes that predict the distribution of jellyfish in Europe include EOJelly (= Star Jelly) (www.starlab.org) which also provides a 7-day advanced 5-point Jellyfish Prediction Index (JPI) for the NW Mediterranean coast and northern Irish Sea, and Aviso (www.aviso.oceanobs.com)

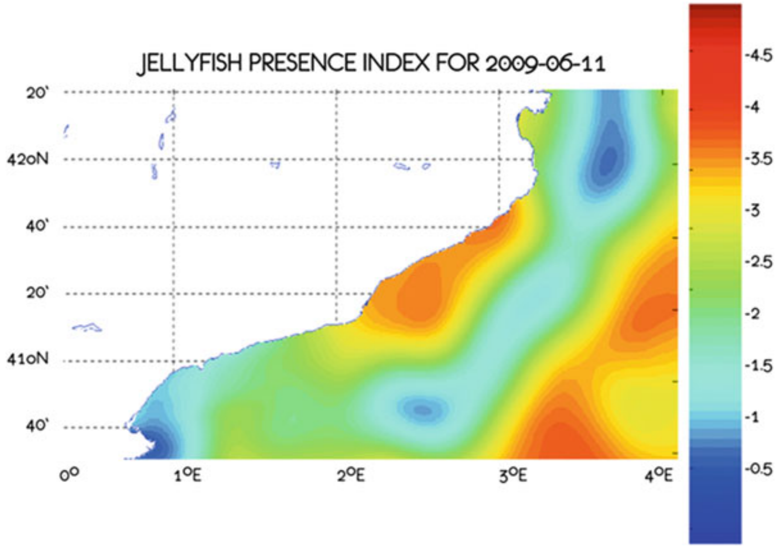

Fig. 6.4 Forecasting the appearance of jellyfish along the NW Mediterranean coast with the Jellyfish Presence Index, a 5-point probability rating from 0 (no risk) to 5 (maximum jellyfish alert) generated using models of particles (jellyfish) movement based on current strength and wind direction and taking into account jellyfish diel vertical migration (Reproduced by permission of EOJelly, www.starlab.es)

which uses Lagrangian analysis of 3D mesoscale dynamics from altimetry which describe ocean currents and coastal modelling to predict jellyfish distribution over the NW Mediterranean Sea. In Chesapeake Bay, USA, the likelihood of encountering sea nettles (*Chrysaora quinquecirrha*) is forecast by the National Ocean and Atmospheric Administration (NOAA). Forecasts are based on maps of surface salinity, and forecasts are validated by field observations made by scientists working in Chesapeake Bay and volunteer citizens (http://chesapeakebay.noaa.gov/forecasting-sea-nettles).

6.4 Concluding Remarks

While it is very true that some jellyfish blooms are economically detrimental to the livelihoods of local fishermen, tourist industries and power and water operations, much of people's perception of jellyfish is rather negative, which is partly driven by poor understanding of their diversity, biology and ecology. Understanding how the public engage with jellyfish in combination with education campaigns is a vitally important mechanism to rectify this. Scientists from the National Center for Ecological Analysis and Synthesis (NCEAS)-funded project '*Global expansion of jellyfish blooms*' participated in two public outreach events: the first at the

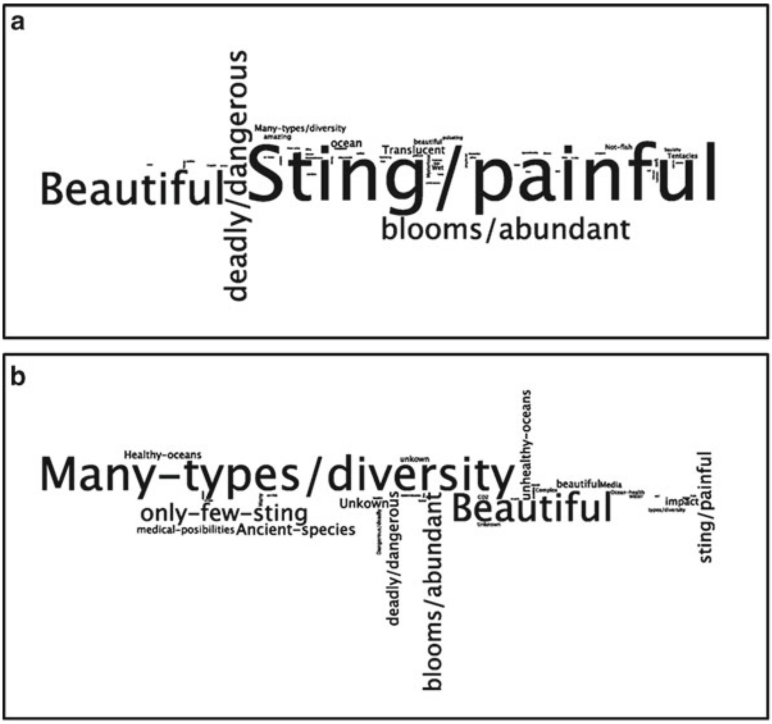

Fig. 6.5 (**a–b**) Tag clouds summarising the change in public perception of jellyfish, (**a**) before and (**b**) after a series of talks and videos presented by jellyfish scientists at a public outreach event held at the Santa Barbara Museum of Natural History in November 2010 (Data were collected using questionnaires)

Santa Barbara Museum of Natural History in November 2010 and the second, hosted and funded by the Fundación BBVA in Madrid in September 2011. At the Santa Barbara event, the audience was invited to fill out a questionnaire before and after a series of talks and videos, the results of which are illustrated in the form of 'tag clouds' (Fig. 6.5). The combination of scientific outreach events, aquarium displays of jellyfish, websites and citizen science-based programmes all help to educate and engage the public in jellyfish. On 1 August 2012, Jellywatch.org released Apps for iPhones and Android phones to enable the public to more easily submit sightings and photos to the global database.

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Part II
Case Studies

Chapter 7
Population Fluctuations of Jellyfish in the Bering Sea and Their Ecological Role in This Productive Shelf Ecosystem

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Robert Lauth, Richard D. Brodeur, and Kenneth O. Coyle**

Abstract A long-term fisheries monitoring program operating in the southeastern Bering Sea detected a biomass increase of large jellyfish in the 1990s. However, medusa biomass declined to lower levels after 2000, but then increased once again in 2009. Similar population fluctuations are revealed in other monitoring efforts that extend to the northeast Bering Sea and to the west in Russian waters. Decadal oscillations in climate, rather than overfishing or other anthropogenic factors, are thought to be responsible for these trends. This case study of Bering Sea jellyfish blooms demonstrates that apparent increases in jellyfish populations may not necessarily be sustained and that increases may occur in response to climate variability. Herein we review what is known about the abundance and distribution of the dominant species of jellyfish in the Bering Sea and their potential interactions with other parts of the ecosystem, particularly those of interest to humans.

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7.1 Introduction

7.1.1 The Bering Sea: A Productive, Dynamic Shelf Ecosystem

The Bering Sea lies between 52° and 66° north latitude and 162° east and 157° west longitude (Fig. 7.1). It is bounded by the Bering Strait to the north, the Aleutian Islands to the south, and the Alaskan and Russian coasts to the east and west, respectively. The eastern Bering Sea features a broad (~500 km wide) shelf of <200-m depth extending northwestward from the Alaska Peninsula to the eastern tip of Siberia. Sea ice covers the eastern Bering Sea shelf each winter, but the variability in sea ice extent among years is large (e.g., Niebauer 1983) because the region can be dominated by air masses of either maritime or arctic origin (Rodionov et al. 2007). The maximum ice extent and timing of the ice retreat in spring represent the primary factors controlling physical conditions on the Bering Sea shelf throughout the year (Stabeno et al. 2001, 2012). Seasonal ice cover is also a major driver of Bering Sea ecology (Hunt et al. 2011). However, summer weather conditions (e.g., storminess/wind mixing and amount of insolation) can also be important to the water properties (Bond and Overland 2005) and production (Napp and Hunt 2001). The physical conditions of the western Bering Sea also show similar biophysical regions as the east (Khen 1999), but the general oceanography of this narrow shelf region is dominated by the Kamchatka Current and its meanderings (Hunt et al. 2010).

The eastern Bering Sea is a productive and economically valuable ecosystem, supporting rich populations of zooplankton, forage fish, groundfish, crabs, marine birds, and mammals. Alaskan commercial fisheries are among the largest in the world, with combined annual landings of nearly two million metric tons valued at 1.6 billion $US (NMFS 2010). The primary fisheries are for groundfish (walleye pollock, flatfish, and Pacific cod), crabs (tanner and king), but also some fisheries exist for salmon, herring and other pelagic fishes. Landing data are less complete for the western Bering Sea, but in recent years these have averaged by weight to only be about 20–25 % of the eastern Bering Sea biomass (Hunt et al. 2010). Both biomass and production of the western Bering Sea is dominated by pelagic nekton rather than demersal nekton (Shuntov and Radchenko 1999). The highly productive Bering Sea ecosystem also supports large populations of seabirds and marine mammals that enter the Bering Sea mainly during their summer feeding migrations, but some islands such as the Pribilof Islands and Commander Islands are home to some breeding populations that spend the majority of their lives in the Bering Sea.

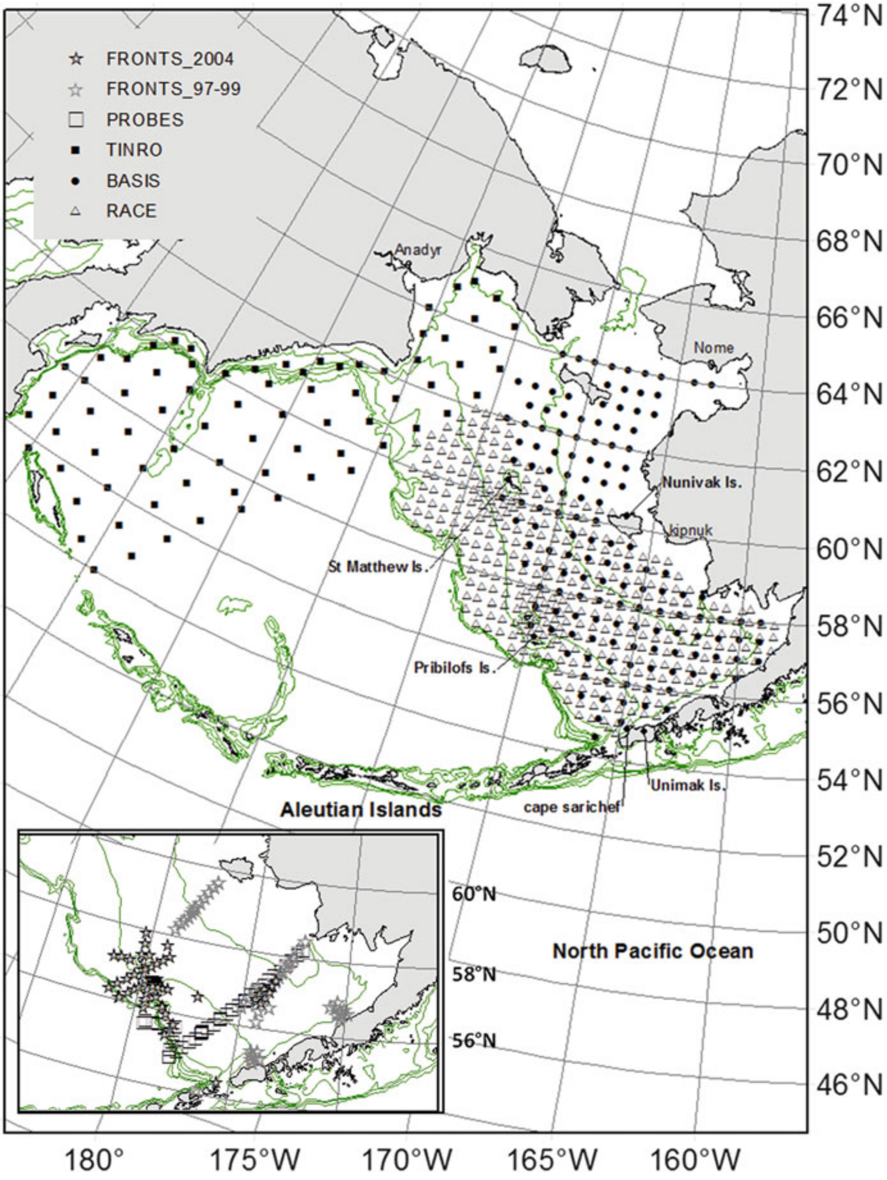

Fig. 7.1 Station map of annual Bering Sea surveys. The main portion of map displays Russian TINRO, US RACE, and US BASIS research cruises. Map insert at *bottom left*, displays PROBES and FRONTs research cruises in southeastern Bering Sea

7.1.2 Historical Accounts of Jellyfish in the Bering Sea

Rathbun (1894) described an area in the eastern Bering Sea called "Slime Bank," known for large jellyfish aggregations. The *Albatross* delineated the region in 1890 as beginning "directly off Cape Sarichef, the northwest cape of Unimak Island… The bank derives its name from the presence of immense numbers of a large jellyfish, brownish or rusty in color, measuring 6–18 in. across the disk, and provided with long slender tentacles having great stinging powers. It is said by the fishermen that the jellyfish are never observed upon the surface of the sea, but seem to occupy an intermediate zone toward the bottom. They claim that these animals sometimes interfere with the hooks reaching bottom, and by covering the bait render it unattractive to the fish. When brought to the surface they are uncomfortable objects for the fishermen to disentangle from the hook and line. They do not become abundant until the latter part of June, when fishermen generally move on…"

Bigelow (1913) assembled the first species list of gelatinous zooplankton for the Bering Sea based on a subsequent *Albatross* survey in 1906. Although the taxonomy was uncertain for many species, he lists 38 medusae and 4 siphonophores for the Bering Sea, with all but two of the medusae species found elsewhere in the world at that time. In the most complete literature survey of the Bering Sea jellyfish fauna to date, Mills (1997) lists 56 Hydromedusae, 8 Scyphomedusae, 9 Ctenophora, and 15 Siphonophora.

7.1.3 Jellyfish Species Composition in the Eastern and Western Bering Sea

One of the earliest studies of eastern Bering Sea jellyfish was conducted as part of the Processes and Resources of the Bering Sea Shelf (PROBES) program (Fig. 7.1) by Hamner (1983). He noted that the Bering Sea, with its stable water masses, shallow shelf waters, and high abundance of zooplankton in summer, is an ideal region for supporting the production of dense populations of scyphomedusae and hydromedusae. Hamner (1983) used net tows, surface, and SCUBA observations to determine the species composition, abundance, distribution, and diets of medusae in July–August 1982, with respect to water mass (oceanic, outer shelf, middle shelf, and coastal domain). Twenty-two species of medusae were found, including 2 Scyphomedusae, 7 Anthomedusae, and 7 Leptomedusae. Certain medusae were associated with particular water masses. Numerous species of hydromedusae occurred at high densities in the outer shelf domain, whereas a different assemblage of hydromedusae occupied the middle and coastal shelf waters. Four large medusae were conspicuous in the region: *Chrysaora melanaster*, the largest and most abundant, dominated the cnidarian biomass in the middle domain, whereas *Aequorea* sp., *Cyanea* sp., and *Staurophora mertensii* occupied oceanic and outer shelf waters. Hydromedusae and scyphomedusae formed dense aggregations of up to 1,000 m^{-3} in surface convergences apparently produced by Langmuir circulation (Hamner and Schneider 1986). However, these medusae also occurred at depth in diving surveys, particularly in the mid-water near the pycnocline (~35 m), but at lower densities, e.g., 0.02 *C. melanaster* m^{-3} (Hamner 1983).

Coyle and Cooney (1993) conducted hydroacoustic and net studies within an 80-mile radius of the Pribilof Islands in the eastern Bering Sea during the summers of 1987 and 1988. They found a general pattern of high acoustically determined biomass (ADB) in the upper 30 m and also in epibenthic layers 15–20 m above the bottom, but found little biomass in between the two layers. The upper layer ADB consisted of primarily large medusae, namely, *Aequorea* sp., *S. mertensii,* and *C. melanaster*, while smaller medusae, such as *Euphysa flammea*, *Sarsia princeps,* and *Catablema* sp., were numerically abundant. Overall, the average biomass (g m^{-3}) of cnidarians was 1.43 (±4.04 SD) in the mid-water layer, 8.91 (±15.8 SD) in the surface-scattering layer at night, and 0.95 (±2.03 SD) in the epibenthic scattering layer. The cnidarian biomass in the upper water column was often associated with specific hydrographic features, such as salinity and temperature fronts near the islands, which may have concentrated the medusae as well as their prey.

Coyle et al. (2008) estimated cnidarian biomass with a 1 m^2, 500-μm-mesh MOCNESS near the Pribilof Islands and on the middle shelf of the eastern Bering Sea in August 1999 and 2004. Between these two periods, significant declines were observed in the biomass of large scyphozoans (*C. melanaster*), as was also apparent in shelf-wide trawl surveys (Brodeur et al. 2008a). By contrast, higher densities of small hydromedusae (*E. flammea*) were observed in 2004 relative to 1999. Shifts in the crustacean community were also observed over this period, as were changes in the diet of age-0 pollock from large to small copepods in 2004 relative to 1999. Warmer conditions and increased water-column stability in summer 2004 may have influenced the zooplankton community by decreasing primary production and selecting for species more tolerant of warmer, oligotrophic conditions.

Previously unpublished information on regional species composition from the Coyle et al. (2008) study is reported here (see Table 7.1). There are trends in the data by domain: inner (<=50 m bottom depth), middle (>50 and<=150 m), and outer (>150 m). Some taxa did not occur in the inner domain (e.g., *Aegina, Dimophyes,* and *Ptychogena*), and others did not occur in the outer domain (many of the hydromedusae and all of the scyphozoans). *Periphylla* is an oceanic animal so its absence from the middle and inner domains is expected. Note that some not occurring in the outer domain had insignificant P-values so they tended to be rare in the samples or had very high variance. Similarly, although the ANOVA determined that *Rathkea* biomass differed among regions, the Bonferroni comparison indicated that this species did not exhibit any significant differences among the pairs. Thus, we conclude that there were no significant differences in *Rathkea* biomass among domains.

7.2 Large-Scale Surveys of Jellyfish in the Bering Sea

Determining trends in jellyfish biomass is difficult due to there being very few cases of large coverage annual surveys past or present being conducted for the sole purpose of targeting macro jellyfish (Purcell 2009). In the Bering Sea, data collected from

Table 7.1 Mean biomass (g 1,000 m^{-3}) of major gelatinous zooplankton taxa from MOCNESS tows in the eastern Bering Sea (July–August 1997–1999, 2004) by domain: inner ($\leq$ 50 m bottom depth), middle (>50 and $\leq$ 150 m), and outer (> 150 m). The values were raised to the power of 0.15 for computing the ANOVAs, but the means reported here are arithmetic untransformed values. P-values indicate significant differences via ANOVA at level $\leq$ 0.05. The Bonferroni method compares mean biomass among domains, where *I* is inner, *M* is middle, and *O* is outer

Genus	Inner	Middle	Outer	P-value	Bonferroni
Aegina	0	<0.01	0.04	<0.01	*O* > *I*&*M*
Aequorea	2.89	27.21	0.32	<0.01	*M* > *I*
Aglantha	2.47	1.61	8.02	<0.01	*O* > *M*&*I*
Aurelia	92.82	159.93	0.03	0.61	
Bougainvillia	0.45	0.04	0	<0.01	*I* > *O* = *M*
Calycopsis	0	<0.01	0.25	<0.01	*O* > *I* = *M*
Chrysaora	1,392.01	2,203.49	0	<0.01	*M* > *I* > *O*
Corymorpha	0.27	4.31	0.01	<0.01	*M* > *I* = *O*
Coryne	1.90	0.16	0.32	<0.01	*I* > *M* = *O*
Cuspidella	0.29	5.99	0	0.65	
Cyanea	2.56	4.28	0	0.18	
Dimophyes	0	0.01	0.81	<0.01	*O* > *M* = *I*
Eirene	4.65	2.15	0.15	0.01	*I* = *M* > *O*
Eperetmus	0	<0.01	0	0.69	
Gonionemus	<0.01	0.11	0	0.22	
Lar	0.04	0.01	0	0.24	
Melicertum	0.01	0.01	0	0.22	
Obelia	0.06	0.02	0	<0.01	*M* > *O* = *I*
Peachia	<0.01	<0.01	0	0.93	
Perigonimus	4.63	6.79	0	<0.01	*I* = *M* > *O*
Periphylla	0	0	0.93	<0.01	*O* > *I*&*M*
Phacellophora	0.24	1.72	0.70	0.32	
Phialidium	0.29	1.43	0	0.52	
Polyorchis	0.01	0.07	0	0.87	
Ptychogena	0	0.03	0.02	0.14	
Rathkea	0.01	<0.01	0.03	0.02	*I* = *M* = *O*
Stomotoca	0.10	<0.01	0	0.43	
Tiaropsis	0.51	<0.01	0	0.57	

trawl surveys targeting fish have been used to determine macro jellyfish biomass (Brodeur et al. 2002, 2008a). In particular, three different surveys, which are described in detail below, utilized different gear (surface and bottom trawls) and sampled locations with some to no overlap. Survey coverage includes both the western and eastern Bering Sea (Fig. 7.1), which for the purposes of comparison were split into four regions: Northeast, Southeast, Northwest, and Southwest. The Southeast region encompasses the area between the Alaska Peninsula to 400 km north, extending east to the 20-m isobath and west to the 200-m isobath. The Northeast region's southern boundary parallels the Alaska Peninsula, starting from the 200-m isobath, running north of St. Paul Island ending in line with the town of Kipnuk (regions described in detail at the Bering Sea Project http://bsierp.nprb.org). The north and west boundary coverage is from the 200-m isobath running along the EEZ to 64.5°N, and the east extends to the 20-m isobath but also includes Norton Sound. The northwest region includes Anadyr Bay and adjacent shelf areas, which extends southeast to the Russian EEZ border and southwest to the 200-m isobath. The southwest region is primarily a deep-water area that ranges from the Commander Islands in the south along the EEZ border to the northwest region in the north.

7.2.1 RACE Surveys

Since 1979, the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (AFSC) has been conducting annual summer bottom trawl surveys to determine the condition of groundfish and invertebrates in the eastern Bering Sea. The sample area includes coverage from the Alaska Peninsula north to 60°50′N, extending out to the 200-m isobaths (Fig. 7.1). The sampling is on a grid system with fixed stations at the center of each 20 × 20 nautical mile square. The trawl is towed on the bottom for 30 min. Catches of all large jellyfish (bell diameters >50 mm) are weighed at sea and standardized to kg ha^{-1} (see Brodeur et al. 2008a for details). Species composition of the catch has only been an endeavor for approximately the last decade of effort (Lauth pers. obs.).

7.2.2 BASIS Surveys

The Bering-Aleutian Salmon International Survey (BASIS) surface trawl surveys have been conducted annually by the AFSC since 2002, targeting forage fish and invertebrates from mid-August to early October. The sampling grid covered the shelf off western Alaska, from 159°W to 174°W longitude and 54.5° N to 64° N latitude (Fig. 7.1). All stations were approximately 30 nautical miles (55.6 km) apart. All tows were standardized for gear (50 m wide by 18 m deep) and duration of tow (30 min at 3.5–5 kts, covering 2.8–4.6 km). Fish and jellyfish were collected using a midwater rope trawl, at or near the surface, with typical spreads of 66.4 m horizontally and 14.6 m vertically (see methods in Cieciel et al. 2009). All sampling was performed during daylight hours.

7.2.3 TINRO Surveys

Data from the western Bering Sea are derived from epipelagic trawl surveys that the TINRO-Center (Pacific Research Fisheries Center, Vladivostok) conducted from 1991 to 2011. All 20 surveys were carried out in the Russian exclusive economic zone beyond the 12-mile territorial seas (Fig. 7.1). Most of the surveys were in summer (11 surveys, 925 tows) and fall (13 surveys, 984 tows). Only three surveys (81 tows) were performed in winter. Jellyfish were caught using large pelagic trawls with a vertical opening of 30–60 m and a horizontal opening of 28–52 m and equipped with a 1 cm meshed cod end liner (see methods in Volvenko (1998) and Zavolokin et al. (2008)). No corrections were made for extrusion of jellyfish through the larger mesh of the trawl nets; therefore, these estimations of jellyfish biomass and abundance are substantially underestimated.

7.3 Spatiotemporal Patterns of Biomass

7.3.1 Regional Interannual Variability

Recent Bering Sea surveys by Russian and US fisheries agencies (i.e., RACE, BASIS, and TINRO) have described jellyfish species composition and biomass in the early 2000s to present for both the western and eastern side of the Bering Sea (Figs. 7.2, 7.3 and 7.4). The eastern portion of the Bering Sea can be readily described as being dominated by *C. melanaster*; surveys report high catches of *C. melanaster*, especially in recent years (Fig. 7.2). Summer and fall jellyfish species proportions in the eastern Bering Sea are very similar, and since 2008, increases

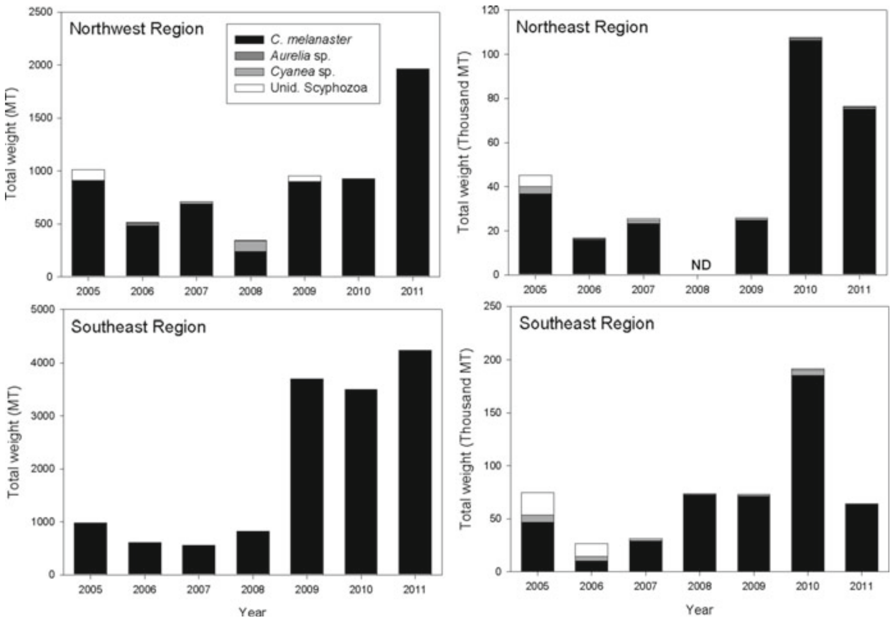

Fig. 7.2 Interannual comparison of the dominant species collected in summer during US RACE bottom trawl surveys (*left*) and in fall during the US BASIS research cruises (*right*). Jellyfish biomass units are MT and 1,000 MT for the RACE and BASIS surveys, respectively

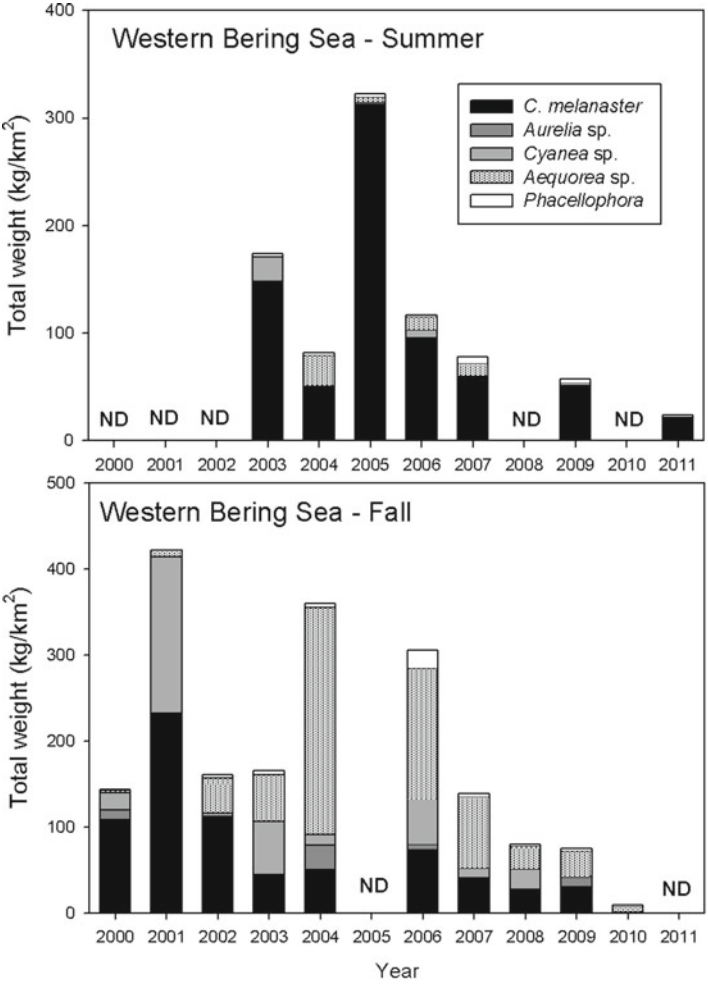

Fig. 7.3 Jellyfish biomass (kg km^{-2}) for the dominant species by season (summer, *upper*; fall, *lower*) during Russian TINRO research cruises. *ND* = no cruises done that year

have been observed in the numbers of large jellyfish species present in reported survey catches, with *Aequorea* sp. and *Cyanea* sp. being two species that were once present in higher abundances than in recent years.

In the western Bering Sea (i.e., Russian waters), trends for macro jellyfish species indicate an overall decline in biomass over the period 2000–2011 (Fig. 7.3). These patterns persist when the TINRO survey data are plotted by region (Fig. 7.4). The eastern Bering Sea (i.e., US waters) exhibits the opposite pattern for the same time period, showing dramatic increases in the summer for the Southeast and in the fall for the Northeast regions (Fig. 7.2). Biomass remains steady in the Northeast in

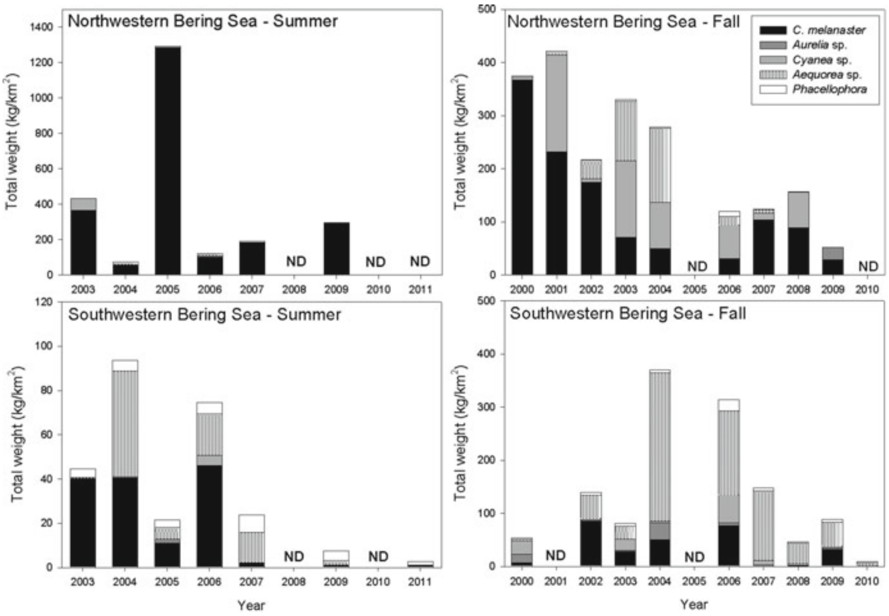

Fig. 7.4 Interannual comparison of summer (*left panels*) and fall (*right panels*) jellyfish biomass for the dominant species by geographic area from Russian TINRO research cruises. *ND* = no cruises done that year

summer and in the Southeast regions in fall (Fig. 7.2). The western side of the Bering Sea differs from the east in that its jellyfish species composition is more varied. In the south, highest abundances are seen in *Aequorea* sp., *C. melanaster*, and most recently *Phacellophora camtschatica* (Fig. 7.4). Northern waters were dominated by *C. melanaster*, though in recent years, species compositions are unknown due to lack of surveys.

7.3.2 *Seasonal Patterns*

As in many other systems, it is generally assumed that most of the large Scyphomedusae have annual life cycles and the medusa stage dies after reproduction sometime during the fall or early winter. Although there are few winter surveys available from the Bering Sea because of the extended sea ice, there have been wintertime observations of jellyfish along the ice edge, and some large and apparently overwintering jellyfish have been observed in May at the ice edge (G.L. Hunt, University of Washington, personal communication), but this may be a rare occurrence.

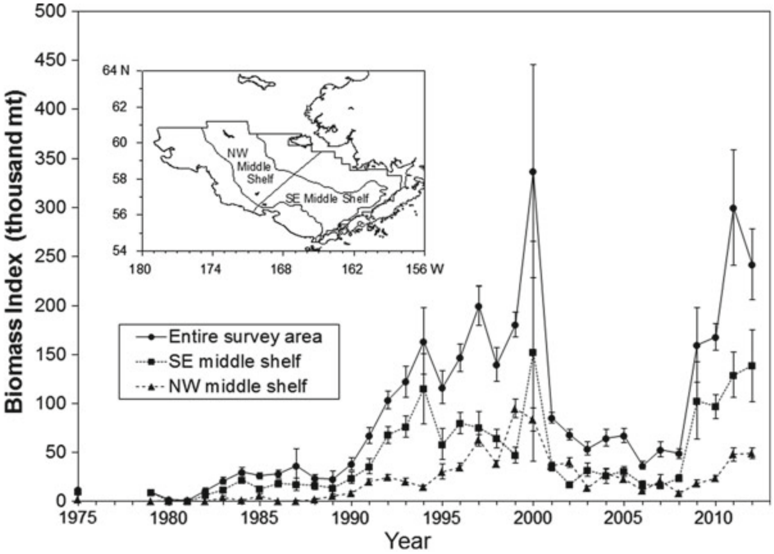

Fig. 7.5 Trend in jellyfish biomass from standardized bottom trawl surveys in the Bering Sea since 1975. Shown are the total biomass (*solid line*) and subsets for the Southeast (*SE*, *long dashed line*) and Northwest, (*NW*, *short dashed line*) middle shelf domains. Bars are standard errors. The inset shows the sampling areas on the Bering Sea shelf

Both the east and west are heavily dominated by *C. melanaster* in summer (Figs. 7.2, 7.3 and 7.4). Fall brings some change, with western *C. melanaster* starting to dissipate, whereas other large jellyfish (e.g., *Aequorea* sp. and *Cyanea* sp.) increase in biomass (Figs. 7.3 and 7.4). The eastern Bering Sea surveys recorded *C. melanaster* at high levels of abundance, and in recent years, few other large jellyfish species were caught (Fig. 7.2).

7.3.3 Horizontal Distribution

Significant changes in the abundance and distribution of large medusae have been observed during the summer RACE surveys, since the start of this time series in the early 1980s (Figs. 7.5 and 7.6), with a dramatic distributional shift occurring after 1990, as indicated by a constrained zero-inflated generalized additive model (Liu et al. 2011). In the early period of low jellyfish biomass (1982–1989; Fig. 7.5), the largest biomass was mainly in the southern part of the survey area, over the middle shelf (Fig. 7.6a). During the first escalating phase (1990–2000; Fig. 7.5), jellyfish biomass increased in the northern part of the survey area, also on the middle shelf (Fig. 7.6b). At the peak (2000; Fig. 7.5), biomass was high in both the north and

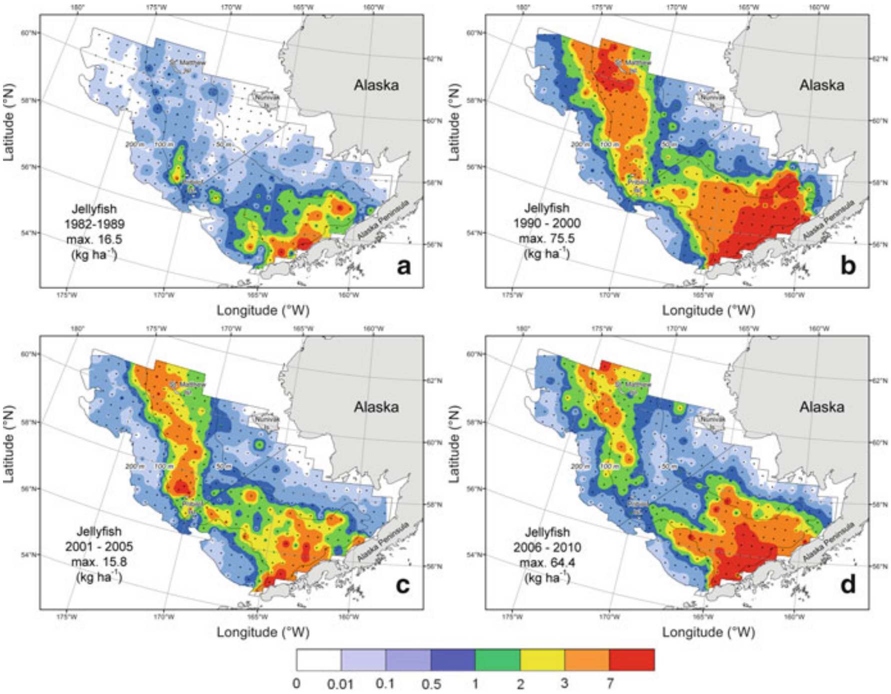

Fig. 7.6 Spatial distributions during the RACE eastern Bering Sea surveys of average jellyfish biomass (kg ha^{-1}) for the periods (**a**) 1982–1989, (**b**) 1990–2000, (**c**) 2001–2005 (an anomalously warm period), and (**d**) 2006–2010 (a very cold period)

south portions of the middle shelf and extended into the southern inner (<50 m depth) shelf region. During a period of warming (2001–2005) and declining jellyfish biomass (Fig. 7.5), concentrations of jellyfish were located near the Alaska Peninsula and northwest of the Pribilof Islands (Fig. 7.6c). During a cold period (2006–2012), jellyfish biomass increased to peak 2000 levels. Dispersion about 2011 and 2012 biomass estimates indicates that these values are nonoverlapping with 2009–2010 (Fig. 7.5). The 2011–2012 peak stands out in the time series and is perhaps even more dramatic than the earlier, but highly variable, peak in 2000 (Fig. 7.5). This increase occurred primarily on the middle shelf, north of the Alaska Peninsula (Fig. 7.6d).

Large jellyfish were observed during fall BASIS surveys in the eastern Bering Sea, starting with 2004 catch data when reporting began to include jellyfish species. Combined jellyfish species distribution for averaged warm years 2004 and 2005 showed evenly distributed jellyfish catches across the middle domain in both the north and southeastern Bering Sea (Fig. 7.7). During warm years, relatively high catches were observed in the north (above 60°N) and lower catches in the inner and outer domains (Fig. 7.7a). The cold year average for 2006–2010 distribution varied but was consistent with the warm years and showed evenly distributed catches in the

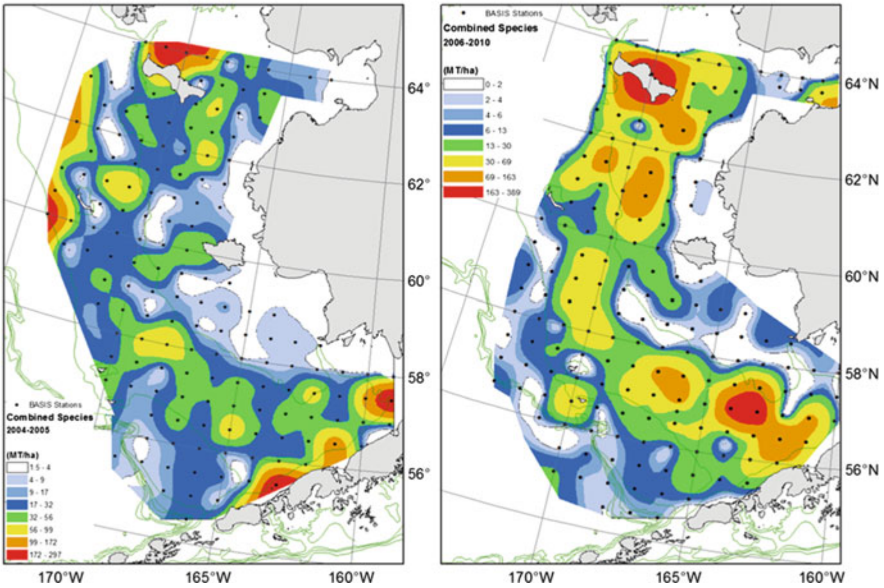

Fig. 7.7 Spatial distributions of average biomass (kg ha^{-1}) in warm (2004–2005, *left*) and cold (2006–2010, *right*) years from the BASIS eastern Bering Sea Surveys

Table 7.2 The mean biomass ± SE of jellyfish in the epipelagic layer of the western Bering Sea during 1991–2011 by seasons, kg km^{-2}

Class, species	Summer	Fall	Winter
Scyphozoa	111.6 ± 18.2	87.1 ± 9.3	7.5 ± 1.5
Aurelia sp.	0.2 ± 0.1	5.0 ± 1.6	–
Chrysaora melanaster	105.4 ± 18.1	54.7 ± 8.4	5.1 ± 1.4
Cyanea sp.	3.0 ± 0.7	23.0 ± 3.3	0.1 ± 0.1
Phacellophora camtschatica	2.8 ± 0.2	4.2 ± 0.3	1.6 ± 0.7
Hydrozoa	8.6 ± 1.2	53.0 ± 4.6	0.6 ± 0.2
Aequorea sp.	8.5 ± 1.2	52.7 ± 4.6	0.5 ± 0.2
Number of stations	868	1,074	81

middle domain and lower catches in the South inner and outer domains (Fig. 7.7b). Based on surveys in the fall, the highest concentrations of combined jellyfish catch occurred in the northern portion of the survey area during both warm and cold years (Fig. 7.7).

In the western Bering Sea, the highest concentrations of jellyfish occurred on the shelf near Gulf of Anadyr (Fig. 7.1) and in adjacent waters (Fig. 7.8). Jellyfish biomass reached a maximum in summer due to high numbers of the large *C. melanaster* at that time of year (Table 7.2). The relative biomass of jellyfish generally declines with increasing distance offshore (Fig. 7.8).

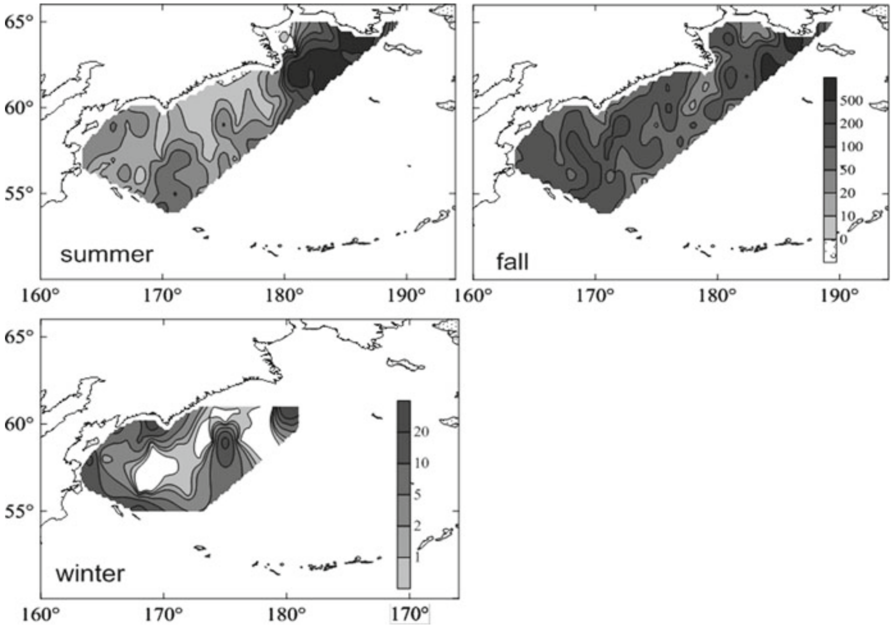

Fig. 7.8 Distribution of total jellyfish biomass (predominantly *Chrysaora, Cyanea*, and *Aequorea*) combined for all years combined by season from Russian TINRO research cruises (Note the winter surveys do not extend as far north due to the presence of seasonal sea ice)

Distributions of the dominant species had different patterns. *C. melanaster* was widespread throughout the western Bering Sea, but was the most numerous on the outer shelf off the Gulf of Anadyr (Fig. 7.9). *C. melanaster* concentrations decreased from summer to fall on the shelf region but increased in the deep-water areas. *Cyanea* sp. inhabited mostly shallow regions of the Gulf of Anadyr in summer but is found along the entire coast in the fall (Fig. 7.9). Concentrations of *Cyanea* sp. decreased sharply from the shelf to deep-water basins. *Aequorea* sp. were concentrated mainly in the deep-water regions in the summer (Fig. 7.9), but by fall, its distributional area was more widespread, and it became very abundant in the shallower waters of the Gulf of Anadyr.

7.3.4 Basin-Wide Distribution Patterns

Large-scale pelagic fish and invertebrate surveys were conducted throughout the Bering Sea except for international waters in the center (i.e., "Donut Hole") by the Russian research vessels *Darwin* and *Gnevny* during August and September of 1987

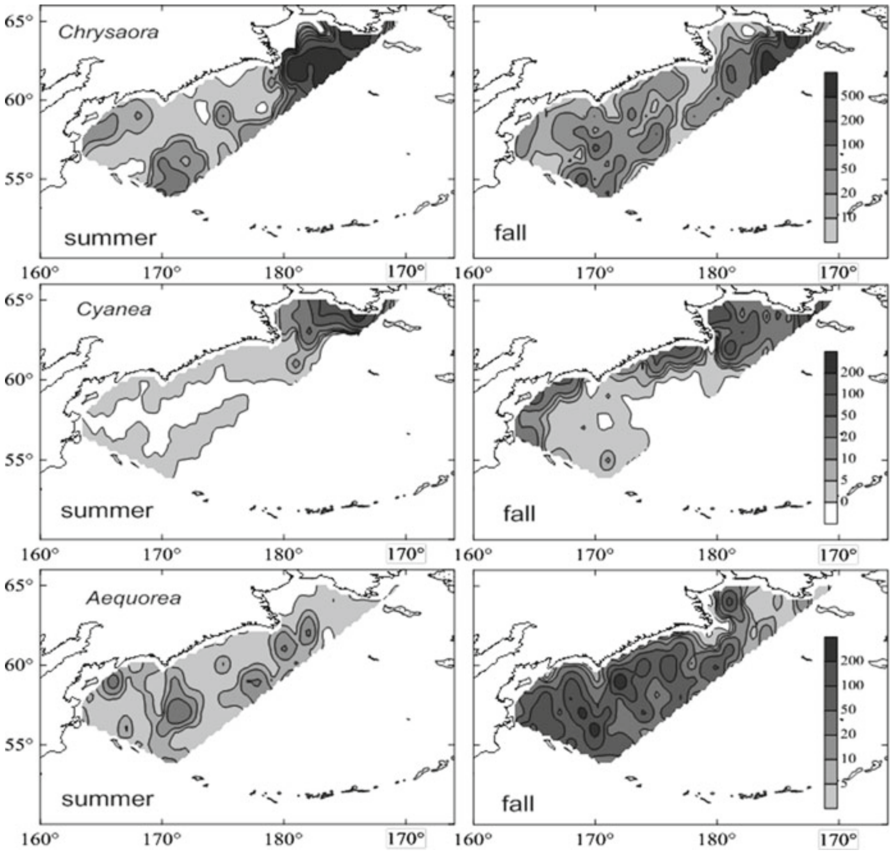

Fig. 7.9 Distribution of biomass (kg km^{-2}) of *Chrysaora* (*top*), *Cyanea* (*middle*), and *Aequorea* (*bottom panels*) for all years combine by summer (*left panels*) and fall (*right panels*) from Russian TINRO research cruises

(Fig. 7.10). Although the gear was slightly different during the two surveys, catch data were standardize to the same sampling area and to weight per hour towed (see Brodeur et al. (1999) for detailed sampling methodology). Cnidaria were the most frequently occurring taxa in both the eastern (139 out of 149 tows) and western (150 out of 183 tows) Bering Sea. They were second most important (after age 2+ walleye pollock) in mean biomass in the survey in the eastern part and fourth in the western part of the survey (Brodeur et al. 1999). Overall jellyfish biomass was substantially higher in the eastern Bering Sea, concentrated mainly on the shelf north of the Alaskan Peninsula (Fig. 7.10) although most stations recorded jellyfish. This distributional pattern was similar to what was seen during the RACE surveys in the late 1980s (Fig. 7.6).

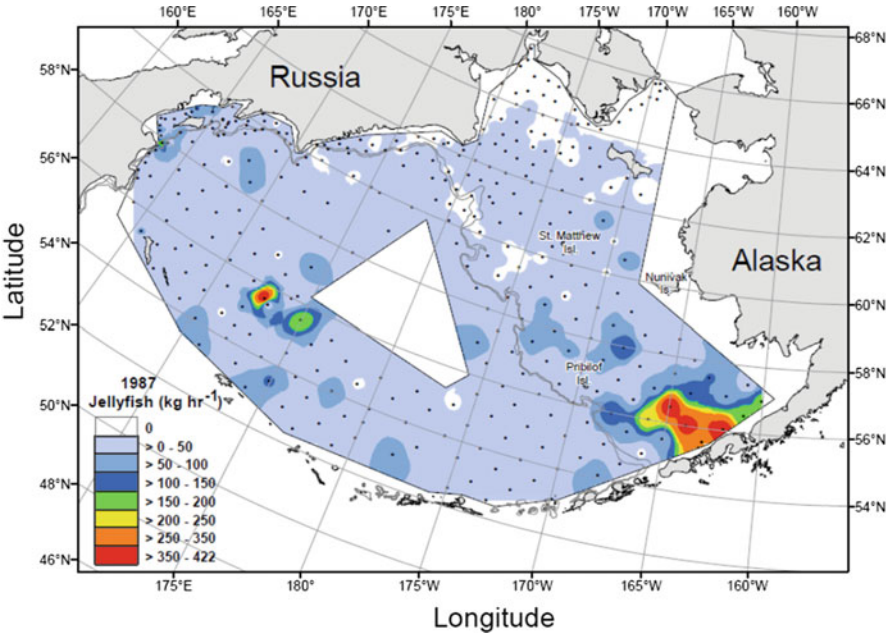

Fig. 7.10 Inverse Distance Weighted (*IDW*) plot combining the 1987 *Darwin* and *Gnevny* jellyfish catches in kg hr^{-1}. Trapezoid polygon in the middle of the map where there was no sampling

7.4 Vertical Distribution and Migration

7.4.1 Biomass and Abundance

During the TINRO surveys, a single station was occupied in the southwestern Aleutian basin (58° N, 172° E) for 14 days on August 23–September 5, 2004 and 75 tows were conducted at depths 0, 40, 80, 120, 160, 200, 350, 500, and 750 m to look at diel vertical distribution. There were 6–7 tows at each depth (from 0 to 750 m) within a 4-h time span followed by an additional 13 tows in the surface layer (0 m). Jellyfish occurred in all the layers trawled from 0 to 750 m (Fig. 7.11). Highest concentrations overall occurred in the upper epipelagic zone (0–50 m). Biomass and abundance of jellyfish decreased tenfold from the surface to the lower layers (50–200 m). By contrast, jellyfish abundance increased steadily from 400 m down to the deepest layer trawled (750 m, Fig. 7.11).

Only three (*C. melanaster*, *Aequorea* sp., and *Calycopsis nematophora*) of eight jellyfish species occurred at all depths throughout the water column from 0 to 750 m (Table 7.3). *C. melanaster* and *Aequorea* sp. were abundant in the surface layer, and their biomass and abundances significantly decreased from the surface to deep layers, whereas *C. nematophora* had the highest concentrations in upper mesopelagic

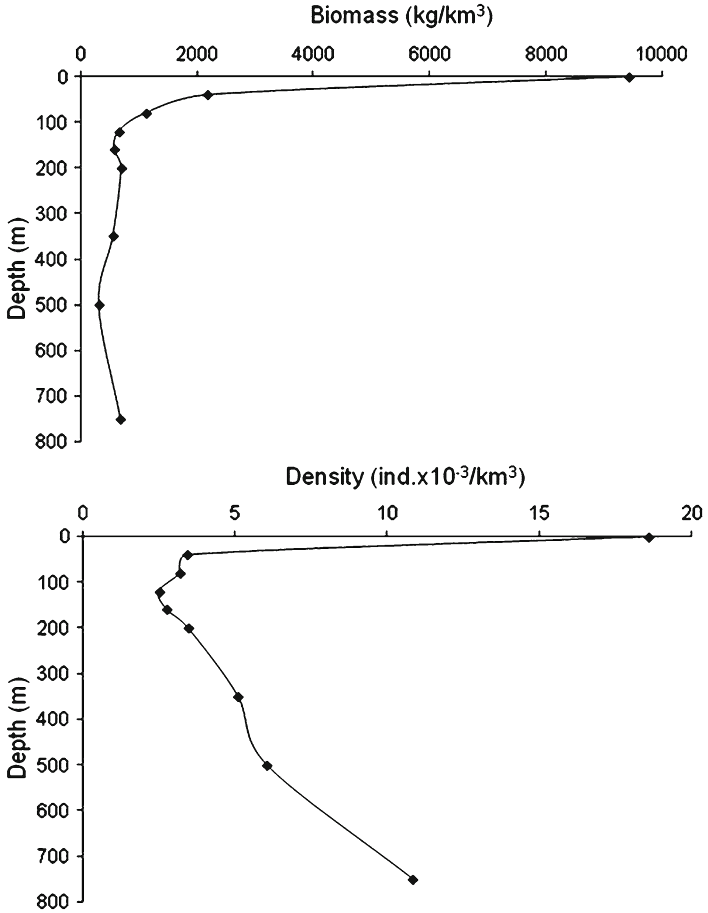

Fig. 7.11 Vertical distribution of total jellyfish biomass (*top*) and density (*bottom*) at a diel station in the western Bering Sea in 2004 for all species combined (Reproduced from Zavolokin (2010) with permission from the Pacific Scientific Research Fisheries Center)

zone. *P. camtschatica* and *Periphylla periphylla* also had a wide vertical distribution but were missing from some depth intervals (Table 7.3). *P. camtschatica* was more numerous in the epipelagic zone, whereas *P. periphylla* concentrated mainly in the mesopelagic zone. Only *Aurelia* sp. inhabited exclusively epipelagic waters (Table 7.3) and was generally confined to the surface layer. *Atolla wyvillei* inhabited the deep mesopelagic layers (Table 7.3), occurring at 350, 500, and 750 m. Biomass and abundance of *A. wyvillei* increased sharply from upper to lower layers, and it is possible that high numbers of this species were concentrated below the maximum depth of sampling, 750 m. *Ptychogena lactea* occurred in the lower epipelagic and in mesopelagic zones from 120 to 750 m (Table 7.3) and was most abundant in the upper layers of this zone. *Aequorea* sp., *C. melanaster,* and *Aurelia* sp. dominated

Table 7.3 Vertical distribution (depth in m) of mean ± SE jellyfish biomass (kg km^{-3}) and abundance (1,000 individuals km^{-3}) of the dominant species at a diel station in the western Bering Sea in 2004. *Dashes* indicate zero catch (Reproduced from Zavolokin (2010) with permission from the Pacific Scientific Research Fisheries Center)

Depth	*Atolla wyvillei*	*Aurelia* sp.	*Chrysaora melanaster*	*Periphylla periphylla*	*Phacellophora camtschatica*	*Aequorea* sp.	*Calycopsis nematophora*	*Ptychogena lactea*	Tows
	Biomass								
0	–	2,860 ± 1,794	2,847 ± 433	–	169 ± 53	3,557 ± 824	3.5 ± 1.7	–	20
40	–	–	1,017 ± 226	1.2 ± 1.2	208 ± 78	954 ± 374	0.9 ± 0.8	–	7
80	–	70 ± 61	193 ± 97	0.1 ± 0	158 ± 59	694 ± 210	3.4 ± 2.5	–	7
120	–	–	56 ± 24	2.5 ± 2	51 ± 47	539 ± 182	4.5 ± 2.8	0.7 ± 0.4	7
160	–	–	84 ± 48	–	7.3 ± 4.2	478 ± 142	7.2 ± 4.5	0.2 ± 0.1	7
200	–	–	234 ± 74	2.7 ± 2.2	–	448 ± 113	8.4 ± 3.1	0.6 ± 0.4	7
350	1 ± 1	–	146 ± 79	6.5 ± 3.4	2.3 ± 1.7	387 ± 117	11.6 ± 3.8	0.5 ± 0.1	6
500	12 ± 5	–	44 ± 31	31.2 ± 10.7	14.2 ± 11.7	207 ± 52	3.5 ± 0.8	0.4 ± 0.2	7
750	129 ± 26	–	31 ± 16	48.6 ± 14.9	13.7 ± 9.7	460 ± 124	3.9 ± 0.8	0.3 ± 0.2	7
	Abundance								
0	–	5,533 ± 3,631	3,086 ± 522	–	283 ± 73	8,651 ± 1,806	1,060 ± 515	–	20
40	–	–	799 ± 130	55 ± 55	180 ± 86	2,123 ± 855	261 ± 240	–	7
80	–	163 ± 142	184 ± 88	18 ± 18	287 ± 147	1,530 ± 478	1,009 ± 728	–	7
120	–	–	95 ± 39	74 ± 55	78 ± 50	946 ± 255	1,161 ± 722	148 ± 105	7
160	–	–	72 ± 37	–	73 ± 37	896 ± 242	1,685 ± 1,073	37 ± 24	7
200	–	–	191 ± 54	168 ± 117	–	780 ± 122	2,214 ± 812	109 ± 72	7
350	73 ± 36	–	165 ± 61	916 ± 481	75 ± 38	921 ± 245	2,847 ± 888	111 ± 29	6
500	789 ± 375	–	34 ± 22	3,128 ± 1,165	48 ± 33	577 ± 132	1,340 ± 241	131 ± 75	7
750	4,056 ± 1,149	–	47 ± 23	2,639 ± 837	163 ± 123	2,484 ± 1,020	1,325 ± 331	130 ± 112	7

the jellyfish biomass and abundance in the epipelagic zone (Table 7.3). *Aequorea* sp., *C. melanaster,* and *A. wyvillei* were also present at high biomasses in mesopelagic layer. *C. nematophora, P. periphylla,* and *A. wyvillei* were abundant at depth.

7.4.2 Diel Vertical Migration

Chrysaora melanaster, P. camtschatica, and *Aequorea* sp. were concentrated mainly in the upper 120 m during day and night (Fig. 7.12a–c) and did not appear to migrate extensively. Most of the *C. melanaster* and *Aequorea* sp. inhabited the surface layer, whereas *P. camtschatica* had high concentrations in the two depth strata below the surface. In contrast, the diel vertical distributions of *P. periphylla*, *C. nematophora,* and *P. lactea* clearly show that they migrated up from mesopelagic depths to the surface during the nighttime and migrated down during the daytime (Fig. 7.12d–f). The broadest range of distribution was shown by *C. nematophora* which showed a high biomass in deeper waters up to 750 m in the daytime and primarily in surface waters at night. *P. periphylla* ascended to only the 40-m layer in the nighttime and was not caught in surface waters. *P. lactea* occurred from 120 to 500 m at night and from 350 to 750 m during the day. *C. nematophora* was most abundant at 160–200 m in the nighttime and at 350 m in the daytime (Fig. 7.12e). *P. lactea* concentrated mainly at 120–200 m at night and at 500–750 m during daytime (Fig. 7.12f). *P. periphylla* showed the highest biomass at 500 and 750 m during both at day and night (Fig. 7.12d).

7.4.3 Jellyfish Size

Evidence of changes of body size with depth occurred only for *P. camtschatica* (Table 7.4). The mean, minimum, and maximum bell diameter clearly decreased from surface to deep waters. Size ranges of *P. camtschatica* were 8–47 cm for medusae caught in the upper 200-m layer and 6–22 cm for medusae caught deeper. The average body size of *P. periphylla* was greater in the epipelagic (3–8 cm) than in mesopelagic zone (3–4 cm) (Table 7.4), suggesting that large medusae migrate more extensively at night. Bell diameters of *C. melanaster, Aurelia sp.,* and *Aequorea* sp. were similar at most of depth layers and did not show any trends (Tables 7.4 and 7.5). Size ranges of these jellyfish were 10–44, 9–32, and 6–29 cm, respectively. The smallest individuals of *Aequorea* sp. (6–7 cm) occurred only at the deep layers (500–750 m). The high abundance of *Aequorea* sp. and *P. camtschatica* in the deep-water regions and the occurrence of small medusae mainly in mesopelagic layers suggest that the polyps of these species inhabit generally greater depths. No apparent differences in body size of *C. nematophora* and *P. lactea* were evident (Table 7.5), but these species are relatively small even as adult individuals, and may not be adequately sampled by conventional net sampling.

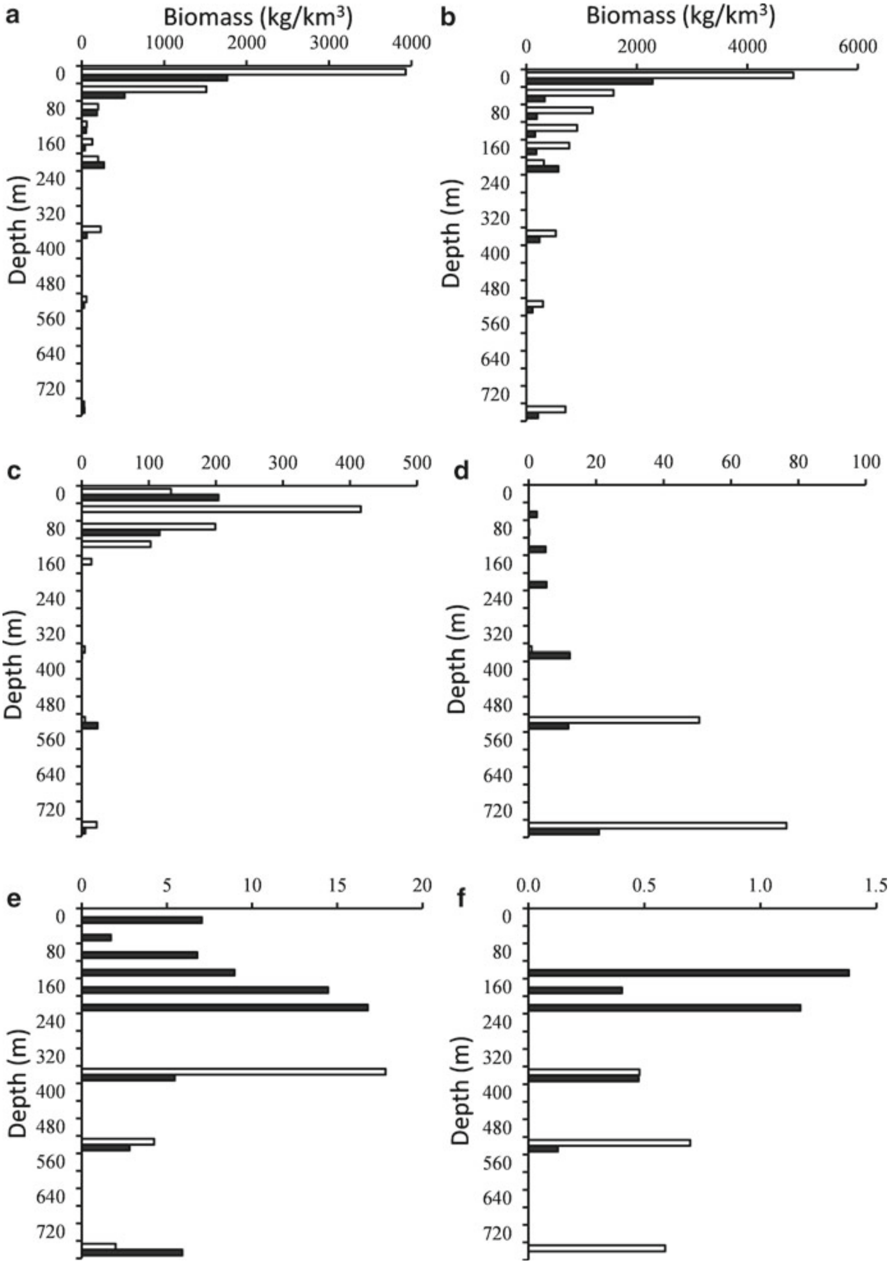

Fig. 7.12 Vertical profiles of jellyfish (kg km^{-3}) during day (*open bars*) and night (*filled bars*) by depth in the layer 0–750 m at a diel station in the western Bering Sea in 2004 for the dominant species: (**a**) *Chrysaora melanaster*, (**b**) *Aequorea* sp., (**c**) *Phacellophora camtschatica*, (**d**) *Periphylla periphylla*, (**e**) *Calycopsis nematophora*, and (**f**) *Ptychogena lactea* (Reproduced from Zavolokin (2010) with permission from the Pacific Scientific Research Fisheries Center)

Table 7.4 Vertical profiles of mean scyphomedusae bell diameter (cm) in the western Bering Sea in 2004. *Min* minimal diameter, *Max* maximal diameter, *N* number of individuals (Reproduced from Zavolokin (2010) with permission from the Pacific Scientific Research Fisheries Center)

Species	Depth (m)	Bell diameter	95 % C.I.	Min.	Max.	N
Atolla wyvillei	350	4.5	1.1	4	6	4
	500	5.2	0.4	4	9	23
	750	6.5	0.4	2	13	48
Aurelia sp.	0	20.0	0.3	9	32	61
	40	–	–	–	–	–
	80	20.6	4.1	13	28	9
Chrysaora melanaster	0	25.2	0.5	14	44	278
	40	28.5	1.6	17	38	32
	80	27.5	3.4	23	35	9
	120	26.5	2.5	25	30	4
	160	27.3	15.2	15	38	4
	200	28.8	3.6	22	38	11
	350	23.1	7.4	10	32	7
	500	31.0	19.1	30	33	2
	750	23.2	10.0	19	26	3
Periphylla periphylla	0	–	–	–	–	–
	40	7.5	4.3	7	10	2
	80	2.5	–	–	–	1
	120	5.9	3.0	4	9	4
	160	–	–	–	–	–
	200	3.6	1.2	2	6	9
	350	2.6	0.3	2	6	30
	500	3.7	0.2	2	12	115
	750	4.4	0.3	2	9	57
Phacellophora camtschatica	0	20.2	2.6	8	47	40
	40	27.0	4.8	18	42	7
	80	21.4	3.8	9	37	9
	120	21.5	13.9	11	29	3
	160	11.5	38.1	9	15	2
	200	–	–	–	–	–
	350	7.0	4.8	6	12	4
	500	13.7	20.6	6	22	3
	750	10.7	2.6	7	16	6

7.4.4 Direct Observations

Data on vertical distribution of large jellyfish in the eastern Bering Sea is more limited since the trawls used generally fish only a single layer quantitatively. However, detailed in situ observations have been made using underwater video cameras on remotely operated vehicles. Brodeur et al. (2002) showed that the five most dominant jellyfish species observed in the videos were primarily distributed between 15 and

Table 7.5 Vertical profiles of mean hydromedusa bell diameters (cm) in the western Bering Sea in 2004. *Min* minimal diameter, *Max* maximal diameter, *N* number of individuals (Reproduced from Zavolokin (2010) with permission from the Pacific Scientific Research Fisheries Center)

Species	Depth (m)	Bell diameter	95 % C.I.	Min.	Max.	N
Aequorea sp.	0	18.9	0.1	12	29	143
	40	19.1	0.5	10	28	43
	80	19.1	0.7	14	27	41
	120	19.6	0.7	15	26	30
	160	20.0	0.8	15	28	35
	200	19.5	0.6	15	24	19
	350	19.3	1.0	14	27	29
	500	19.8	1.5	6	25	18
	750	13.6	0.9	7	25	74
Calycopsis nematophora	0	1.9	0.1	1	3	54
	40	2.1	0.2	2	3	4
	80	1.9	0.1	1	3	20
	120	2.0	0.1	1	3	28
	160	2.0	0.1	1	3	28
	200	1.9	0.1	1	3	41
	350	2.1	0.1	1	4	64
	500	1.9	0.1	1	3	66
	750	1.8	0.1	1	3	52
Ptychogena lactea	120	3.8	0.5	3	6	5
	160	3.9	7.6	3	5	2
	200	3.1	1.2	3	5	5
	350	3.7	0.9	3	5	6
	500	4.1	0.4	4	5	5
	750	4.4	0.1	4	5	2

40 m in the water column, although some *Chrysaora* were found as deep as the observations were made (95 m). Both acoustic and video observations showed that the jellyfish (primarily *C. melanaster*) had a shallower distribution at night than during the day (Brodeur 1998).

7.5 Possible Causes of Boom and Bust Cycles

7.5.1 Relation of Jellyfish Trends to Climate

In the relatively pristine Bering Sea, only climate variability and fishing are likely causes for changes in the jellyfish population (Brodeur et al. 2008a). Although the groundfish fishery is the largest in the USA (NMFS 2010), fishing effort (i.e., number of trawls) was lower in the period 1998–2008 than in 1990–1997. Thus, the jellyfish biomass peak in 2000 is not associated with changes in commercial fishing intensity (Olson 2009). However, climate variability is known to be an important driver of change in the Bering Sea ecosystem, from primary production to zooplankton biomass, including jellyfish (Hunt et al. 2011).

A steep increase in jellyfish biomass was documented over the eastern Bering Sea shelf throughout the 1990s (Brodeur et al. 2002, Fig. 7.5). Biomass peaked in summer 2000 and then declined precipitously, stabilizing at a moderate level during 2001–2008. The onsets of the biomass increase during the 1990s and decline in 2000 coincided with transitions between climatic regimes. Brodeur et al. (2008a) used a 27-year time series to examine relationships between eastern Bering Sea jellyfish biomass and temperature, ice cover, atmospheric variables, current patterns, zooplankton biomass, and associated fish biomass using Generalized Additive Models (GAMs). These analyses indicated that jellyfish outbreaks during 1982–2004 were influenced regionally by interacting variables such as sea ice cover, sea surface temperature, currents, wind mixing, and food availability. Likewise, large-scale atmospheric and oceanic indices such as the Pacific Decadal Oscillation and Aleutian Index are correlated with jellyfish biomass trends in the western Bering Sea (Zavolokin 2011).

7.5.2 *Climate Effects on Zooplankton Communities*

The eastern Bering Sea shelf is a dynamic ecosystem, forced by a variable climate (Bond and Adams 2002; Aydin and Mueter 2007). Changes in ice conditions and timing of the spring bloom have been hypothesized to affect eastern Bering Sea zooplankton biomass (Hunt et al. 2011), and recent ecosystem studies indicate that with cooling from 2006 to 2009, populations of large zooplankton (i.e., *Calanus marshallae* and euphausiids) have increased (Coyle et al. 2011; Hunt et al. 2011). Likewise, surveys in 2009–2011 indicate that jellyfish biomass has increased once again to late-1990s levels (Fig. 7.5). Using updated environmental data from 1982 to 2009, Decker et al. (in preparation) reran the Brodeur et al.'s (2008a) GAMs to determine if previously developed models would accurately predict recent increases in Bering Sea jellyfish. GAMs predicting jellyfish biomass for the period 1982–2009 explained 85–90 % of the variance for the survey area (Decker et al. in preparation). Peaks in zooplankton biomass during the time series precede increases in jellyfish biomass, suggesting that food availability is an important factor contributing to fluctuations in eastern Bering Sea jellyfish populations. These jellyfish appear to be responding to both physical conditions and the abundance of crustacean zooplankton, and understanding environmental changes and the dynamics of their prey resources may be key to understanding jellyfish population changes in the eastern Bering Sea.

7.5.3 *Changes in Circulation and Dispersal*

In addition to temporal changes in biomass, the horizontal distribution of jellyfish has also shifted since the start of the RACE time series. Jellyfish expanded their range after 1990 to include the northern portion of the bottom trawl survey area (Liu et al. 2011), forming distinct centers of distribution in the southeastern portion of the survey and to the north near St. Matthew Island (Brodeur et al. 2008a; Fig. 7.6). Medusae collected in the bottom trawl are distributed primarily at bottom depths between approximately 50 and 100 m (Liu et al. 2011), which are depths corresponding to the middle shelf of the eastern Bering Sea.

The region along the Alaska Peninsula (i.e., "Slime Bank") is known for large jellyfish aggregations. The bifurcating flow through Unimak Pass, which travels more strongly to the northwest along the 100-m isobath in winter and more strongly eastward along the Alaska Peninsula in summer (Stabeno et al. 2002), may be in part responsible for the observed spatial patterns of jellyfish in the survey area. That is, benthic jellyfish polyps, likely to be located along the rocky shorelines of Unimak Pass and the Alaska Peninsula, release juvenile medusae, which would be advected to the northwest and eastward along the Alaska Peninsula by the predominant flow patterns. By contrast, the source of medusae for the northern aggregation may be the rocky coast of the Pribilof Islands, and the northwestern flow along the shelf in this region may contribute to the observed spatial pattern of jellyfish to the north. Drift simulations are in agreement with these speculations (Chen et al. in preparation).

7.6 Interaction of Jellyfish with Other Ecosystem Components

7.6.1 Fish Predators on Jellyfish

Numerous studies have examined the diets of many of the dominant groundfish species in the Bering Sea. Mito et al. (1999) summarized diet information on 64,652 fish from 47 species collected on the eastern Bering Sea shelf from 1972 to 1975. The only species they found which consumed appreciable amounts of medusae was prowfish (*Zaproa silenus*, n = 56) which consumed only gelatinous material. Brodeur and Livingston (1988) examined the diets of 25 elasmobranch and fish predators (n = 2,242) from the eastern Bering Sea in 1985 and 1986 and found that four species (sablefish *Anoplopoma fimbria*, yellow Irish lord *Hemilepidotus jordani*, flathead sole *Hippoglossoides elassodon*, and Alaska plaice *Pleuronectes quadrituberculatus*) consumed jellyfish, but the frequency of occurrence and weight percentage of jellyfish consumed were low, generally less than 1 %. An assessment of the Alaska Fisheries Science Center RACE demersal fish diet database (1985–2011) found 20 species had consumed Scyphozoa (mainly Alaska plaice, sablefish, walleye pollock, and yellowfin sole), 16 species had eaten Ctenophora (primarily sablefish, walleye pollock, and snailfishes), and only three species had consumed salps (data provided by Troy Buckley and Geoff Lang, AFSC, Seattle). Stomachs that were analyzed fresh at sea often contained a higher proportion of gelatinous prey than those that were preserved and analyzed in the lab, suggesting rapid breakdown of gelatinous material and hence underestimates of the contribution of these prey to predators (Troy Buckley, pers. comm.).

Pelagic fish predators on gelatinous taxa have also been reported for the Bering Sea. Many common myctophid and especially bathylagid midwater fishes are known to consume medusae and ctenophores, although gelatinous prey is secondary to crustacean prey (Gorbatenko and Il'inskii 1992; Balanov 1994; Balanov et al. 1995). In addition, juvenile and adult salmon are known to consume gelatinous prey, particularly chum salmon (Azuma 1992; Sakai et al. 2012), and this may allow them to avoid competition with other salmon despite the low nutritive value of jellyfish (Davis et al. 1998).

7.6.2 Predation on and Competition with Fish

Due to their high abundance and spatial overlap (e.g., Brodeur et al. 1999) with many commercially important fish species in the Bering Sea, there is a potential for jellyfish and especially *C. melanaster* to negatively impact the early life stages of fish through direct predation or competition for resources. In other systems, the spatial distributions of jellyfish and early life stages of commercial fish and forage fish overlap significantly (Brodeur et al. 2008b; Eriksen et al. 2012). Although the distributions of jellyfish and forage fish in relation to the environment are fairly well known in the Bering Sea (Brodeur et al. 1999; Cieciel et al. 2009; Hollowed et al. 2012), we know little about how the distributions of these important planktivores overlap in space and time.

There also is relatively little known about the diets of the dominant jellyfish in the Bering Sea. As mentioned previously, Hamner (1983) found juvenile walleye pollock in the oral pouches of *C. melanaster,* but the sample size was limited. Brodeur et al. (2002) also found walleye pollock juveniles in about 20 % of the stomachs examined during two different years, but no other fish species were identified. They estimated that this species was consuming 2.8 % of the pollock on a daily basis. They also estimated that *C. melanaster* consumed roughly 32 % of the standing stock of zooplankton on the shelf during summer and as such could be a substantial competitor with many pelagic species. These pollock consumption values were much higher than those (0.03 % of pollock eggs and 0.003 % of the larvae) calculated for the nearby Sea of Okhotsk by Gorbatenko et al. (2009). In the western Bering Sea, jellyfish collected from trawls in fall 2006 generally contained zooplankton (copepods, euphausiids, amphipods, pteropods, chaetognaths, ostracods, and larval decapods; Table 7.6). However, *C. melanaster* guts also contained lanternfish and unidentified fish in its diet unlike the other jellyfish species examined (Zavolokin et al. 2008). Clearly more information is needed on the feeding ecology and predation potential of jellyfish upon fish species, especially in the spring when more eggs and larvae are present in the water column.

Table 7.6 Summary of dominant jellyfish diets (% by weight) in the western Bering Sea in September–October 2006. Summaries by major taxonomic groups are in *bold italic* type. SCI (Stomach Content Index) is the prey weight × 10,000/body weight (%00). "+" = <0.5 %. *Dashes* indicate zeros

Prey	*Aequorea* sp.	*Aurelia* sp.	*Chrysaora melanaster*	*Cyanea* sp.	*Phacellophora camtschatica*
Copepoda	**59**	–	–	**10**	–
Pseudocalanus sp.	+	–	–	–	–
Paraeuchaeta japonica	+	–	–	–	–
Neocalanus plumchrus	57	–	–	–	–
Neocalanus cristatus	–	–	–	10	–
Metridia pacifica	2	–	–	–	–
Euphausiacea	–	–	**3**	**2**	**85**
Euphausia pacifica	–	–	2	–	85
Thysanoessa longipes	–	–	1	2	–
Euphausia sp.	–	–	+	–	–
Amphipoda	**35**	–	**+**	**5**	–
Themisto pacifica (1–2 mm)	–	–	+	5	–
Themisto pacifica (2–3 mm)	35	–	–	–	–
Themisto pacifica (3–4 mm)	+	–	+	–	–
Chaetognatha	*3*	–	–	–	–
Sagitta elegans	3	–	–	–	–
Pteropoda	*1*	–	**+**	*5*	–
Limacina helicina	1	–	+	5	–
Ostracoda	–	–	**50**	–	–
Decapoda zoea	**2**	**100**	**13**	**78**	**15**
Cephalopod paralarvae	–	–	**2**	–	–
Teleosts	–	–	**32**	–	–
Stenobrachius leucopsarus	–	–	32	–	–
Unid. fish bones	–	–	+	–	–
SCI (%00)	0.53	0.07	0.70	1.18	0.16
Mean bell diameter (cm)	20.2	16.3	38.2	26.6	36.5
Mean weight (g)	444	327	2,515	946	2,300
Number of stomachs	11	5	6	8	2

Hamner (1983) also reported gut contents for the predominant eastern Bering Sea hydromedusae and scyphomedusae. *C. melanaster* fed primarily on pteropods and also on euphausiids, medusae, and crustacean zooplankton. Larger (7–50-cm bell diameter) *C. melanaster* were also observed consuming juvenile walleye pollock (*Theragra chalcogramma*). *Cyanea* sp. consumed the medusae *E. flammea*, *C. melanaster, Aequorea* sp., and *S. princeps*. Pteropods, crustaceans, and larval fish were also found in *Cyanea* sp. guts; however, it was not possible to determine if *Cyanea* sp. were feeding directly on these prey or if these items were the prey of the medusae consumed by *Cyanea* sp. The leptomedusan *S. mertensii* fed nearly exclusively on *Pseudocalanus* copepods, whereas *Aequorea* sp. fed upon mesozooplankton (i.e., copepodites, zoeae, and juvenile pteropods). Laboratory and field observations indicate that the anthomedusans *Catablema* sp. and *Stomotoca atra* also feed on other medusae.

7.6.3 Commensal Relationships with Juvenile Walleye Pollock

The first mention of age-0 pollock found in association with jellyfish in the Bering Sea was anecdotal in the form of scuba diver observations reported in Hamner (1983). A quantitative analysis was done by Brodeur (1998) who examined ROV videos from 27 dives over 2 years in the eastern Bering Sea. Juvenile pollock were commonly found swimming around the tentacles of *C. melanaster* and to a lesser extent *Cyanea* sp., exclusively during daylight hours. At night, the pollock left the jellyfish layer (~ 30–40 m) and ascended to the surface to feed. These observations did not show that the pollock consumed either the jellyfish or their prey which suggests that this is a facultative association to avoid predation in the pelagic zone where little other shelter exists. However, since *C. melanaster* consumes larval and juvenile pollock, it is uncertain whether this relationship benefits walleye pollock recruitment overall.

7.6.4 Avian Predators

In a separate study as part of the PROBES work, Harrison (1984) determined that scyphozoan jellyfish are preyed on by 11 species of birds in the Bering Sea: *Fulmarus glacialis, Puffinus griseus, Puffinus tenuirostris, Oceanodroma furcata, Larus hyperboreus, Rissa tridactyla, Rissa brevirostris, Uria aalge, Uria lomvia, Aethia psittacula,* and *Aethia cristatella*. Birds ingested *Chrysaora* and *Cyanea*, as well as other unidentified medusae. Hyperiid amphipods, which are parasitic on scyphomedusae (Laval 1980; Harbison et al. 1977; Towanda and Thuesen 2006), also contributed to avian diets. Harrison (1984) found that birds feeding on jellyfish contained a greater diversity of prey than non-jellyfish-eating birds and suggested that gelatinous zooplankton are important in structuring the Bering Sea food web. The jellyfish associates are of higher nutritional value (Percy and Fife 1981) than jellyfish tissue (Larson 1986), and thus, medusae and their symbionts are a concentrated food patch for birds and other higher trophic-level organisms.

7.7 Importance to the Ecosystem Energy Cycling and Relationship to Management

Jellyfish are important zooplankton consumers and can restructure food webs when their abundance is high (Kideys et al. 2005). Field and modeling studies in other ecosystems indicate that jellyfish can negatively impact fisheries because they compete with zooplanktivorous fish, feed on early life stages of fish, and divert lower trophic-level production away from upper trophic levels (Ruzicka et al. 2007; Brodeur et al. 2008b, 2011). Specifically, in the northern California Current, where the jellyfish taxa are similar to that of the Bering Sea, gelatinous predators can consume up to 150 % of the energy relative to forage fish, but only pass on 2 % of this production to upper trophic levels while forage fish pass on 10–15 % (Ruzicka et al. 2007). We currently lack similar, specific understanding of how Bering Sea jellyfish affect energy flow through the ecosystem and how commercially important fish in the region may be impacted. However, given their seasonal blooms, particularly during periods of high abundance of *C. melanaster* (e.g., Brodeur et al. 2008a; Fig. 7.5), Bering Sea jellyfish can represent a significant energy shunt in marine pelagic food webs during high biomass years, given that they are not consumed by many pelagic predators. Currently, our understanding of gelatinous zooplankton and its role within the Bering Sea food web is limited, despite these species' important role in the ecosystem, both as predator and prey. More information (i.e., consumption estimates, food web modeling) is required to determine the ecological impacts of Bering Sea jellyfish blooms and to guide ecosystem-based management efforts.

7.8 Future Studies and Projections

Population trends of Bering Sea jellyfish do not support the hypothesis that jellyfish are exhibiting a sustained population increase, but rather, Bering Sea jellyfish populations exhibited variable oscillations over decadal time scales similar to many other populations worldwide (Condon et al. 2013). Given the implications of jellyfish blooms for fisheries, these observations indicate that Bering Sea jellyfish populations should continue to be monitored and perhaps forecasted so that we can better prepare for the economic impacts of jellyfish on the Bering Sea ecosystem. Moreover, the ecological consequences of the large blooms need to be further investigated, particularly how they impact the fish and other higher trophic levels of interest to humans.

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Chapter 8
The Giant Jellyfish *Nemopilema nomurai* in East Asian Marginal Seas

Shin-Ichi Uye

Abstract The giant jellyfish *Nemopilema nomurai* is unique in both its enormous body size and its propensity for occasional population explosions in the East Asian Marginal Seas (i.e., the Bohai, Yellow, East China, and Japan Seas). Its frequent blooms in the last decade (i.e., in 7 out of 10 years between 2002 and 2011) have caused severe damage to local fisheries in Japan and Korea. The blooms may be attributable to environmental/ecosystem conditions conducive to such outbreaks that have prevailed in Chinese coastal waters, which are a seeding and nursery ground. One of the most characteristic features of the asexual reproduction of this species lies in its podocysts, a resting stage capable of dormancy for at least 6 years prior to excystment into active and strobilating polyps. Thus, the abundance and behavior of podocysts in a given season may determine the population size of medusae in the next season. At present, the year-to-year variation in bloom intensity can be forecast in early summer based on on-deck sighting surveys from ferries of young medusae en route from the seeding waters to the Japan Sea. Thereby, fishermen can prepare countermeasures well in advance for likely jellyfish outbursts.

Keywords Jellyfish blooms • Giant jellyfish • East Asian Marginal Seas • Sexual reproduction • Asexual reproduction • Scyphozoan polyps • Podocysts • Feeding ecology • Over-fishing • Eutrophication • Forecasting blooms

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8.1 Introduction

Nomura's jellyfish, *Nemopilema nomurai* (Scyphozoa: Rhizostomeae), is one of the largest of all jellyfish species, attaining a bell diameter of ca. 2 m and a wet weight of ca. 200 kg (Fig. 8.1, Shimomura 1959; Yasuda 2007). It was first described as a new genus and species by Kishinouye (1922) based on a formalin-preserved specimen caught in 1920 and live specimens taken in 1921, both in the Fukui Prefecture area of the Japan Sea. Uchida (1954) later regarded *Nemopilema* as a junior synonym of *Stomolophus* without any plausible reason and referred to this species as *S. nomurai*. Furthermore, Kramp (1961) and Hon et al. (1978) regarded this species as a synonym of *S. meleagris*. However, *N. nomurai* differs greatly from *S. meleagris* in morphology, size, and geographic range. Finally, Omori and Kitamura (2004) revised the taxonomy of three rhizostome species from Japanese waters and concluded that this jellyfish should be reassigned to the genus *Nemopilema*. They also reinstated the species name *nomurai*.

Prior to modern scientific study, this large species was perhaps recognized in China as one of the edible jellyfish, since the commonly eaten species, *Rhopilema esculenta*, that often co-occurs with *N. nomurai*, was described by Zhang Hua (232–300 AD) in his book "Natural History" during the Tsin Dynasty (Wu 1955). A large jellyfish, similar to *N. nomurai,* was first recorded in the southern Yellow Sea as "Haepaleo" meaning jellyfish in a book by the Korean author Chong (1814). In Japan, a jellyfish likely to be *N. nomurai* was reported for the first time by William Griffis, an American teacher who lived in Fukui (formerly Echizen)

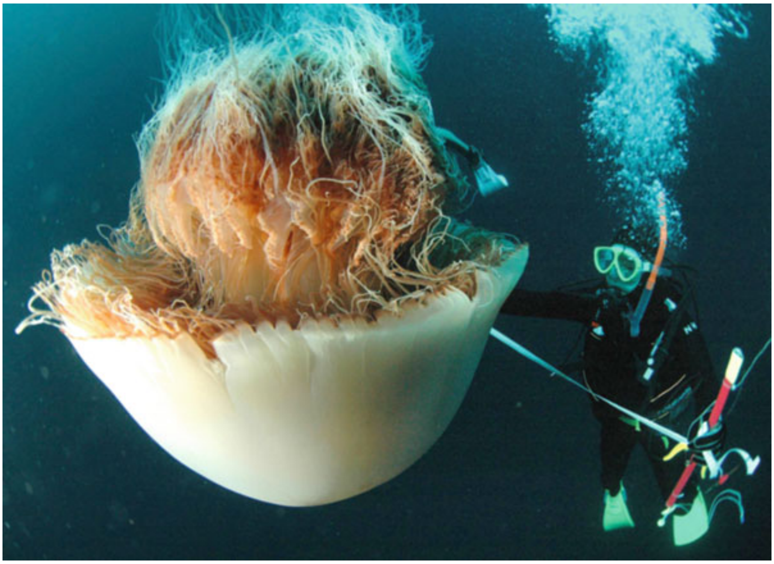

Fig. 8.1 The giant jellyfish *Nemopilema nomurai* with divers trying to measure its body size (Credit owned by Yomiuri Shimbun)

Prefecture in 1871 and 1872, when he encountered this peculiar jellyfish at sea. He described it as a brilliantly colored, Japanese-parasol-like jellyfish (Griffis 1887). These early records did not give any information about the bloom intensity but showed that the geographical range of this species expanded into almost the entire East Asian Marginal Seas, which consists of the Bohai, Yellow, East China, and Japan Seas. Although occasional population outbreaks probably occurred, *N. nomurai* only appeared in numbers that could be quantified in the Japan Sea. Japanese fishermen have long sought these medusae to use as bait for red sea bream and filefish, and this traditional fishing method still remains today.

8.2 Recurring Blooms and Their Impact on Fisheries

In the Japan Sea, a prominent bloom of *Nemopilema nomurai* was first recorded in 1920 (Kishinouye 1922), followed by two more records in 1958 (Shimomura 1959) and 1995 (Yasuda 2007), a rate of about one per 40 years in the twentieth century. In the present century, there has been a remarkable change in bloom frequency; in 2002, only 7 years after the previous bloom, enormous numbers of *N. nomurai* medusae appeared in Japanese coastal waters, causing severe damage to fisheries. Since then, blooms (e.g., >2,000 medusae entrapped per set net per day) have occurred almost annually, except for 2008, 2010, and 2011 when medusae were scarce (e.g., <10 medusae).

In bloom years, massively aggregated medusae have devastated various types of net fisheries (i.e., seine, gill, trawl, and set), with set nets consistently the most susceptible to jellyfish damage. In late July of 2005, *N. nomurai* damaged set nets at Tsushima Island in the Tsushima Strait, before the bloom shifted northward along the coast of the Japan Sea carried by the Tsushima Current. The damage was most serious and widespread in late October, when significant numbers of medusae were transported into the Okhotsk Sea, north of Hokkaido, and some were also transported by the Kuroshio Current along the southwestern Pacific coast of Japan (Fig. 8.2, Uye 2008). Thereafter, the medusa population began to diminish, and it almost disappeared by late February. Complaints from fishermen to the Fisheries Agency of Japan exceeded 100,000, and monetary loss to fisheries was estimated to be ca. 30 billion JPY in 2005. The problems to fisheries consist of (1) clogging and bursting of fishing nets, (2) decrease of fish catch, (3) killing and spoiling of fish, (4) stinging of fishermen, (5) increased time and labor required to remove entrapped medusae from the nets, and (6) increased risk of capsizing to trawl boats.

I visited a fishery cooperative operating three salmon set nets in Iwate Prefecture, northern Japan, in December 2005, when approximately 200 medusae with average bell diameter of ca. 1 m were entrapped in a net (Fig. 8.3, Uye 2008). Some fishermen scooped individual salmon and other valuable fish with a dip net, while the others sliced medusae with a long-handled steel cutter. After the medusae in the net were sliced into small parts, the debris was removed repeatedly with a big scoop net hoisted by the ship's crane. Then, the salmon remaining at the bottom of the net

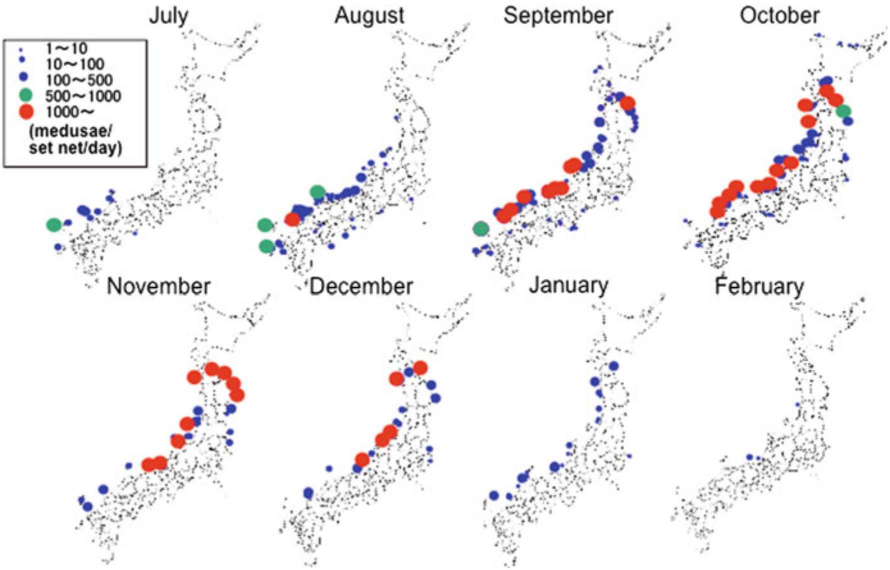

Fig. 8.2 Spatial distribution of *Nemopilema nomurai* from July 2005 to February 2006 determined from numbers of medusae trapped in set nets (Courtesy of the Japan Fisheries Information Center, which drew these maps based on data compiled by the Japan Sea National Fisheries Research Institute)

Fig. 8.3 Fishermen struggling with *Nemopilema nomurai* medusae entrapped in a set net off the coast of Iwate Prefecture, in December 2005 (From Uye 2008)

were harvested, many dead and pale from jellyfish stings. It took 1.5 h to process the single net, nearly three times longer than the time it usually takes without jellyfish. The captain of the ship told me, "It is not too bad today, but it was very bad last month, when a net was clogged with several thousands of medusae so that plastic floats tied along the net sank below the sea surface." The only solution for the fishermen to prevent the nets from bursting was to undo the seams of the nets to release both entrapped jellyfish and fish. On other occasions, they had to remove medusae twice a day in order to keep their nets operable. In 2005, many fixed nets were broken and burst (the exact numbers are not known), so that owners of these nets were forced to stop fishing prior to the end of the fishing season.

8.3 Life Cycle

8.3.1 Sexual Reproduction

Nemopilema nomurai is a gonochoristic jellyfish having a ribbon-like ovary and testes at the bottom of its pleated, interradial gastric pouch, which protrudes beneath the bell (Fig. 8.4). In August and September, the immature gonads of young medusae (wet weight: ca. 10 kg) are largely transparent. In October some medusae (ca. 60 kg)

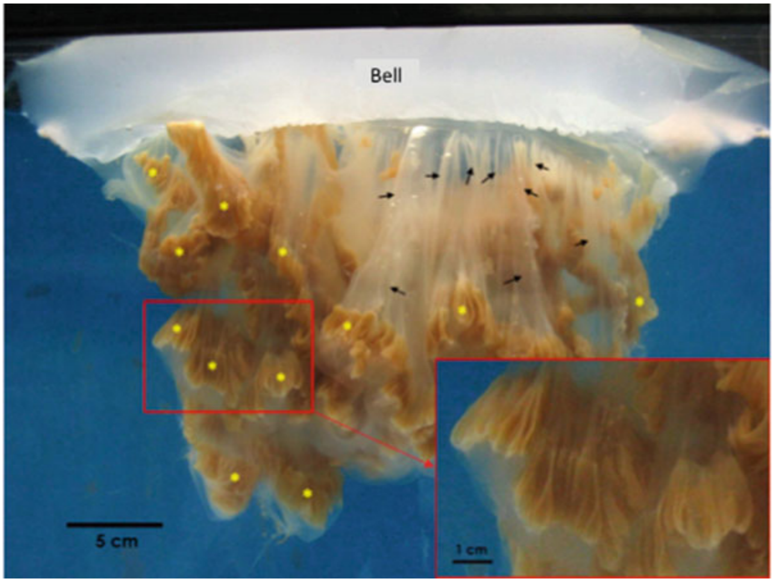

Fig. 8.4 View of a *Nemopilema nomurai* ovary contained in the gastric pouch protruding beneath the bell. The gastric pouch is a large sac with numerous folds (indicated by *arrows*) like drapes. The ovarian tissue (*asterisks*) is located at the bottom of each fold (From Ohtsu et al. 2007)

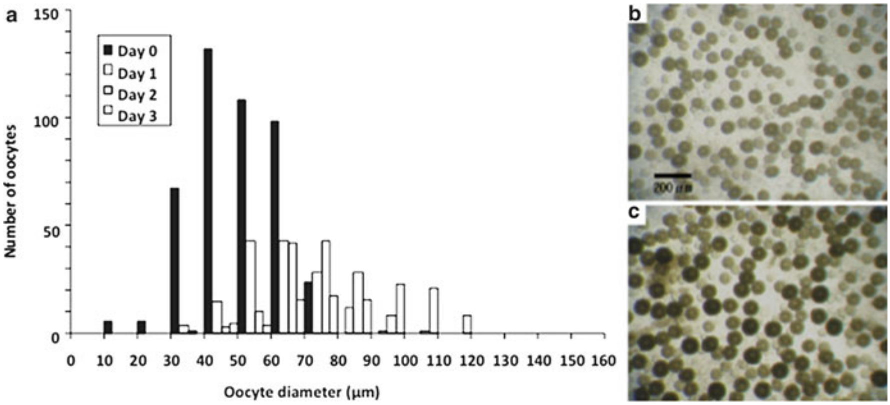

Fig. 8.5 (**a**–**c**) Maturation of oocytes in *Nemopilema nomurai* (**a**) Daily changes in the diameter distribution of oocytes in a female medusae during captivity in a net near the shore (From Ikeda et al. 2011a). (**b**) Transparent oocytes on the day of capture (day 0). (**c**) Oocytes become darker and larger (day 2) and have extraordinarily large nuclei (From Ohtsu et al. 2007)

begin to have colored gonads, varying from milky white through to pink and dark brown, and in November and December more medusae mature sexually, indicating that late fall and early winter are the main spawning season (Kawahara et al. 2006; Ohtsu et al. 2007; Iguchi et al. 2010). Neither fertilized eggs nor planulae are found in the ovary or on the oral arms, indicating that fertilization is external in this species.

Even during the main spawning season, there is a large individual difference in the maturation stage. It is peculiar that physically intact and vigorously swimming medusae have exclusively immature gonads and their gonadal maturation is induced when the medusae are fatally damaged. Ohtsu et al. (2007) and Ikeda et al. (2011a) detailed the induction of gametogenesis after immature medusae were arrested in a net on the beach. On day 0, when a female medusa was caught, only transparent oocytes less than 70 µm diameter were present in her ovary. On days 2–3, oocytes became larger and darker (Fig. 8.5) with extraordinarily large nuclei, or germinal vesicles, indicating that they were still in a primary oocyte stage with their maturation arrested at the prophase of the first meiotic division. The maturation division, observed as breakdown of the germinal vesicles, was induced by light exposure, and spawning of eggs or mature secondary oocytes (ca. 110 µm diameter) from the ovary occurred 80–100 min after light exposure (Fig. 8.6). For males, on day 0 the testis consisted of small ovoid sperm follicles (long axis: ca. 80 µm) devoid of spermatozoa. By day 5, the follicles were enlarged (ca. 120 µm) and filled with spermatozoa. Light exposure also acted as a trigger for sperm release, which was complete within 30 min after illumination. In the field, dawn can function as a light trigger for spawning of both eggs and sperm. Both are shed into the gastrovascular cavity and then released from the body through small orifices on the scapulets and oral arms. In the majority of adult medusae, however, physical damage, and hence their gonadal maturation, may progress relatively slowly due to predation by fish and parasitic shrimp (*Latreutesanoplonyx*).

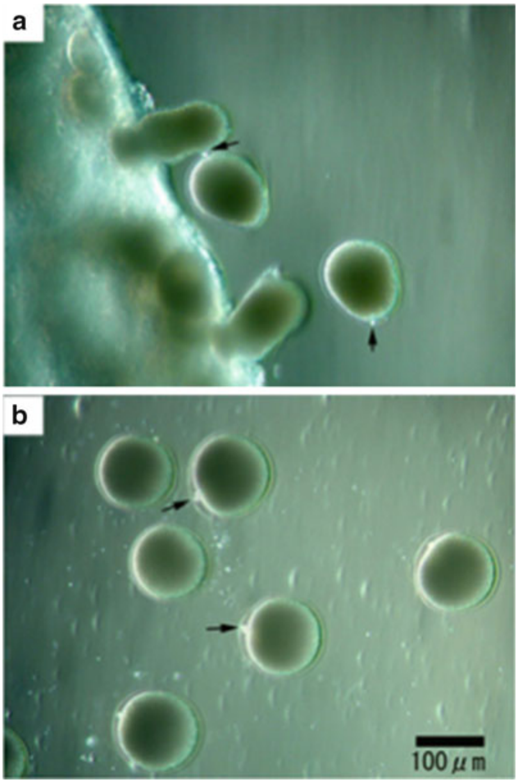

Fig. 8.6 (**a**–**b**) Spawning of secondary oocytes from *Nemopilema nomurai* (**a**) Oocytes with a single polar body and (**b**) completely matured secondary oocytes with two polar bodies (From Ohtsu et al. 2007)

Fertilization of eggs may take place not only in the female's gastrovascular cavity into which sperm are drawn in from the surrounding water but also in the ambient water, suggesting that the proximity of mature females and males is important to ensure high rates of fertilization. Fertilized eggs develop and hatch into planula larvae about 24 h after fertilization at 20 °C. Planulae are ca. 170 μm long and ca. 130 μm wide, with 10 μm long cilia over their surface. Planulae swim for several days until they settle on hard substrates, either of natural (e.g., pebble, bivalve shell, wood) or artificial materials (e.g., ceramic, glass, various plastics) (Kawahara et al. 2006).

8.3.2 Asexual Reproduction

It takes 2 days for settled planulae to completely metamorphose into polyps (scyphistomae) with 4 tentacles and a calyx diameter of 250–300 μm. Young polyps develop in 6–10 days after settlement to an intermediate stage with 8 tentacles and calyx diameter of ca. 500 μm. Fully developed polyps with 16 tentacles and 800–1,100 μm calyx diameter are found 10–20 days after settlement, when they start asexual reproduction by means of podocyst production. A stolon protrudes from the bottom of the calyx and attaches to the substrate ca. 10–300 μm away from the base of the polyp. Then, the polyp body mass gradually moves to the new attachment site, leaving a podocyst behind at the former position. The newly produced podocysts are whitish and ca. 300 μm in diameter. New polyps excyst from the podocysts after variable dormant periods (see details below). In the laboratory, a single, very productive original (or founder) polyp formed a colony consisting of 18 podocysts and 6 polyps when kept at 18 °C for 6 months (Kawahara et al. 2006).

In the laboratory, polyps kept at temperatures ≥19 °C never strobilated, but those kept at ≤15 °C did; it took at least a month to start strobilation at 11 and 15 °C and 3 months at 9 °C (Kawahara et al. 2013). These results suggest that seasonal chilling could be a trigger inducing strobilation in wild polyps. When strobilation commenced, the calyx became elongated and segmented; in 1.5 days, rhopalia with statoliths became apparent; and in 2 days, ephyral lappets were elongated and pulsated rhythmically. Fully developed strobilae, 2.2–2.8 mm long from the base of the polyp to the top of the ephyral mouth, liberated ephyrae one by one into the water. The average number of ephyrae formed by a strobila was ca. 5 (Kawahara et al. 2006).

Newly liberated ephyrae were 2.2–3.8 mm wide from lappet tip to lappet tip; were able to ingest food, such as *Artemia* nauplii; and grew at temperatures ≥18 °C. However, they were unable to catch sufficient food to sustain net growth at ≤11 °C. Therefore, the seasonal warming, i.e., above around 15 °C, might enable and accelerate ephyral growth. At 22 °C ca. 10 days post liberation, the ephyrae had grown to metephyrae, with the secondary lappets extended outwards to the primary lappets such that the bell margin looked polygonal and was 8–14 mm wide from lappet tip to lappet tip. They had eight clearly defined oral arms, and each arm branched into two wings at the tip. In advanced metephyrae (14–18 mm wide; ca. 20 days post liberation), a reddish filiform appendage developed at the junction point of the wings, and the central mouth was still open. After the central mouth closed, the metephyrae advanced to the medusa stage and grew to a bell diameter of 40–110 mm at 40–50 days post liberation. Numerous appendages were present on the oral wings and scapulets. Further rearing of medusae was not possible in small laboratory aquaria (volume: ca. 50 l), perhaps because repeated bumps into the wall were fatal for them. In the barrier-free open sea, *N. nomurai* grows much larger, attaining sexual maturity in late fall and early winter and dying off by midwinter. Their planktonic life span is less than a year, but their benthic life span may be multiple years.

8.4 Seasonal Geographical Distribution

The large bay system flanked by the Korean Peninsula and the mainland of China (i.e., the Bohai, Yellow, and East China Seas) is the geographical origin of the early pelagic stages. Although the polyps have not yet been found, this area is likely to be

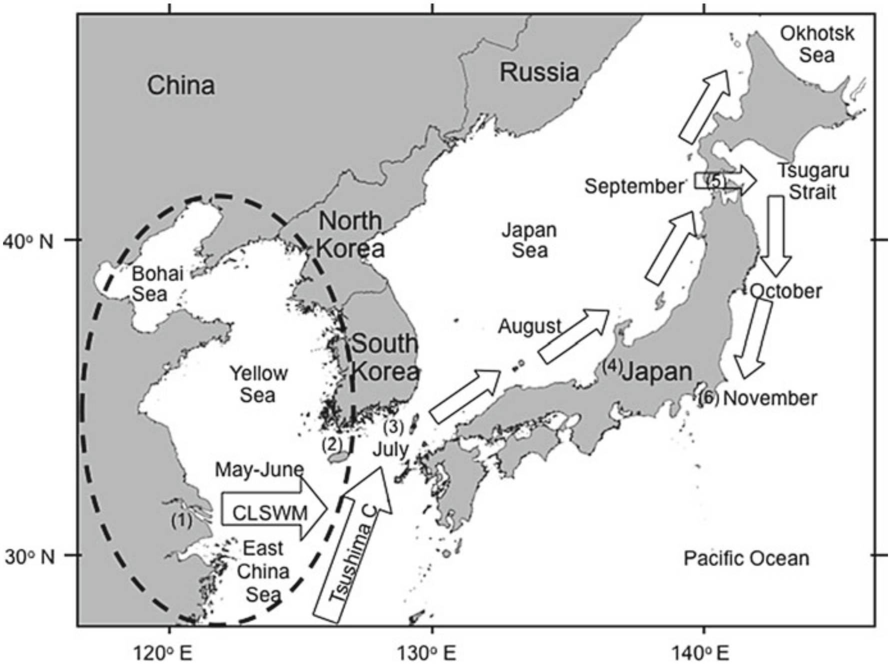

Fig. 8.7 Schematic representation of the advective transport of *Nemopilema nomurai* medusae from their seeding and nursery ground (indicated by *dashed line*) to the Japan Sea showing major hydrographic features: Changjiang Low Salinity Water Mass (*CLSWM*) and the Tsushima Current. (*1*) Changjiang River Estuary, (*2*) Cheju Island, (*3*) Tsushima Strait, (*4*) Fukui Prefecture, (*5*) Tsugaru Strait, and (*6*) Boso Peninsula. See text for detail (Modified from Uye 2008)

the main benthic habitat of *N. nomurai* (Hon et al. 1978; Zhang and Li 1988; Cheng et al. 2004; Kawahara et al. 2006), because ephyrae and small (bell diameter: <10 cm) medusae have been collected (Toyokawa et al. 2012) and sighted (see below) only in this region. The ephyrae are released into the plankton from the benthic polyps during spring to early summer. Many individuals spend their planktonic life as medusae in this area until they die in winter (Zhang et al. 2012), and thereby the endemism of this species is maintained. However, the majority of medusae originating in the southern Yellow Sea and northern East China Sea are expatriated by currents (Fig. 8.7). Due to monsoonal rainfall in June and July in temperate East Asia, the Changjiang (Yangtze River) low salinity water mass (LSWM) forms, and its front extends close to Cheju Island, Korea. The young medusae are entrained into this offshore-spreading LSWM and are then transported northward by the Tsushima Current to the Tsushima Strait between Japan and Korea in July and August (Chang and Isobe 2003; Reizen and Isobe 2006; Uye 2008). The medusae are transported farther into the Japan Sea as described in the previous section. In September, the population front passes through the Tsugaru Strait to the Pacific Ocean and is transported south as far as the Boso Peninsula.

To date, ephyrae and small medusae of *N. nomurai* have never been found in Japanese coastal waters, indicating that the settlement of new polyp populations in Japanese waters remains unsuccessful. However, the recurrent blooms could someday establish new outpost populations of polyps and podocysts in Japanese waters.

8.5 Feeding and Growth

Nemopilema nomurai polyps can capture only small (body length: ≤ 0.5 mm) and slow-swimming prey such as ciliates, their own planulae, rotifers, copepods, planktonic larvae, and *Artemia* nauplii in the laboratory. It is worth noting that *N. nomurai* planulae were suitable food for young polyps with 4–8 tentacles and also that excess feeding of *Artemia* nauplii (≥ 2 nauplii polyp^{-1} d^{-1}) resulted in high polyp mortality. Ephyrae with a mouth peduncle can eat essentially the same foods as polyps, except for planulae.

Medusae have two elaborate feeding apparatuses: scapulets and branched oral arms beneath the bell. Food organisms near the upper portion of the bell are entrained toward the lower bell in the flow generated by pulsation and are then transported posteriorly among the scapulets and oral arms. Prey are stunned by nematocysts, captured by cirri and ingested through "mouthlets" on the scapulets and oral arms. Since the diameter of the mouthlets remains unchanged (ca. 1 mm) throughout the medusa stage, their food is confined to micro- and mesozooplankton that can pass through these openings. Examination of the gastric pouch contents of wild medusae revealed that copepods were usually the dominant food items (Uye 2008), and occasionally many fish eggs were also eaten (unpublished). Thus, *N. nomurai* outbursts may have a negative impact on fish reproduction. The difficulty of retrieving all food items from the intricate gastric pouch precludes estimation of in situ feeding rates of medusae.

The weight-specific growth rate of *N. nomurai* in the laboratory at 22–28 °C fed with excess *Artemia* nauplii (Kawahara et al. 2006) was 0.30 d^{-1} from 1-day-old ephyra (wet weight: 0.0035 g) to 20-day-old medusa (1.5 g), then decreased to 0.11 d^{-1} for 20- to 48-day-old medusae (29 g). The average growth rate of medusae caught in southwestern Japan Sea (temperature: 22–28 °C) was 0.03 d^{-1} from July (3.4 kg) to November (108 kg) in 2005. A similar growth rate was determined for wild medusae in 2009 (unpublished). After November, medusae shrank due to energy expenditure for reproduction in addition to senescence.

The food requirements of wild medusae can be estimated based on their metabolic (i.e., respiration) and growth demands. The respiration rates of *N. nomurai* were measured on board our research vessel (*Toyoshio Maru*) in the Tsushima Strait in July 2005 for specimens weighing from 0.8 to 8.0 kg WW. The weight-specific respiration rate was constant irrespective of medusa weight, i.e., 12 ml O_2 kg^{-1} of WW h^{-1} (Uye 2008). Assuming that (1) the weight-specific respiration and growth rates of medusae during the main growth seasons, e.g., from July to November, are constant (see above), (2) the carbon content is 0.54 % of wet weight (unpublished),

Table 8.1 Estimated feeding and clearance rates of a representative body size of *Nemopilema nomurai* medusae in early summer, midsummer, and fall, assuming the weight-specific growth rate of 0.03 d^{-1} throughout the period (see text for other assumptions)

Seasons	Early summer	Midsummer	Fall
Body weight (kg WW)	2	20	100
Feeding rate (g C $medusa^{-1}$ d^{-1})	0.735	7.35	36.6
Clearance rate (m^3 $medusa^{-1}$ d^{-1})	73.5	735	3,660

and (3) the respiratory quotient and assimilation efficiency are 0.85 and 0.80, respectively (Schneider 1989), the food requirement can be estimated for a medusa in July (wet weight: 2 kg), September (20 kg), and November (100 kg) (Table 8.1). A medusa in these months is required to ingest 0.735, 7.35, and 36.6 g C d^{-1}, respectively. Assuming that the ambient micro- and mesozooplankton biomass is 10 mg C m^{-3}, similar to the average biomass in the East China Sea (unpublished), a medusa would process 73.5, 735, and 3,660 m^3 of seawater to capture prey per day, respectively, to meet the above ingestion rates. In the Tsushima Strait, medusae (wet weight: 3.0 kg) occurred at a density of 2.5 medusae 1,000 m^{-3} (= 40.5 mg C m^{-3}) in late July 2005 (Uye 2008), when the *N. nomurai* population dominated zooplankton carbon biomass. They would have ingested 28 % of the total micro- and mesozooplankton biomass per day, a significant predation pressure. It is not unusual for *N. nomurai* medusae to aggregate at much higher densities than those reported in 2005, and thus their predation pressure on the micro- and mesozooplankton communities could often be much greater.

8.6 Possible Causes for Blooms

The recent frequent blooms of *N. nomurai* may possibly be attributed to regional environmental changes rather than to decadal climate changes or regime shifts as suggested for jellyfish blooms in other waters (Lynam et al. 2004; Purcell 2005; Attrill et al. 2007; Brodeur et al. 2008). It is difficult, however, to specify which factors are really responsible for the increasing *N. nomurai* population. As has already been argued in previous studies (Arai 2001; Graham 2001; Uye and Ueta 2004; Purcell 2005, 2012; Purcell et al. 2007; Condon et al. 2012), the following factors, which are evident in Chinese coastal waters, are thought to be among the causes (Uye 2008, 2011).

8.6.1 Overfishing

The stock sizes of fishes, which are predators of, as well as competitors with, jellyfish for zooplankton prey, are declining in the East Asian Marginal Seas. For example, in the Bohai Sea, the catch per unit effort declined by ca. 95 % during the period from 1959 to 1998 (Tang et al. 2003). In the Yellow Sea, according to Korean fish-catch statistics (National Fisheries Research and Developmental Institute, Korea), the annual fish catch declined from ca. 13×10^4 t in the mid-1980s to less than 5×10^4 t in 2004. Furthermore, Japanese fish-catch statistics (Fisheries Agency, Japan) shows that the annual fish catches in both the East China and Japan Seas have more than halved since the 1990s. Such an extreme reduction of fish populations may reduce predation rates on planulae and ephyrae and also result in an open ecological niche into which jellyfish populations could expand and fill.

8.6.2 Global Warming

Due to recent global warming, the surface temperature in the Yellow Sea increased by 1.7 °C from 1976 to 2000 (Lin et al. 2005). Our laboratory experiments have demonstrated that the asexual reproduction rate of polyps accelerates by nearly 20 % with a similar temperature increase (unpublished). Hence, global warming may lead to higher reproduction rates of polyps as well as both earlier and longer seasonal occurrences of medusae.

8.6.3 Eutrophication, Change in Nutrient Composition, and Hypoxia

Because of increased anthropogenic activity in East Asia, particularly in China's eastern coastal zone, nutrient loading from the land is rapidly increasing, as evidenced by dissolved inorganic nitrogen (DIN) and phosphorus (DIP) concentrations in the Changjiang River water (Fig. 8.8). At the same time, the concentration of dissolved silica (Si) is decreasing. The input of nitrogen and phosphorus into coastal waters has certainly enhanced phytoplankton production; chlorophyll *a* concentration in the surface water of the Changjiang plume increased by a factor of 4 from 1984 to 2002 (Wang 2006), which could be expected to enhance zooplankton production and to supply more food to jellyfish. Furthermore, the changing nutrient composition (e.g., N/P and Si/N ratios of 35 and 0.85, respectively, in 2002, as compared with the "normal" Redfield ratios of 16 and 1.0, respectively) might have changed phytoplankton taxonomic composition from diatoms to harmful non-diatom species, including toxic dinoflagellates *Alexandrium* and *Gymnodinium*, blooms of which have increased dramatically in frequency from less than five per year in the 1990s to 58 in 2003 (Wang 2006). Such cultural eutrophication may intensify hypoxia or anoxia in the lower part of the water column as a result of decomposition of excess organic matter, as in the Changjiang outflow area (Chen et al. 2007; Wei et al. 2007). This condition would result in the reduction of both habitat space and reproduction of most marine species but not of jellyfish or scyphozoan polyps, which are tolerant of low oxygen concentrations (Condon et al. 2001; Shoji et al. 2005; Ishii et al. 2008; Thein et al. 2012).

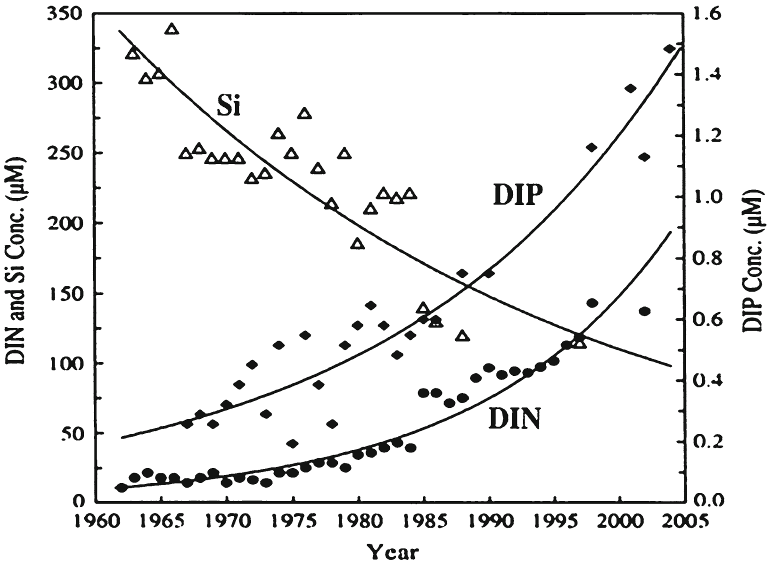

Fig. 8.8 Variation in nutrients (*DIN* dissolved inorganic nitrogen; *DIP* dissolved inorganic phosphorus; *Si* dissolved silica) concentrations in Changjiang River water from 1962 to 2002 (From Wang 2006)

8.6.4 Marine Infrastructure and Coastal Garbage

Marine infrastructure, such as harbors, waterfronts, docks, and aquaculture facilities, has developed rapidly in China's coastal waters. These have increased the availability of overhanging areas, into which jellyfish polyps selectively settle and form colonies (Brewer 1978; Watanabe and Ishii 2001; Duarte et al. 2013). Although the actual attachment sites of polyps of *N. nomurai* have not yet been found, they attach exclusively to hard substrates, including plastic plates and sheets in the laboratory. Hence, the marine installations, as well as plastic trash dumped on the sea floor, may provide new substrates to which polyps can attach.

8.7 Intermittent Blooms and Their Possible Mechanisms

The recent increase in the frequency of blooms of *N. nomurai* might be attributed to the changing environmental conditions conducive to population outbreaks in Chinese coastal waters. Nevertheless, medusae did not bloom in 2008, 2010, and 2011, and no plausible explanations can be given for these gaps in the series of blooms. On the other hand, intermittent blooms are common in rhizostome species, including commercially harvested edible species (Omori and Nakano 2001), and the mechanisms have not yet been elucidated.

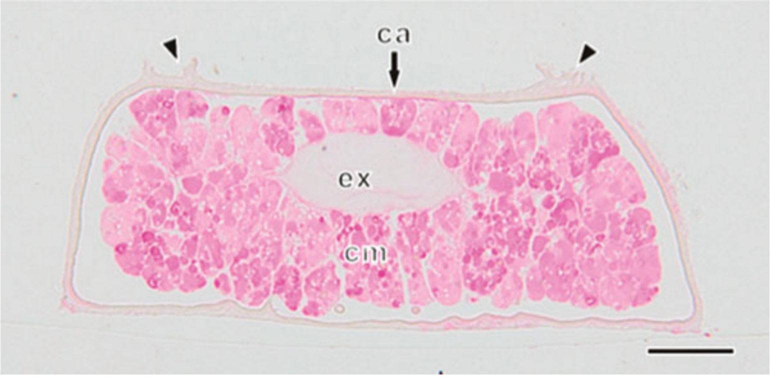

Fig. 8.9 Light photomicrograph of a sagittal section of a *Nemopilema nomurai* podocyst stained with hematoxylin and eosin. The cyst encapsulates a cell mass (*cm*) containing nutrient reserves. At the center of the cell mass is an extracellular matrix (*ex*). *Arrowheads* indicate the edge of the roof of the capsule (*ca*). Scale bar = 50 μm (From Ikeda et al. 2011b)

Polyps of *N. nomurai*, like those of other rhizostome species, produce podocysts as a form of asexual reproduction (Calder 1982; Arai 1997; Kawahara et al. 2006; Ikeda et al. 2011b), initiating a long-lived dormant phase. Ikeda et al. (2011b) detailed the histology and histochemistry of *N. nomurai* podocysts, which consist of a dome-shaped chitinous cuticle that encapsulates a mass of cyst cells filled with nutrient reserves (Fig. 8.9). The metabolic activity of podocysts was extremely low as evidenced by scarcity of mitochondria, rough endoplasmic reticulum, and Golgi complexes. They were capable of dormancy for as long as 6 years in the laboratory (Kawahara et al. 2013). Although excystment was very rare (ca. 1 %) for podocysts maintained in well-aerated seawater at constant temperature (19 °C), it increased significantly (20–55 %) when they were exposed to such extreme environmental conditions as abnormally high temperatures (≥27 °C) or low salinities (8–24). In addition, the excystment of 8–25 % of polyps was induced when they were returned to well-aerated seawater (DO: >5.0 mg O_2 l^{-1}) after they had been exposed to hypoxia (DO: 1.0 mg O_2 l^{-1}) for 12 days or burial in organic-rich mud (inducing hypoxia) for up to 3 years (Kawahara et al. 2013).

Taking the above-mentioned physio-ecological properties of *N. nomurai* podocysts into consideration, enormous numbers of them may exist on the bottom of the seeding grounds. Hence, the behavior of these podocysts (e.g., maintaining dormancy or mass excystment into polyps) could be a significant determinant of the population size of medusae in the following season. For example, if only a few podocysts excyst and the total polyp population stays at a low level, then a non-bloom year would be expected (Fig. 8.10). On the other hand, if massive accumulations of podocysts excyst and form large polyp populations, a bloom year would be forecast. The factors that induce dormant podocysts to excyst are still unclear, but reduced salinity (Xu et al. 2008), hypoxia (Chen et al. 2007; Ning et al. 2011), and burial in the mud are suspected.

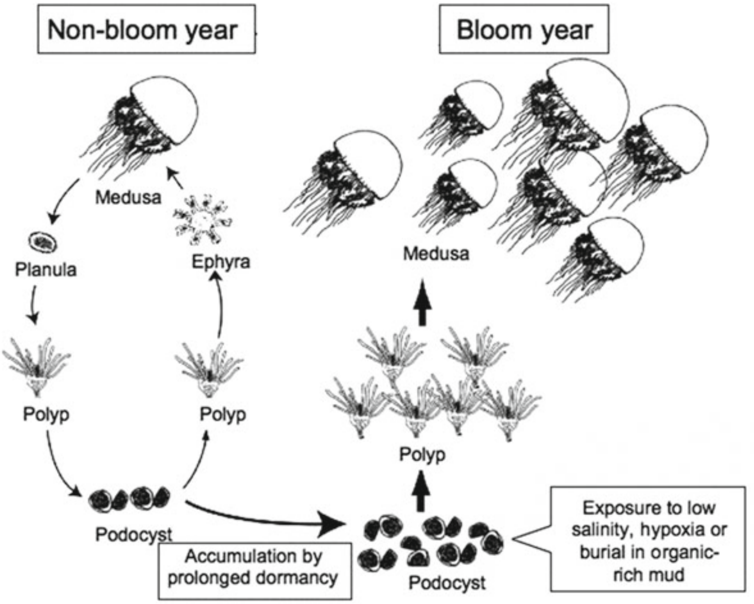

Fig. 8.10 Schematic representation of the possible distinction in podocyst abundance and behavior (e.g., dormancy or excystment) between bloom and non-bloom years of *Nemopilema nomurai* medusae (From Kawahara et al. 2013)

8.8 Bloom Forecasting, Countermeasures, and Future Prospects

At present, year-to-year variations in environmental parameters, which may affect annual jellyfish proliferation, such as seawater temperature, chlorophyll *a* concentration, and Changjiang River water discharge, do not allow us to predict whether *N. nomurai* will bloom. However, it has become possible to predict the bloom intensity in June–July of each year, 1–3 months prior to massive occurrences of medusae in Japanese coastal waters, based on on-deck sighting surveys from ferries. Our jellyfish team from Hiroshima University has been conducting such surveys since 2006 of young medusae along the ferry route between Japan (Shimonoseki, Osaka, and Kobe) and China (Qingdao, Shanghai, and Tianjin). From the ship deck, medusae near the surface (≤ca. 3 m deep) in a 10-m wide lane (narrowed when medusae were numerous) next to the ship's side were counted for 5-min intervals, and the ship's position was monitored by a GPS at 15-min intervals during daytime.

Nemopilema nomurai have never been sighted before June, when they grow large enough (bell diameter: ≥ca. 10 cm) to be recognized from the ca. 15-m-high deck of the ferry cruising at ca. 40 km h^{-1}. In early June 2009, a prominent bloom year, young medusae occurred only in a relatively small area off the Changjiang Estuary.

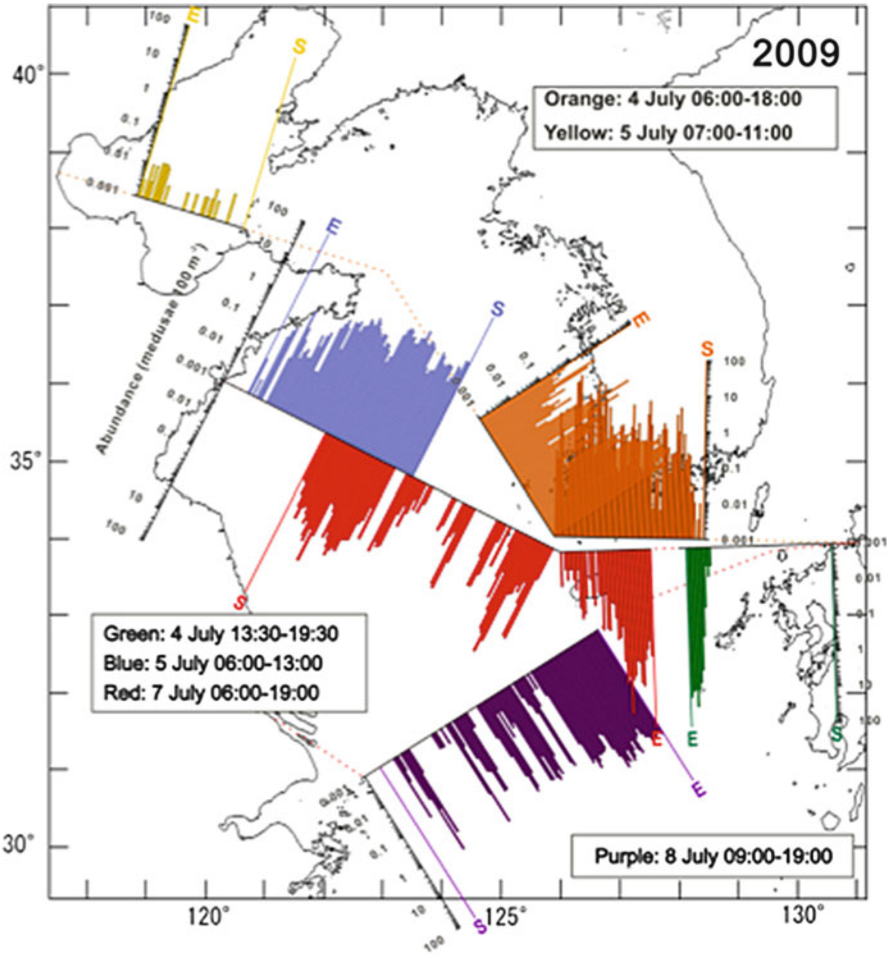

Fig. 8.11 Occurrence of *Nemopilema nomurai* medusae in the Bohai, Yellow, and East China Seas along three cruise lines of ferries between Japan and China during 4–8 July 2009. *S* and *E* denote the start and end points of daily sighting surveys. Each column represents the number of medusae counted in each 5 min (From Uye 2010)

In late June, they were distributed in an extended area over the northern East China Sea and the central Yellow Sea at relatively high density (average and maximum: 0.71 and 21 medusae 100 m^{-2}, respectively). Immediately after this ferry survey, an early warning of the bloom was announced nationwide. In early July, *N. nomurai* occurred over the entire Bohai, Yellow, and East China Seas, and a highly aggregated frontal population (33 medusae 100 m^{-2}) was about to clog fishing nets at Tsushima Island (Fig. 8.11). Medusa density reached its peak for 2009 in July, and then it declined due to transport into the Japan Sea. The average medusa density in the Yellow Sea in July has shown remarkable year-to-year differences: it was 1.97,

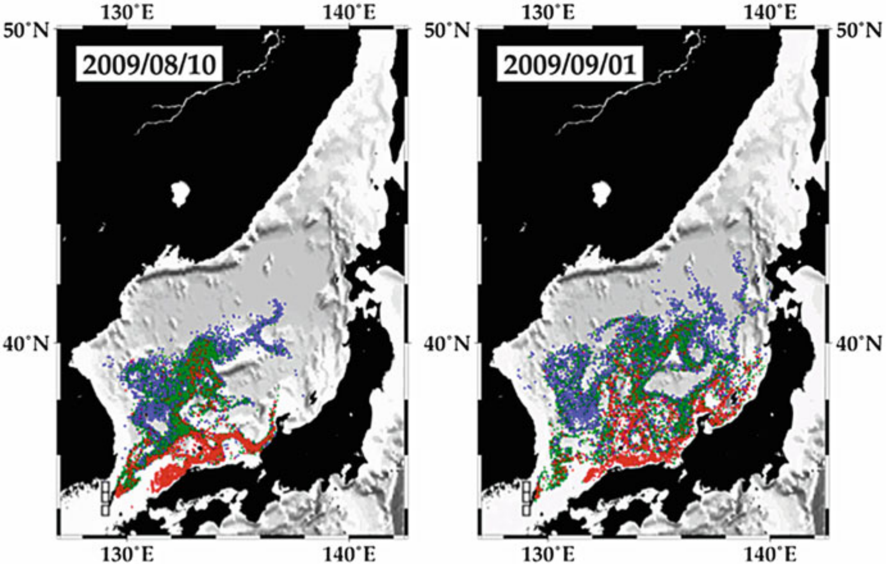

Fig. 8.12 Horizontal trajectory of *Nemopilema nomurai* medusae in the Japan Sea predicted by a numerical simulation model on 10 August and 1 September 2009. *Red*, *green*, and *blue* particles mimic medusae released from the inshore, intermediate, and offshore area (designated as a box with 1, 2, and 3, respectively) across the Tsushima Current during 25 June and 7 July 2009 (Courtesy of Drs. Tatsuro Watanabe and Akira Okuno)

3.17, and 2.29 medusae 100 m^{-2} in bloom years 2006, 2007, and 2009, respectively, and 0.02, 0.0006, and 0.05 medusae 100 m^{-2} in non-bloom years 2008, 2010, and 2011, respectively. By knowing the bloom forecast derived from the on-deck-ferry sighting survey, fishermen can prepare for possible jellyfish encounters well in advance.

After passage through the Tsushima Strait, the transport of *N. nomurai* medusae into the Japan Sea is essentially controlled by the Tsushima Current, and hence, a numerical simulation model can predict the horizontal trajectory of the medusae on given dates (e.g., Fig. 8.12). Therefore, local fishermen can receive more detailed information about when the frontal medusa population can be expected to arrive at their location.

One of the countermeasures to alleviate the problems caused by *N. nomurai* is to slice up medusae by towing a trawl with fine steel wires at the cod-end through the Tsushima Strait, an entry area of the Japan Sea. However, the volume of seawater swept clear by this trawl net is too meager in the vast space of the strait, and hence this may not kill significant numbers of medusae in the field. Various types of jellyfish excluders have been applied to trawl nets, and Matsushita et al. (2005) and Okino et al. (2009) have examined their operation. In addition, traditional set nets, to which the damage by medusae is always greatest, have been modified by (1) enlargement of the mesh size of the leading nets in order to let the medusae pass

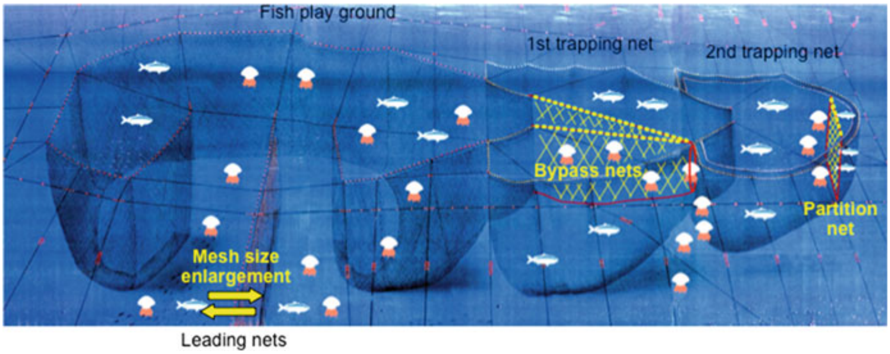

Fig. 8.13 Schematic representation of a traditional set net modified to exclude *Nemopilema nomurai* medusae by (1) enlargement of mesh size of the leading nets, (2) installation of bypass nets, and (3) installation of a partition net (Courtesy of Mr. Ryosuke Matsuhira)

through, (2) installation of bypass nets to deflect approaching medusae outside the net, and (3) installation of a partition net to separate medusae from fish and enable the jellyfish to be removed from outside the net (Fig. 8.13). Since it costs 5–10 million JPY to introduce such modifications for a large set net, only wealthy net owners can invest in effective countermeasures of these types. Such modified set nets did function effectively to remove entrapped medusae (hence, usually less than a hundred medusae were trapped per net per day) and yielded regular fish catches even during the months of heaviest aggregation (October–December) in 2009. On the other hand, many unmodified set nets were so severely damaged by numerous entrapped medusae as to halt operation during the regular fishing season.

The environmental deterioration in Chinese coastal waters, which are the seeding and nursery ground of *N. nomurai*, will perhaps continue in the future, due to ongoing Chinese economic development and mega-scale infrastructure projects such as the Three Gorges Dam (completed in 2006) and the South–north Water Transfer Project (to be completed in several decades). To tackle these expected advances in conditions promoting jellyfish plagues, the following countermeasures should be adopted in order to sustain fisheries. The first step is to continue early forecasting of blooms by the on-deck-ferry sighting survey. If a bloom is forecast, the second step is to simulate the spatiotemporal transport of medusae by numerical models. When medusae arrive in local fishery grounds, the third step is for fishermen to deploy jellyfish-excluding nets. When the jellyfish aggregation is so intense as to overwhelm excluders and cause serious damage to nets, it may be necessary to stop their operation and accept a fishing moratorium.

The East Asian Marginal Seas are one of the world's most productive fishery grounds (total fish catch in 2003: 9.0×10^6 t, or 11 % of the world marine fish catch, Fisheries Center, University of British Columbia, Canada). The international collaboration between Japan, China, and Korea needs to be strengthened for preservation of this very productive ecosystem. International law enforcement of both environmental protection (e.g., regulation of total nutrient loads) and fishery management measures is urgently needed to avoid chronic dominance of jellyfish, one of the more unfortunate end points of the marine ecosystem deterioration forced by unwise human activity.

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Chapter 9
Contrasting Trends in Populations of *Rhopilema esculentum* and *Aurelia aurita* in Chinese Waters

Zhijun Dong, Dongyan Liu, and John K. Keesing

Abstract *Rhopilema esculentum* and *Aurelia aurita* are the most common scyphozoan species in Chinese waters. Here the population trends of *R. esculentum* and *A. aurita* are described and compared. The possible causes of their contrasting population trends are discussed by reviewing the status of existing information and introducing new data collected on blooms and reproduction of *A. aurita* in northeastern China. The population change of *R. esculentum* was described based on the annual harvest of *R. esculentum* in Chinese waters since 1955. It is generally accepted that a stock enhancement program has been successful in increasing the total catches of *R. esculentum*. However, the catches have declined since 1998, and this may be due to current stock enhancement levels exceeding the carrying capacity of the fishery ground or deterioration in the coastal marine environment. In contrast, blooms of *A. aurita* are causing increasing problems in the coastal waters of northern China with suitable settlement substrate provided by expansive coastal aquaculture implicated in these population increases. In addition to anthropogenic influences such as fishing, stock enhancement, and the proliferation of coastal infrastructure, the variation in reproductive and life history traits between *R. esculentum* and *A. aurita* may also explain the different recruitment potentials of the two species.

Keywords Jellyfish blooms • *Rhopilema esculentum* • *Aurelia aurita* • Chinese coastal waters • Jellyfish fisheries • Stock enhancement • Population dynamics • Polyps • Aquaculture rafts • Life histories

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9.1 Introduction

There are 35 species of scyphomedusae belonging to 20 genera in 16 families that have been recorded in Chinese seas. Of these *Aurelia aurita*, *Cyanea nozakii*, *Nemopilema nomurai, Rhopilema esculentum*, and *Rhopilema hispidum* are the most common scyphozoan jellyfish species in the Yellow Sea and East China Sea (Hong and Lin 2010). The edible jellyfish *R. esculentum* has been exploited in Chinese waters for more than 1,700 years (Omori and Nakano 2001) and is one of the most abundant fishery species in China (Fig. 9.1a, b), while the moon jellyfish *A. aurita*, which is not edible, is one of the most common jellyfish species along the coast of northern China (Fig. 9.1c, d). Blooms of *A. aurita*, *C. nozakii*, and *N. nomurai* have had severe deleterious consequences for both industry and recreational users of the coastal environment (Dong et al. 2010). In contrast, the population of *R. esculentum* has declined to the extent that has necessitated using stock enhancement to ensure a viable fishery. In this chapter, the population trends of *R. esculentum* and *A. aurita* are described and compared, and possible causes of their contrasting population trends are discussed by reviewing the status of existing information and introducing new data collected on blooms and reproduction of *A. aurita* in northeastern China.

Fig. 9.1 (**a**–**d**) (**a**) Harvesting of *Rhopilema esculentum* in Yingkou, Liaoning Province (Bohai Sea); (**b**) processing of *R. esculentum* in Yingkou, Liaoning Province (Bohai Sea); (**c**) bloom of *Aurelia aurita* in a sea cucumber pond in Yantai, Shandong Province (Yellow Sea); (**d**) *A. aurita* clogging power plant cooling water intakes in Qingdao, Shandong Province (Yellow Sea)

9.2 Population Changes of *Rhopilema esculentum* with Special Reference to Its Fishery and Stock Enhancement

Rhopilema esculentum inhabits a wide range of the northwestern Pacific region including seas around Japan, Korea, and China. In China, *R. esculentum* is widely distributed in the Bohai Sea, the Yellow Sea, the East China Sea, and the northern South China Sea (Dai et al. 2004; Jiang et al. 2007, Fig. 9.2). Adult medusae can

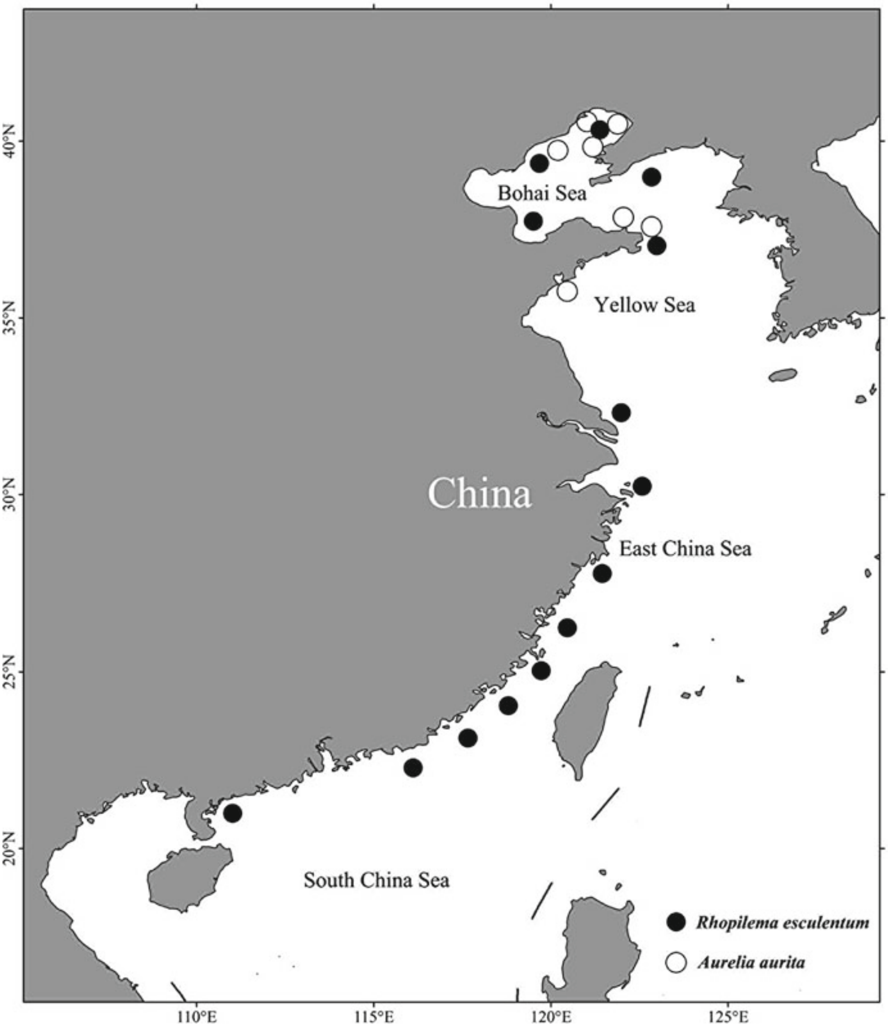

Fig. 9.2 The main fishery regions for *Rhopilema esculentum* and location of blooms of *Aurelia aurita* in Chinese waters (From Dai et al. 2004; Jiang et al. 2007; Dong et al. 2010; Wan and Zhang 2012; Wang et al. 2012a, b)

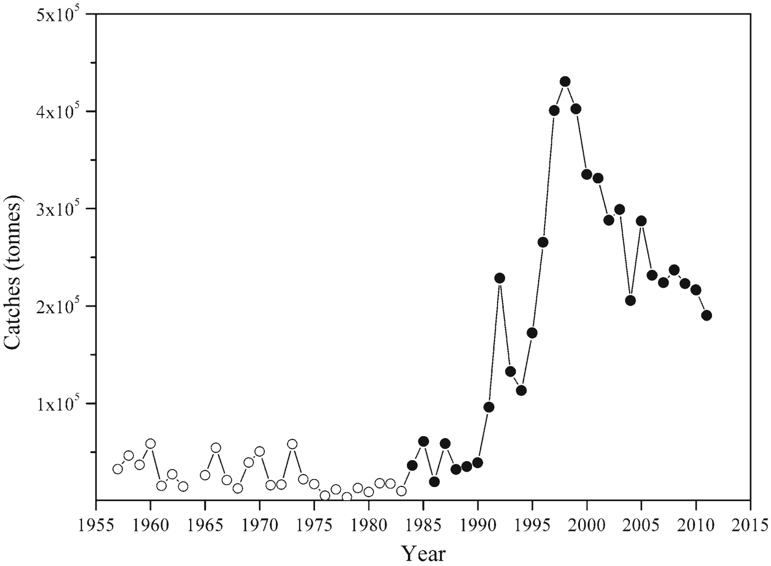

Fig. 9.3 Annual harvest of the edible jellyfish *Rhopilema esculentum* in Chinese waters in tonnes wet weight. *Open circles*: harvest before stock enhancement; *solid circles*: harvest after stock enhancement (From Jiang and Wang 1991; China Fishery Statistical Yearbook 1997–2006; FAO Statistics 2012)

grow to 25–60 cm bell diameter, with the largest individuals exceeding 100 cm. The body color is variable: red, white, pale blue, or yellow in the Bohai Sea and the Yellow Sea and reddish brown in the East China Sea (Jiang et al. 2007). The Chinese population of *R. esculentum* is thought to consist of a series of local subpopulations which have different breeding habits and migration patterns (Ding and Chen 1981; Huang et al. 1985; Jiang et al. 2007).

The fishery for *R. esculentum* can be divided into two periods, before and after 1984, when stock enhancement via the release of cultured juveniles of *R. esculentum* commenced (Fig. 9.3). From when records were first kept in 1955 until 1975 annual catches fluctuated between 0.01 and 0.06 million tonnes. But after 1975 there was a sharp decline in the catch due to overexploitation (Huang et al. 1985; Liu et al. 1992) which was confirmed by surveys in the southern Zhejiang Sea area and Hangzhou Bay conducted by the Marine Fisheries Research Institute of Zhejiang Province (Huang et al. 1985). In the northern Yellow Sea, surveys by the Liaoning Ocean and Fisheries Science Research Institute also showed that there was a significant decline in the size of the stock since 1975 (Liu et al. 1992) and the annual catches remained extremely low between 1976 and 1983 (Fig. 9.3).

In order to meet the increasing demand for jellyfish, intensive research on reproduction, culturing, and stock enhancement of *R. esculentum* was undertaken during the 1980s and 1990s (Ding and Chen 1981; Huang et al. 1985; Huang and Wang 1991; Chen et al. 1994; Wang et al. 1997, see also review by Dong et al. 2009). Pilot projects of stock enhancement were conducted between 1984 and 2004 in Liaodong Bay, Liaoning Province (Chen et al. 1994; Liang et al. 2007) and since 1994 in the

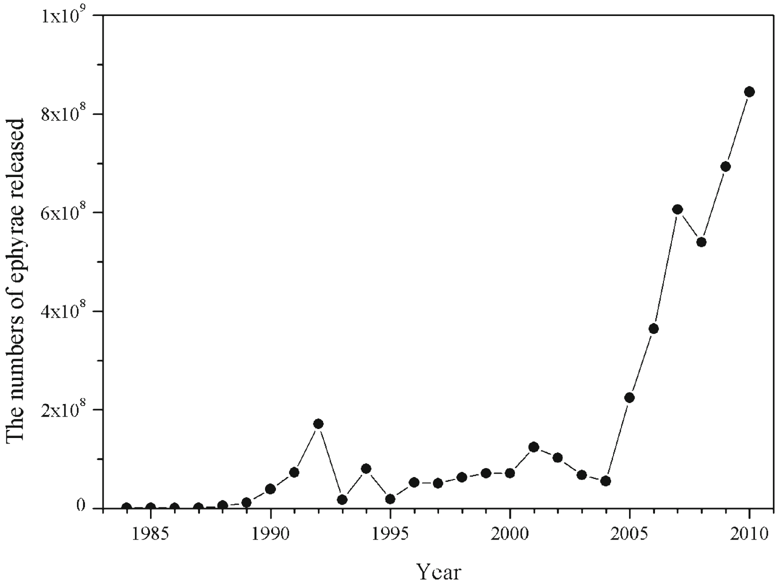

Fig. 9.4 Release of cultured *Rhopilema esculentum* in coastal waters of Liaoning Province and Shandong Province (From Chen et al. 1994; Liang et al. 2007; Zhang et al. 2009, http://www.moa.gov.cn)

coastal waters of Shandong Province (Zhang et al. 2009). During the pilot trials in Liaodong Bay, ≤17.3 million juvenile medusae were released annually. In 2005, a large-scale release (156 million juvenile *R. esculentum*) was conducted in Liaodong Bay for the first time (Dong et al. 2009), and since then the numbers released have increased sharply to a maximum of 845 million in coastal waters of Liaoning Province and Shandong Province in 2010 (Fig. 9.4).

The stock enhancement of *R. esculentum* was effective in increasing the annual catches of *R. esculentum* in Liaodong Bay, with recapture rates ranging between 0.07 % and 3.20 % during the period between 1984 and 2006 (Dong et al. 2009). Since the restocking program commenced, the total harvest of *R. esculentum* has grown rapidly and has exceeded 0.10 million tonnes since 1992, with a maximum harvest of 0.43 million tonnes occurring in 1998 (Fig. 9.3). However, the exact contribution of the stock enhancement program to the increased catch is difficult to quantify due to concurrent changes in fishing effort and management practices which may have independently affected catch rates. Indeed the number of fishing boats in Liaodong Bay increased from less than 500 in 1980 to approximately 9,000 in1989 (Jiang et al. 2007, Fig. 9.5). However, the increase in the number of fishing boats partially predates the rapid increase in catches that occurred between 1991 and 1997, indicating that restocking may have had a beneficial effect on catches. Further confounding the assessment of how effort has changed in the fishery are the reductions in the fishing season and the introduction of fishing moratoria. Before 1980, the fishing season of *R. esculentum* lasted for 2 months between August and October because the fishing boats were relatively few in number. In the 1980s, as boat numbers increased, the fishing season of *R. esculentum* was reduced to

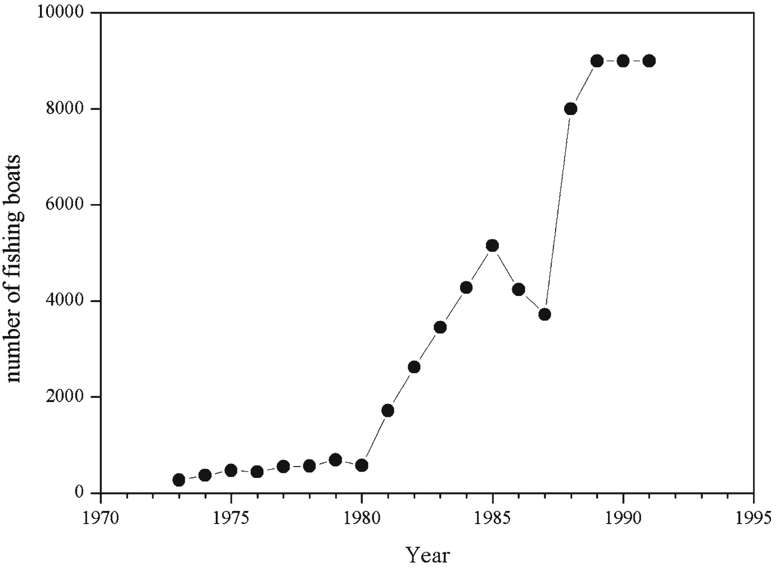

Fig. 9.5 The numbers of fishing boats in Liaodong Bay (From Jiang et al. 2007)

1–3 weeks between August and September. By the 1990s, the fishing season of *R. esculentum* lasted for just a few days (Jiang et al. 2007). Moreover, midsummer fishing moratoria have been enforced in the Bohai, Yellow, and East China Seas since 1995. During the moratoria, generally from June to August, the areas are closed to fishing to protect fish stocks from excessive fishing capacity. The moratoria may have favored an increase in the *R. esculentum* population by protecting the juvenile medusae against trawl and seine net fishing, to which they are vulnerable.

Despite the difficulty associated with trying to disentangle all the factors influencing the catches of *R. esculentum* over time, it is generally accepted that the stock enhancement program was successful in increasing the total catches of jellyfish (Dong et al. 2009). In 2010, however, the catches declined to 0.22 million tonnes, despite the increased stock enhancement. The reasons for this are not clear, but it is likely that the current stock enhancement level may exceed the carrying capacity of the fishery ground or that deterioration in the coastal marine environment has caused conditions which are no longer conducive to supporting large populations of *R. esculentum.*

9.3 Population Changes of *Aurelia aurita*, Consequences, and Potential Impact of Coastal Aquaculture

Aurelia aurita is the most common scyphozoan jellyfish with a wide geographic distribution in subtropical, temperate, and boreal coastal waters (Lucas 2001; Uye et al. 2003; Ki et al. 2008; Lo et al. 2008). Blooms of *A. aurita* have occurred in

Table 9.1 Examples of *Aurelia aurita* blooms in Chinese waters and their negative impacts on human enterprises (Revised from Dong et al. 2010)

Month	Location	Direct consequences	Source
July, 2008	Qinhuangdao, Hebei Province	Over 4,000 tonnes of *A. aurita* were cleaned up in July 2008	Liu (2008)
Sept, 2007	Yantai, Shandong Province	Interference with aquaculture	Su (2007)
Aug, 2008	Weihai, Shandong Province	20–50 tonnes of *A. aurita* were cleaned up each day	Dong et al. (2010)
July, 2009	Qingdao, Shandong Province	Over 10 tonnes of *A. aurita* were cleaned up for 2 days	Lu (2009)
July–Aug, 2009	Yantai, Shandong Province	0.62 medusae m^{-3}during July and September	Dong et al. (2012)
July, 2011	Qingdao, Shandong Province	0.1 and 2.9 ephyrae m^{-3} during April and June; 1.3 medusae m^{-3} in July	Wan and Zhang (2012)
Aug, 2009	Qingdao, Shandong Province	The highest density of *A. aurita* was 123 medusae km^{-2} in August 1	Wang et al. (2012b)
June–July, 2009–2011	Huludao, Yingkou, and Wafangdian, Liaoning Province	Mainly distributed in nearshore waters in southern Liaodong Bay	Wang et al. (2012a)

harbors and coastal waters of the Yellow Sea and the Bohai Sea and are a nuisance to local fisheries, tourism, and coastal power plant operations (Su 2007; Liu 2008; Lu 2009; Dong et al. 2010; Wan and Zhang 2012; Wang et al. 2012a, b, Table 9.1, Fig. 9.2). Jellyfish ingress often causes a reduction in the operating capacity of power plants and in extreme cases has caused plants to temporarily shut down.

Little has been studied on the population dynamics and geographical distribution of *A. aurita* in Chinese waters. The results of research to date indicate that *A. aurita* occurs mainly in nearshore waters (Dong et al. 2012; Wan and Zhang 2012; Wang et al. 2012a, b) and is rare in deep waters (Zhang et al. 2012).

Dong et al. (2012) studied the temporal variation in an *A. aurita* population, which occurred in Yantai Sishili Bay (YSB) in the northern Yellow Sea during the summer of 2009 and in August 2010 (Dong et al. unpublished data). A direct comparison of the populations sampled during August 2009 and August 2010 showed that the population was much greater in 2009 (mean density of 0.79 medusae m^{-3} with a highest density of 2.20 medusae m^{-3}) than 2010 (mean density of 0.01 medusae m^{-3} and a highest density of 0.07 medusae m^{-3}). In YSB the industries of scallop aquaculture, sea cucumber aquaculture, and shipping have been expanded greatly by the Yantai City government. Indeed extensive scallop culture accounted for ca. 70 % of the total area of the bay (Zhou et al. 2006). However, since the end of 2009, the scallop culture rafts have been removed because Yantai City now plans to develop the region for coastal tourism. The removal of scallop culture rafts, which provide suitable substrate for polyps of *A. aurita*, was probably the most important factor causing the decrease of the *A. aurita* population in 2010. Similar decreases in populations of *A. aurita* have been observed following the removal of aquaculture rafts in Tapong Bay, Taiwan (Lo et al. 2008).

Dense populations of *A. aurita* have also been observed in another temperate bay with intense scallop aquaculture activities. Wan and Zhang (2012) investigated the temporal variations in *A. aurita* populations during February and December in 2009 in Jiaozhou Bay. Ephyrae of *A. aurita* occurred from April to June with the mean abundance between 0.1 and 2.9 ephyrae m^{-3}. Adults were present in July and occurred at a mean density of 1.3 medusae m^{-3}. Wang et al. (2012b) investigated the density of *A. aurita* in Jiaozhou Bay by visual observation during August and September in 2011. The highest density of *A. aurita* they measured was 123 medusae km^{-2} in August 2011. The differing survey methods and units of density make it difficult to compare these two studies but suggest a reduction in density between 2009 and 2011.

Because jellyfish polyps require a hard substrate for attachment, an increase in the amount of suitable benthic habitat such as that provided by aquaculture rafts could lead to the proliferation of polyps (Lo et al. 2008; Duarte et al. 2013).We found further indirect evidence of this in Yantai in June 2012. Visual observations were conducted for the occurrence of juvenile medusae in different waters near coastal construction including docks, breakwaters, and aquaculture ponds in the coastal area around YSB. Surface trawls by a zooplankton net (31.6 cm diameter, 140 cm long, and 160 μm mesh) were used to quantify the biomass of juvenile *A. aurita* when juvenile medusae were present. We observed a mass occurrence of juvenile *A. aurita* in the nearshore sea cucumber culture ponds in Yantai during June 2012 (Fig. 9.1c) with the mean density being 15.9 medusae m^{-3}.

The provinces of Liaoning, Shandong, and Hebei are major areas for aquaculture of scallops and in 2010 accounted for 57.0 %, 24.9 %, and 16.2 %, respectively, of the total area used for scallop aquaculture in China (China Fishery Statistical Yearbook 2010). Experimental evidence that *A. aurita* larvae prefer to settle on artificial substrates has been reported by different researchers (reviewed by Duarte et al. 2013). Therefore, the expansion of scallop aquaculture in these coastal areas may be increasing the available habitat for polyps and thus facilitating the proliferation of *A. aurita*.

9.4 Possible Importance of Contrasting Aspects of Reproduction and Life History of *Rhopilema esculentum* and *Aurelia aurita* for Population Trends in Chinese Waters

Although anthropogenic influences such as fishing, stock enhancement, and the proliferation of coastal infrastructure have probably been major determinants of population trends in *R. esculentum* and *A. aurita,* it is likely that natural recruitment to *R. esculentum* and *A. aurita* populations has also been influenced by the contrasting reproductive and life history characteristics of each species.

Table 9.2 Comparison of characters of the planula, polyp, and strobilation process of *Rhopilema esculentum* and *Aurelia aurita*

Species	*Rhopilema esculentum*	*Aurelia aurita*
Planulae brooded	No	Yes
Cultivation temperature	18–22 °C	15–27 °C
Planulae size length/width (μm)	95–150/60–90	52–100/29–38
Settlement (days)	4	2
Polyp fully developed max. height (mm)/tentacles (n)	3.5/16–30	4.2/16–28
Asexual reproduction	Podocysts	Buds, stolons, podocysts, free-swimming particle, fission
Strobilation temperature	Increase to 13 °C	Constant 20 °C/increase to 15 °C
Ephyrae per strobila	4–17	2–18
Sources	Ding and Chen (1981), Chen and Ding (1984)	Present study

Firstly, there are potentially significant differences in recruitment between *R. esculentum* and *A. aurita* as a result of contrasting pressures on reproductive stocks of both species. As well as the large harvests of *R. esculentum*, the timing of fishing has the potential to affect natural levels of recruitment. Because *R. esculentum* generally reproduces sexually in September and October in Liaodong Bay (Chen 1985), it is likely that, as the fishing period contracted to earlier months of the fishing season, *R. esculentum* has been harvested before they are sexually mature, thus reducing natural levels of recruitment. Such pressures have not been exerted on *A. aurita* because it is not harvested.

Secondly, the abundance of adult jellyfish in a population is mostly impacted by the mortality rates of the juvenile benthic and planktonic stages of the life cycles because the mortality of planulae and polyps is relatively higher than ephyrae and medusae (Lucas 2001). The characteristics of the planulae, polyps, and strobilation process of *R. esculentum* and *A. aurita* in China are compared in Table 9.2 using data from Ding and Chen (1981) and Chen and Ding (1984) for *R. esculentum* and from new data collected by us in 2010 in our laboratory. We obtained larvae by artificial fertilization (Chen and Ding 1984) of eggs from medusae collected in the northern Yellow Sea and reared the resulting scyphistomae and ephyrae to the young medusa stage. At 25–27 °C, the fertilized eggs developed into planulae in 1 day. The planulae attached to the substratum and metamorphosed into scyphistomae within 2 days. The scyphistomae grew into mature scyphistomae in 15–35 days with numbers of tentacles varying from 16 to 28. Fully developed scyphistomae increased their population by asexual reproduction. In total, eight types of asexual reproduction were distinguished based on the new polyps formed, including lateral budding, lateral budding by means of stolons, podocyst formation, motile bud-like tissue particles, internally produced propagules, longitudinal fission, and strobilation (Fig. 9.6). The ephyrae were released by strobilation at 20 °C. The ephyrae develop

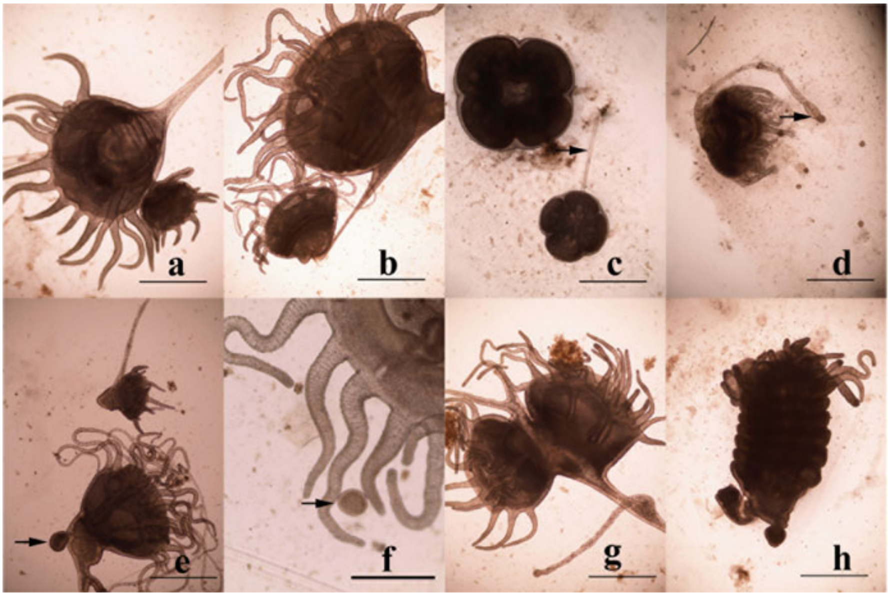

Fig. 9.6 (**a**–**h**) Different types of asexual reproduction in *Aurelia aurita*. (**a**) Typical lateral budding, (**b**) lateral budding by means of stolons, (**c**) reproduction from parts of stolons, (**d**) podocysts, (**e**) motile bud-like tissue particles, (**f**) internally produced propagules, (**g**) longitudinal fission, (**h**) transverse fission. All scale bars = 1 mm

into metephyrae in approximately 15 days and young jellyfish achieve sexual maturity after approximately 80 days. In the Yantai Sishili Bay of the northern Yellow Sea, blooms of moon jellyfish *A. aurita* generally occurred in July and August (Dong et al. 2012). The time taken for planulae of *A. aurita* to form and settle was less than half that observed for *R. esculentum* by Ding and Chen (1981) (Table 9.2). Therefore, the risk of predation on the planulae of *A. aurita* might be significantly lower than for *R. esculentum*. In addition, mortality may be lower in *A. aurita* which brood the planulae within their bodies after internal fertilization than in *R. esculentum* that fertilize eggs externally (Barnes and Hughes 1999). Moreover, scyphistomae of *A. aurita* could reproduce asexually by various types of asexual reproduction modes, such as budding, podocyst, and stolons, while scyphistomae of *R. esculentum* only formed podocysts. The occurrence of different asexual reproduction modes in *A. aurita* offers more flexibility to confront different environmental fluctuations than *R. esculentum*. These factors may help explain the contrasting population trends of the two species in northeastern China in recent years.

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Chapter 10
Chrysaora plocamia: A Poorly Understood Jellyfish from South American Waters

Hermes Mianzan, Javier Quiñones, Sergio Palma, Agustin Schiariti, E. Marcelo Acha, Kelly L. Robinson, and William M. Graham

Abstract Blooms and strandings of *Chrysaora plocamia* are reported to occur along both Atlantic and Pacific South American coasts. First described in Peruvian waters by Lesson (1830) almost two centuries ago as *Cyanea plocamia*, there is surprisingly little ecological information about this conspicuous animal. This chapter reviews current knowledge about *C. plocamia* biology and ecology, its relationship with pelagic fisheries and climate and the problems blooms cause in the Humboldt Current and Patagonian shelf ecosystems. *Chrysaora plocamia* has important ecological roles, including trophic and symbiotic interactions with fish and sea turtles. Population variability has a clear relationship with climate where phases of high *C. plocamia* biomass were associated with El Niño events occurring during warm "El Viejo" regimes. Interestingly, their estimated biomass occasionally approached those of sardines or anchovies. This large jellyfish negatively affects human industries in the region when abundant, including fisheries, aquaculture, desalination plants and tourism. Understanding relationships between jellyfish blooms and environmental drivers (e.g. ENSO, regime shifts) should allow forecasting of the jellyfish abundance and potential vulnerabilities such that resource managers and industrial fisheries owners may prepare for costly outbreaks.

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10.1 Introduction

> J'admirai également de nombreuses méduses, et les plus belles du genre, les **Chrysaores**, particulières aux mers des Malouines [Malvinas Island]. Tantôt elles figuraient une ombrelle demi-sphérique très lisse, rayée de lignes d'un rouge brun et terminée par douze festons réguliers; tantôt c'était une corbeille renversée d'où s'échappaient gracieusement de larges feuilles et de longues ramilles rouges. Elles nageaient en agitant leurs quatre bras foliacés et laissaient pendre à la dérive leur opulente chevelure de tentacules.
>
> [I also admired the numerous jellyfish, particularly the most beautiful of the genus, the Chrysaores, peculiar to Falkland/Malvinas seas. Sometimes they had a very smooth hemispherical umbrella, striped red-brown lines and completed by twelve regular festoons. Sometimes they became upside-down waste-paper baskets, from which grew gracious broad leaves and long red twigs. They swam waving their four leaf-like arms and let them hang drift their opulent hair tentacles.] – 20,000 Leagues Under the Sea, **Jules Verne**, 1869

Chrysaora plocamia (Cnidaria: Scyphozoa: Semaeostomeae) is one of the largest and most conspicuous jellyfish found along the South American Pacific and Atlantic coasts (Fig. 10.1a–c). The bell diameter is typically 50–60 cm with the oral arms reaching lengths of 2–3 m. Rare specimens attain diameters of about 1 m with oral arms extending more than 3 m (Mianzan and Cornelius 1999). There is surprisingly little information about *C. plocamia* despite being first described almost two centuries ago in Peruvian waters by Lesson (1830) as *Cyanea plocamia.* This chapter reviews what is currently known about the biology and ecology of *C. plocamia*, its relationship with pelagic fisheries and climate and the problems *C. plocamia* blooms can cause. Our synthesis is derived from a variety of bibliographic sources, including technical reports, anecdotes and other non-peer-reviewed resources not typically available to the international scientific community.

Chrysaora plocamia can be found across a range that encompasses two major Large Marine Ecosystems (LMEs): the Humboldt Large Marine Ecosystem in the Pacific and the Patagonian Shelf Large Marine Ecosystem in the Atlantic (Heileman 2009; Heileman et al. 2009). These LMEs, with a combined coastline of 13,000 km and surface area of more than 5.5 million km^2, represent a large fraction of South American coastal waters (Miloslavich et al. 2011). High biological productivity here contributes to about 15 % of global fish landings. In the Humboldt LME, *C. plocamia* ranges from Peruvian to Chilean waters. The species is far more concentrated in these northern waters compared to southern Chilean waters (Fig. 10.2). *C. plocamia* in southern waters was reported as *Chrysaora* sp. (Vanhöffen 1888) in the Magellan Strait, as *C. hysoscella* by Vannucci and Tundisi (1962) around the Antarctic Peninsula and as *C. plocamia* in the Beagle Channel (Mianzan and Cornelius 1999), but all these populations have since been recognised as *C. plocamia* (Morandini

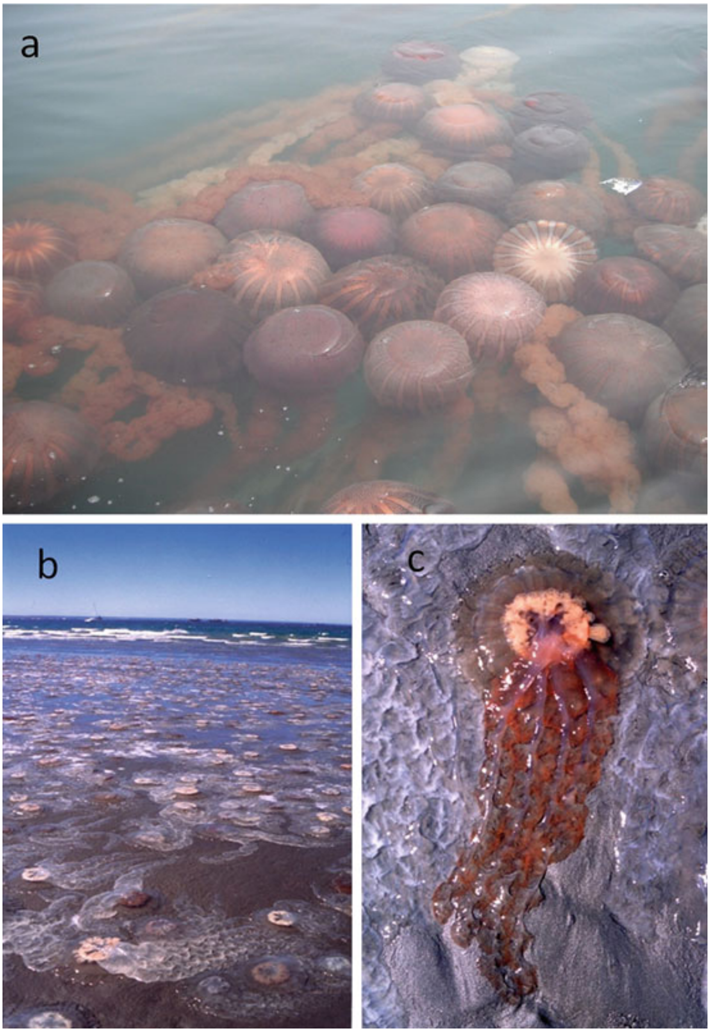

Fig. 10.1 (**a**–**c**) (**a**) Bloom of *Chrysaora plocamia*, May 2012 off Callao (12°04′S), Peru (Photo by Mario Rosina). (**b**) Stranding event of *Chrysaora plocamia* at Puerto Madryn, Chubut, Argentina. (**c**) Detail of a pigmented specimen (Photos by José Luis Esteves)

and Marques 2010). The species is also common in Atlantic waters (Mianzan and Cornelius 1999; Morandini and Marques 2010), where large conspicuous blooms occur with some regularity along the northern Patagonian coast becoming rare northerly (Mianzan and Cornelius 1999; Mianzan et al. 2005). The connectivity of *C. plocamia* between the Pacific and Atlantic oceans is likely facilitated by circulation within the Patagonian cold estuarine zone (Acha et al. 2004).

As with most coastal jellyfish species from temperate waters, *C. plocamia* exhibits strong seasonality. Although information about *C. plocamia's* reproduction is

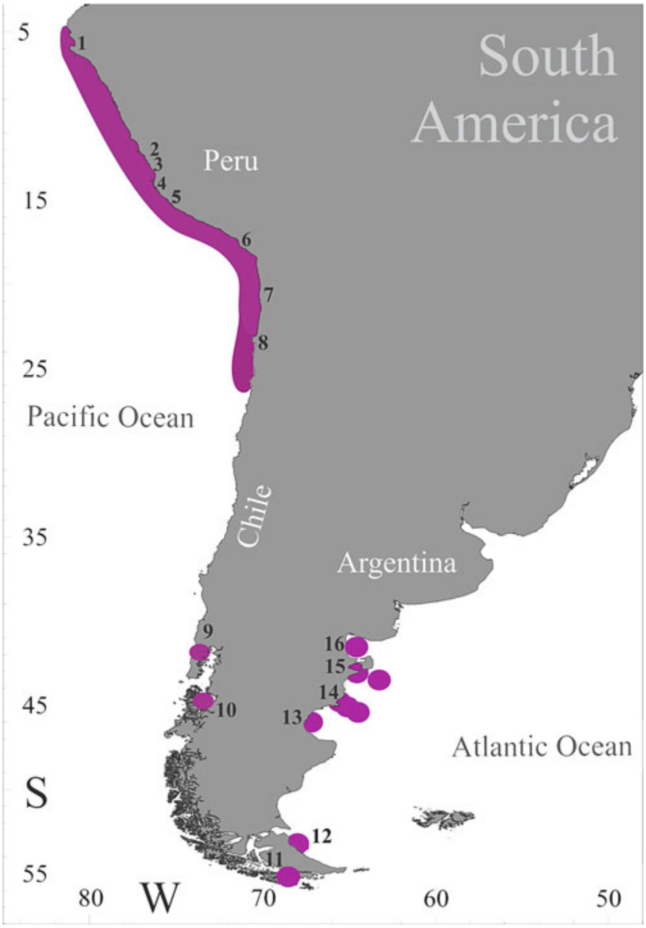

Fig. 10.2 Distribution of *Chrysaora plocamia* in South America. Humboldt Large Marine Ecosystem, **Peru**: *1* Bahía Sechura, *2* Callao, *3* Pisco, *4* Paracas, *5* Bahía Independencia, *6* Ilo; **Chile**: *7* Arica, *8* Antofagasta, *9* Isla Chiloé, *10* Aysén region; Patagonian Shelf Large Marine Ecosystem, **Argentina**: *11* Canal de Beagle, *12* Bahía San Sebastián, *13* Golfo San Jorge, *14* Cabo Dos Bahías, *15* Golfo Nuevo, *16* Golfo San Matías. *Shaded* and *dotted areas* indicate the known distribution of *C. plocamia*

still pending, polyps, strobilae, ephyrae and juvenile medusae were recently reared in the laboratory from planulae collected from mature specimens (Morandini pers. comm.). Post-ephyrae and juvenile stages occur during early austral spring, while adult medusae are common during austral summer–autumn (Mianzan 1986, 1989; Quiñones 2010). Medusae then senesce, losing tentacles and oral arms, and sink to the seabed in late autumn–early winter (Fig. 10.3). Abundance is lowest during winter; however, overwintering medusae are observed. Ephyrae frequently found in Chilean fjords during spring are probably those of *C. plocamia* (Bravo et al. 2011; Palma et al. 2011).

Fig. 10.3 Senescent *Chrysaora plocamia* on the sea floor close to Caleta Olivia, Santa Cruz, Argentina (Photo by José Adrián Acosta Fabio)

Coloration patterns of medusae differ by region from being totally transparent to being whitish with a few irregularly distributed brown-reddish spots to being completely yellow, red or brown with 16 triangular streaks radially distributed on the bell (see Mianzan and Cornelius 1999; Morandini and Marques 2010). Most Peruvian specimens have dark and highly varied coloration. Medusae from southern Chile and Argentina are typically lighter, with only few specimens intensely pigmented (Fig.10.1a–c). Observations of juveniles and even ephyrae in different and separate areas may suggest the existence of local populations. *Chrysaora plocamia* was found to be morphologically identical to *C. achlyos* (Morandini and Marques 2010), and genetic analysis is still needed to establish if differences in distribution reflect separate species (Morandini and Marques 2010, Dawson and Gomez Daglio 2012 pers. comm.).

10.2 Blooms of *Chrysaora plocamia*: Relationship with Climate

Climate is understood to be a main driver of biological productivity in upwelling systems. The Humboldt Current ecosystem is known to respond to climate, including the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) (Bakun 1996; Chavez et al. 2003, 2008). As an example, populations of the

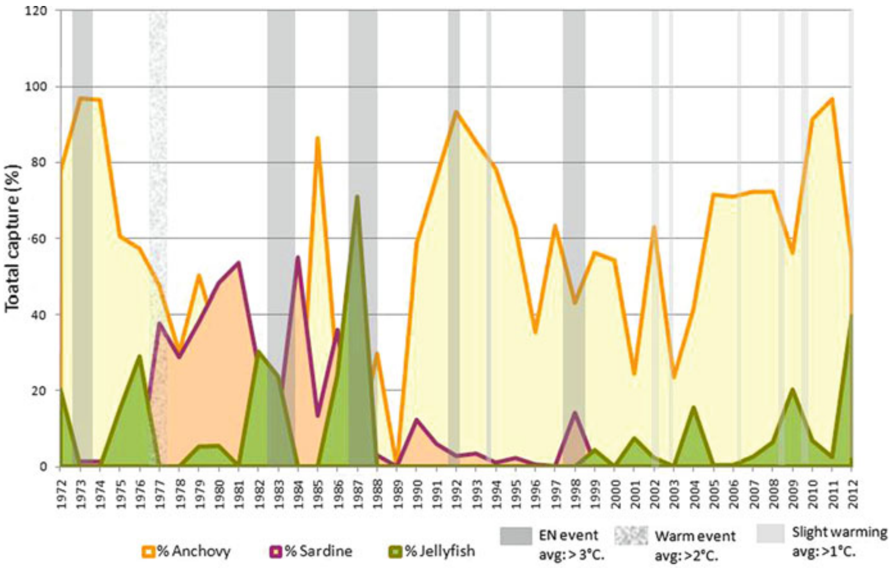

Fig. 10.4 A 40-year time series (1972–2012) of pelagic fishing landings (% wet weight) of anchovy (*Engraulis ringens*), sardine (*Sardinops sagax*) and jellyfish (*Chrysaora plocamia*) from Peru. *Shaded areas* represent ENSO and warm years. *Bar width* indicates the duration of the warm event (in months). The series represent the effort of 11,702 fishing hauls carried out annually during spring–autumn

Peruvian anchovy (*Engraulis ringens*) and sardines (*Sardinops sagax*) undergo interannual and interdecadal fluctuations in response to ENSO (El Niño–La Niña) and the PDO (El Viejo–La Vieja), respectively (e.g. Bakun 1996; Chavez et al. 2003, 2008; Fréon et al. 2008). Strong El Niño or La Niña events have large cascading ecosystem effects. Among these are changes to reproductive strategies of fish and, ultimately, changes to fisheries yields (e.g. Arntz and Valdivia 1985).

Similar climate-driven variability occurs in jellyfish populations (Brodeur et al. 2008; Suchman et al. 2012; Robinson and Graham 2013). *Chrysaora plocamia* biomass varies with ENSO (Quiñones 2010; Quiñones et al. 2010, 2013) as jellyfish biomass is usually high the year immediately preceding and during El Niño events. A long-term data set of jellyfish biomass taken during Peruvian research cruises from 1972 to 2012 indicates that population size fluctuated on annual to decadal scales. The consistency of this pattern during those decades led to this species being proposed as a potential indicator of El Niño phases in Chile (Alvial et al. 1984; Soto 1985). However, low medusa biomass from 1989 to 2009 in spite of several El Niño events occurring during these years suggests that other factors were also influencing its abundance. Variations in *C. plocamia* biomass were strongly matched to interdecadal phases known as "El Viejo" (a warm phase) and "La Vieja" (a cold one). The contribution of *Chrysaora plocamia* to the total pelagic catch was particularly high (20–70 % wet weight) when El Niño occurred during the warm "El Viejo" regime from the mid-1970s to 1980s (Fig. 10.4).

Decades with high medusa biomass coincided with a warm, “sardine-dominated” regime that began in 1975 and continued until the mid-1990s. Conversely, low abundances of medusae occurred during the cool “La Vieja”, anchovy-dominated regime that followed (Fig. 10.4; Chavez et al. 2003, 2008). *Chrysaora plocamia* began to increase in 2007, reaching 40 % of the total pelagic catch in 2012, concomitant with a modest but increasing sardine capture by the artisanal purse seine fishery, suggesting the Humboldt Current ecosystem had undergone a shift once again to a warm, “El Viejo” regime.

10.3 Ecological Interactions of *Chrysaora plocamia* in the Pelagic Realm

Chrysaora plocamia is an important member of the Humboldt and Patagonian Shelf LMEs given its ability to dominate the pelagic biomass. Jellyfish in general consume a wide selection of zooplankton and in large quantities (see Arai 1988), so *C. plocamia* quite possibly exerts strong, top-down ecological forcing when abundant.

Scientific observations of fishes feeding on *C. plocamia* are scarce in both the Humboldt Current and Patagonia shelf ecosystems. However, there are anecdotal suggestions that fish prey on *C. plocamia*. Artisanal fishermen from Bahía Independencia (Peru) used “gonads” of *C. plocamia* as bait to catch the Centrolophid palm ruff (*Seriolella violacea*). This practice makes sense considering *Seriolella violacea* have been shown to eat large quantities of jellyfish including salps, pyrosomes and ctenophores (mainly *Mnemiopsis leidyi*) (e.g. Arai 1988; Mianzan et al. 1996, www.fishbase.org). Recently, large juveniles of *S. violacea* were observed biting the medusae and mesoglea was occasionally found in their stomachs (Riascos et al. 2012a).

Chrysaora plocamia also form part of the diet of some sea turtle species; however, turtles need to consume large volumes of gelatinous prey to meet their nutritional requirements (Hays et al. 2009). Three of the five turtle species reported for Peruvian waters feed specifically (leatherback turtle, *Dermochelys coriacea*) or at least opportunistically (green turtle, *Chelonia mydas agassizii,* and olive ridley, *Lepidochelys olivacea*) on medusae (Quiñones et al. 2010; Goya et al. 2011). *Chrysaora plocamia* biomass appears to be sufficient, particularly during ENSO years, to support *C. m. agassizii* (Quiñones et al. 2010).

Jellyfish like *C. plocamia* provide structure that favour many types of ecological interactions in the pelagic realm; they may be used as a source of shelter and food or a focus for aggregation (e.g. Arai 1997; Towanda and Thuesen 2006). Their large bell and conspicuous oral arms may provide shelter and food for schools of juvenile stages of the starry butterfish (*Stromateus stellatus*) (Elliot et al. 1999) and other stromateid juvenile fish in the Patagonian shelf ecosystem (Mianzan pers. obs., A. Gosztonyi 2012 pers. comm.) (Fig. 10.5). Large scyphomedusae in particular often harbour juvenile or small adult fish under the bell or among the

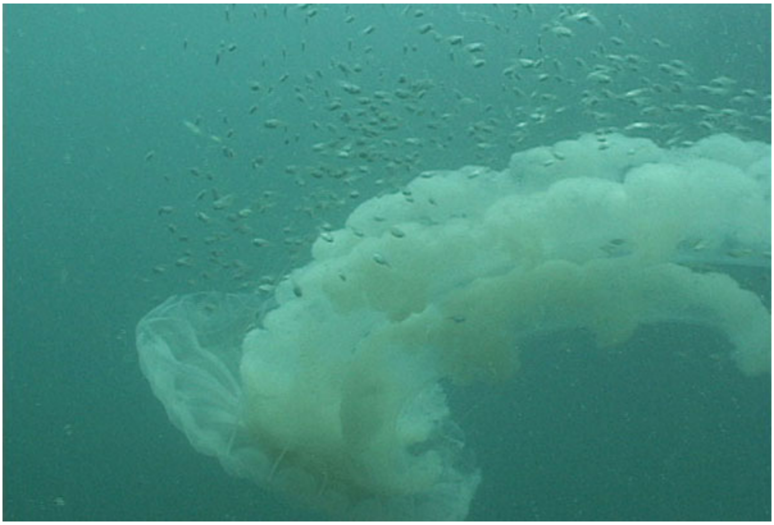

Fig. 10.5 *Chrysaora plocamia* accompanied by a school of stromateid juvenile fish off Puerto Madryn, Chubut, Argentina (Photo by J. Costello)

tentacles and oral arms. These fishes probably find shelter and protection from larger predators and may also benefit from prey stung and caught by the jellyfish (Purcell and Arai 2001).

Numerous invertebrate taxa utilise *C. plocamia* for substrate within the structureless water column. The hyperiid amphipod *Hyperia curticephala* has been described associating with *C. plocamia* medusae in coastal waters of Paita and Mejillones Bays (northern Peru and northern Chile, respectively) (Oliva et al. 2010). The authors reported one of the highest numbers of amphipods per medusa available in literature. Associations between hyperiid amphipods and medusae are widely documented (e.g. Laval 1980; Arai 1997; Towanda and Thuesen 2006, see also Chaps. 4 & 5). These associations are complex and vary greatly in timing, degree of dependence of the hyperiids on their hosts for shelter or for food and extent of maternal care (Gasca and Haddock 2004). The presence of small portions of mesoglea in the gut contents of all amphipods dissected suggests that *H. curticephala* uses *C. plocamia* not only as substrate in the pelagic realm but also as a food source (Oliva et al. 2010). Oliva et al. (2010) considered this association as micro-predation. Predation of hyperiids on medusae suggests that an equilibrium exists between its feeding rate and the regeneration rate of medusa tissue (Laval 1980). It was also proposed that amphipods may constitute a prey item for juveniles of *S. violacea* feeding on them and channelling energy back to fishes. The association between another invertebrate, the parasitic anemone *Peachia chilensis,* and *C. plocamia* as a host has been recently described. The parasite induced castration, reduction of fecundity and host mortality (Riascos et al. 2012a, b).

Table 10.1 Socio-economic impacts of mass occurrences of *Chrysaora plocamia* around South America

Industry	Event	Location	Source
Fisheries	Jellyfish by-catch in Peruvian artisanal fisheries	Pisco, Peru	Dr. Valdivia IMARPE pers. comm.
	Jellyfish by-catch in Peruvian industrial fisheries	Ilo, Peru	Quiñones et al. (2013)
Water inlets	Jellyfish clogging seawater intakes of floating pump stations	Callao, Peru	Federico Iriarte (2012) pers. comm.
	Desalination plant blocked	Antofagasta, Chile	Aldo Pacheco (2012) pers. comm.
	Clogging of ships' seawater intakes	Golfo Nuevo, Argentina	Mianzan (1986, 1989), Mianzan et al. (2005), Ricardo Vera (2012) pers. comm.
Aquaculture	Affected salmon aquaculture facilities	Chiloé, Chile	Palma et al. (2007), Bravo et al. (2011)
Tourism	Mass strandings	Golfo Nuevo, Argentina	Mianzan et al. (2005)
	Mass strandings, stinging	Paracas, Peru	Vera et al. (2004, 2005)
	Mass strandings, stinging	Arica, Iquique and Antofagasta, Chile	Vera et al. (2004, 2005), Vega and Ogalde (2008)

10.4 Economic Impact of *Chrysaora plocamia* Blooms: Is It a Troublesome Species?

There is a growing body of information suggesting *Chrysaora plocamia* is a nuisance for several human industries in South American waters (Table 10.1), which is not surprising given economic losses caused by other jellyfish species elsewhere (Nagata et al. 2009; Purcell 2012). Tourism, fishing, aquaculture and energy production are among the industries most affected by jellyfish (e.g. Chap. 6, Möller 1984; Verner 1984; Mianzan 1986, 1989; Williamson et al. 1996; Uye and Ueta 2004; Uye 2008), and species from the genus *Chrysaora* are sometimes cited as being problematic. For example, it has been suggested that *Chrysaora fulgida* has replaced fishes and has been inhibiting the recovery of sardine stocks in Namibian waters (Lynam et al. 2006; Flynn et al. 2012).

10.4.1 Fisheries

Jellyfish generally cause problems to fishing operations when abundant, and clogging of gear is the most reported effect (e.g. Purcell et al. 2007; Dong et al. 2010). Clogged gear can cause a wide spectrum of issues ranging from increases in fishing effort and gear damage to injuries to fishers and fishery closures that result in severe income loss (e.g. Möller 1984; Graham et al. 2003; Kawahara et al. 2006; Purcell et al. 2007).

Fisheries landings in Peru, Chile and Argentina may represent about 15 % of the world's total marine landings (Official Statistics from each country see Vice Ministry of Fisheries, Peru; National Service of Fisheries, Chile and Ministry of Agriculture, Livestock and Fisheries, Argentina). These fisheries represent nearly 11 million tonnes annually, and the biological productivity supporting these fisheries also supports the production of jellyfish.

The by-catch of *C. plocamia* in Peruvian waters generates economic losses mainly to artisanal and commercial purse seine fisheries. Interference is particularly problematic during warm phases of ENSO when *C. plocamia* are so numerous (Fig.10.6a, b) that fishers had trouble finding waters without jellyfish to operate the gear (Dr. Valdivia, Instituto del Mar del Perú (IMARPE), pers. comm.). These fishing operations are substantial, involving 1,700 vessels each with a hold capacity from <30 to 900 tonnes (Fréon et al. 2008; Alfaro-Shigueto et al. 2010).

Within the artisanal fleet, jellyfish must be removed manually; however, total removal is difficult to achieve at sea (Fig. 10.6b). Thus, jellyfish are manually unloaded with the fish catch and discarded in port. Information from IMARPE fisheries observers from the Pisco area indicated that jellyfish by-catch averaged 10 % annually in 2007, 2008 and 2009. This percentage increases to 20–40 % of the total catch during summer when *C. plocamia* biomass tends to reach its annual peak.

The commercial purse seine fishery operates differently to the artisanal one. Both fish and jellyfish are removed directly from the purse seine net by suction and held within the ship without sorting and discarding jellyfish. These result in a large displacement of fish catch by jellyfish and also result in loss of revenue or even the total catch being rejected by processing plants. *Chrysaora plocamia* by-catch in the southernmost Peruvian fishing harbour of Ilo was enough to cause losses exceeding $200,000 (USD) in 35 summer days (Fig. 10.6c). Fishery factories refused to receive the catch if jellyfish by-catch was greater than 40 % of total weight (Quiñones et al. 2013). Thus, economic losses to both artisanal and commercial fishing have the potential to become substantially high during warm periods like El Niño when *C. plocamia* tend to be more abundant.

10.4.2 Aquaculture

General information about effects of jellyfish on fish aquaculture is limited to relatively few well-documented incidents (Purcell et al. 2007; Doyle et al. 2008; Baxter et al. 2011). There is evidence *C. plocamia* has interfered with salmon aquaculture operations in Chile (southern Humboldt Current). Since 1980, salmon farming in Chile has grown from 10,000 tonnes in 1988 to 470,000 tonnes in 2009 (Soto et al. 2001; Palma et al. 2007; SERNAPESCA 2012).

From February to June 2002, salmon aquaculture facilities were affected by proliferations of *Chrysaora plocamia* (Fig. 10.7a). It is likely that *C. plocamia* caused

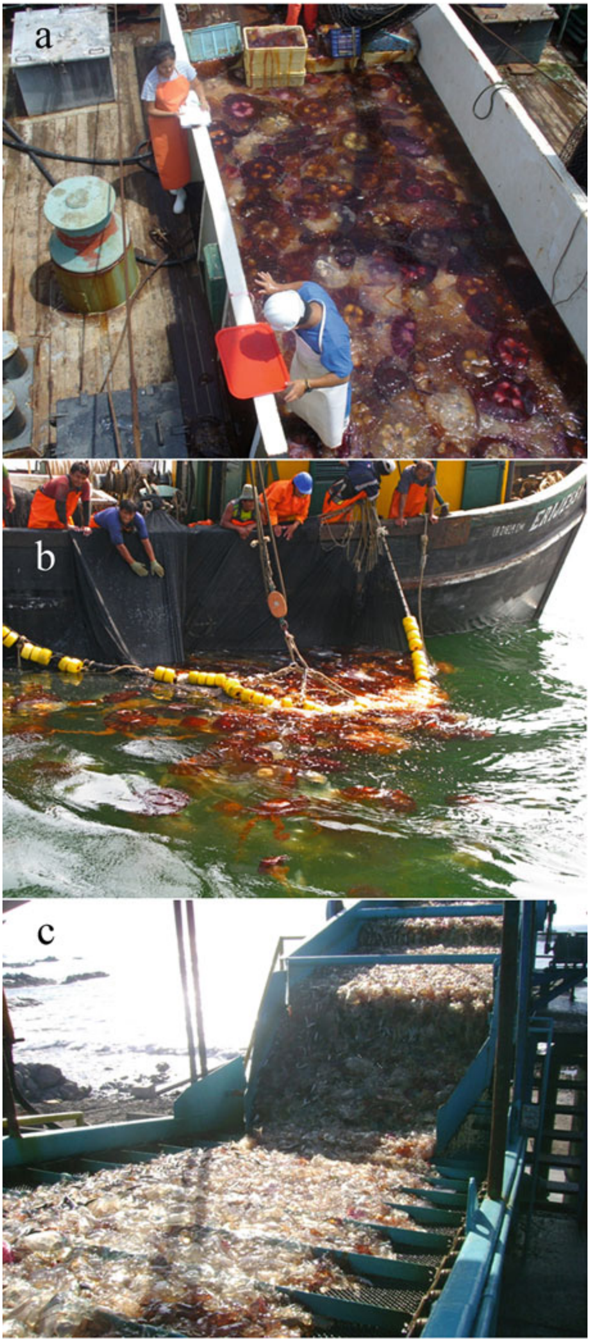

Fig. 10.6 (**a**–**c**) (**a**) Capture of *Chrysaora plocamia* by the Peruvian Research Vessel “José Olaya Balandra” off Peru in summer 2009; (**b**) by-catch of *C. plocamia* by an artisanal purse seine vessel during an anchovy (*Engraulis ringens*) fishing operation off Callao, Peru (Photo by Yuri Hooker); (**c**) anchovy landing of an industrial purse seine vessel with >70 % by-catch of *C. plocamia* in the port of Ilo (Peru—January 2009). The whole catch was discarded

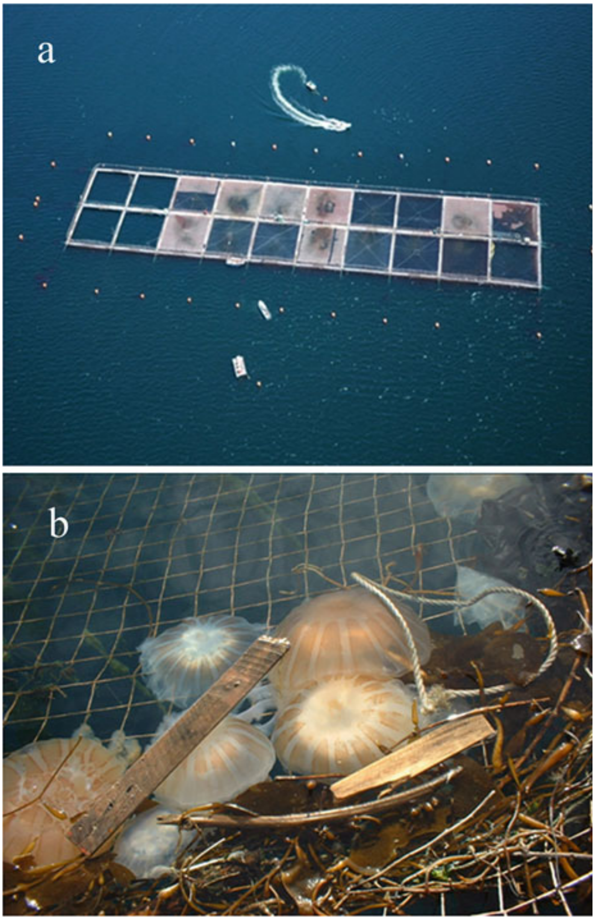

Fig. 10.7 (**a**–**b**) (**a**) Aerial view of salmon farming facilities surrounded by *Chrysaora plocamia* (Chiloe Island, southern Chile). (**b**) Detailed view of broken *C. plocamia* on nets of floating salmon culture cages in Chiloe, Chile

fish mortality by damaging the gill tissue resulting in suffocation (Palma et al. 2007). Medusae become pressed against the nets and their tissues split into several, smaller pieces that passed through the mesh of the floating cages (Fig. 10.7b). It was also proposed that fish were unable to feed inside the floating cages during such events (Bravo et al. 2011) and many died due to stress and starvation. Fish natural mortality doubled during this event and more than 60 % of the dead fishes presented eye injuries (blindness).

10.4.3 Clogging of Cooling Water Intakes

Chrysaora plocamia medusae have been responsible for clogging water intake systems of ships and shore-based facilities. When abundant, this species has caused significant problems in Argentinean and Peruvian harbours (Schweigger 1959 cited in

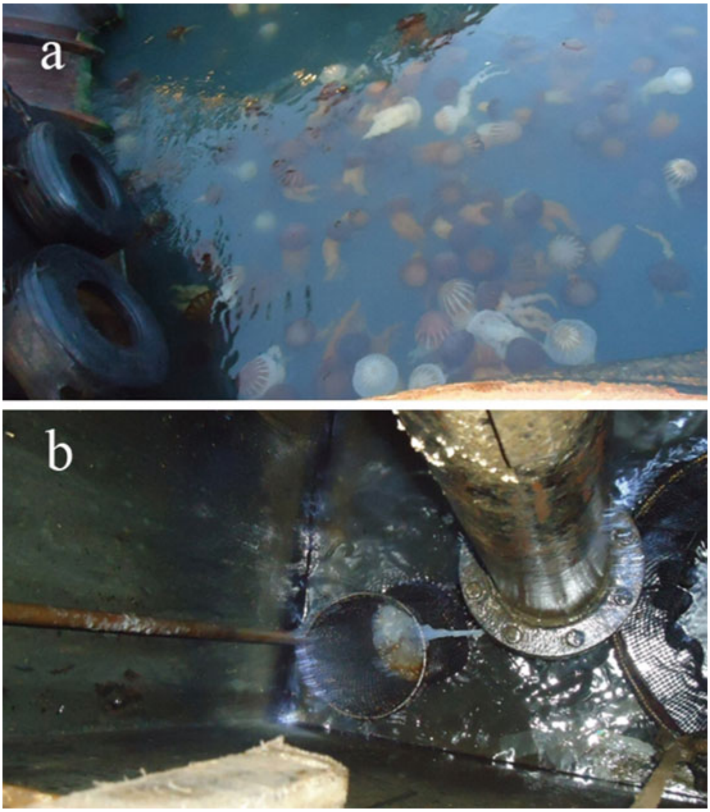

Fig. 10.8 (**a**–**b**) (**a**) Cooling water intakes clogged by *Chrysaora plocamia* in floating structures for industrial fishery landings in Callao harbour Peru (June 2012). (**b**) Manual removal of jellyfish remains from ship pumps

Möller 1984; Mianzan 1989). During the summer of 1999–2000, the water intake systems of ships anchored in the harbour experienced clogging when a massive stranding of *C. plocamia* occurred in Nuevo Gulf (Mianzan et al. 2005) and it required several hours for divers to clear the jellyfish from the system (Ricardo "Bebote" Vera 2012 pers. comm.). In another example from El Callao harbour, Peru, in early 2012, several vessels experienced clogging while transferring fish to factories on land. Here, seawater intakes of floating pump stations called "chatas" that supply water for the operation were blocked. Blockage due to medusae during the bloom resulted in delays and stoppages before jellyfish were manually removed (Fig. 10.8a, b).

Chrysaora plocamia blooms also affected a desalination plant in Chile. The city of Antofagasta is in the middle of Atacama Desert located in northern Chile, where 70 % of the freshwater is supplied by a desalination plant. The water intake pipes are often blocked by *C. plocamia* during summer. Reduced production resulted in social disturbances and economic losses (Aldo Pacheco 2012 pers. comm.).

Fig. 10.9 Skin reactions shortly after *C. plocamia* stings

10.4.4 Tourism

Tourism impacts by jellyfish are widely recognised in tropical and subtropical regions of North America, Europe and Australia, but only a few cases are known from South America. Large numbers of *C. plocamia* or their remains have caused problems in tourist areas of Paracas in Perú; Arica, Iquique and Antofagasta in Chile; and Puerto Madryn in Argentina. Strandings tend to happen in late spring–summer (Vera et al. 2004, 2005) and are especially large during El Niño events in Peru and Chile. Aquatic sports like kayaking, rowing, wake boarding, diving, swimming and sailing are frequent in the area where the jellyfish were aggregated; consequently, *C. plocamia* was responsible for one of the most frequent causes of skin irritations in swimmers (Vera et al. 2005). The mildly toxic venom of *C. plocamia* can cause slight cutaneous and ophthalmologic manifestations within the first 24 h. Delayed long-term reactions in individuals who have been sensitised through previous contacts can result in an immune response such as skin lichenification (Vera et al. 2004, 2005; Vega and Ogalde 2008) (Fig. 10.9).

10.5 Concluding Remarks

Chrysaora plocamia is very large and colourful and therefore a quite conspicuous animal that is difficult to overlook. The species is an important member of the coastal marine ecosystems of South America having important ecological roles, including trophic and symbiotic interactions with fish and sea turtles. Population variability has a clear relationship with climate where phases of high *C. plocamia* biomass were associated with El Niño events that occurred during “El Viejo” warm regime. Interestingly, biomass occasionally approaches sardines or anchovies stock biomass estimates. This large jellyfish negatively affects human industries in the region when abundant, including fisheries, aquaculture, desalination plants and tourism. Understanding relationships between jellyfish blooms and environmental drivers (e.g. ENSO, regime shifts) should allow forecasting of the jellyfish abundance and potential vulnerabilities such that resource managers and industrial fisheries owners may prepare for costly outbreaks.

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Chapter 11
Pelagia noctiluca in the Mediterranean Sea

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Abstract Over recent decades, man's expanding influence on the oceans has begun to cause change in some regions, including in the Mediterranean Sea. New proliferations of jellyfish may be occurring in the Mediterranean Sea, possibly in response to the cumulative effects of some of these anthropogenic impacts. In the Mediterranean Sea, many of these "proliferation events" are due to *Pelagia noctiluca*, an oceanic scyphozoan that has become very abundant along the coasts. *Pelagia noctiluca* is usually considered to be the most important jellyfish species in the Mediterranean Sea due to its widespread distribution, abundance, and ecological role and also because of its negative interaction with humans. Climatic conditions that favor enhanced reproduction by *P. noctiluca* and probably also determine optimal conditions for the formation of blooms are characterized by mild winters, low rainfall, high temperature, and high-atmospheric pressure. The Medusa Project in Catalonia aims to understand the spatiotemporal dynamics of the jellyfish populations in the NW Mediterranean Sea by undertaking daily sampling during summer (May to September) of 243 beaches, covering more than 500 km of coast. Data on beach strandings along the Spanish Catalan coast revealed that jellyfish occur in greatest concentrations along the northern Catalan coast and on beaches located close to marine canyons. The arrival of *P. noctiluca* to the coast depends firstly on the offshore production of jellyfish. Oceanographic structures like fronts, which

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enhance and maintain high levels of biological production and provide ideal conditions for feeding, growth, and reproduction of the jellyfish are present in the NW Mediterranean. The weakening of the front results in large numbers of *P. noctiluca* being driven into the coast by southeast winds. In the NW Mediterranean Sea *P. noctiluca* exert top-down control over a variety of prey including fish eggs and possibly the invasive ctenophore *Mnemiopsis leidyi*. *P. noctiluca* is also responsible for the majority of the stings incurred by bathers along the Catalan coast. Finally, we recommend that similar sampling programs should be done elsewhere to better understand changes in the distribution, abundance, and blooming patterns of dangerous jellyfish species.

Keywords Jellyfish blooms • *Pelagia noctiluca* • NW Mediterranean Sea • Catalan coast • Tourism • Long-term monitoring • Oceanography • Climate variability • Physicochemical variables • Socioeconomic impacts • Jellyfish-fish interactions

11.1 Introduction

Jellyfish are a common component of Mediterranean marine communities (Boero et al. 2008). Their spatiotemporal dynamics are highly variable, and blooms occur irregularly and are difficult to predict (Boero et al. 2008; Brotz and Pauly 2012). In Mediterranean waters, approximately 12 species of scyphomedusae form dense blooms (Axiak et al. 1991; Gili and Pagès 2005). While a possible long-term increase of jellyfish in Mediterranean waters has been noticed in recent years (Brotz et al. 2012; Condon et al. 2012), this general increase seems to be evident for only some jellyfish species (Brotz et al. 2012; Condon et al. 2013), reflecting the large variability of jellyfish dynamics (Brotz and Pauly 2012). Recently, Brotz et al. (2012) used a combination of quantitative and anecdotal data to analyze trends in gelatinous zooplankton (Cnidaria, Ctenophora, and pelagic tunicates) in 66 large marine ecosystems (LMEs). They discovered that the abundances of jellyfish and the frequency of blooms in the Mediterranean LME had increased. This general increase was subsequently corroborated for the Mediterranean Sea by Condon et al. (2013) using only quantitative data.

11.1.1 Ecology of Pelagia noctiluca

The most common and conspicuous jellyfish species in Mediterranean waters is the mauve stinger, *Pelagia noctiluca* (Forsskål 1775). This scyphozoan is a holoplanktonic species (i.e., it lacks a benthic phase in its life history) (Fig. 11.1). This characteristic allows *P. noctiluca* populations to inhabit oceanic as well as coastal ecosystems and may explain its biogeography. *P. noctiluca* is widely distributed from the warm subtropical waters of the Gulf of Mexico and the

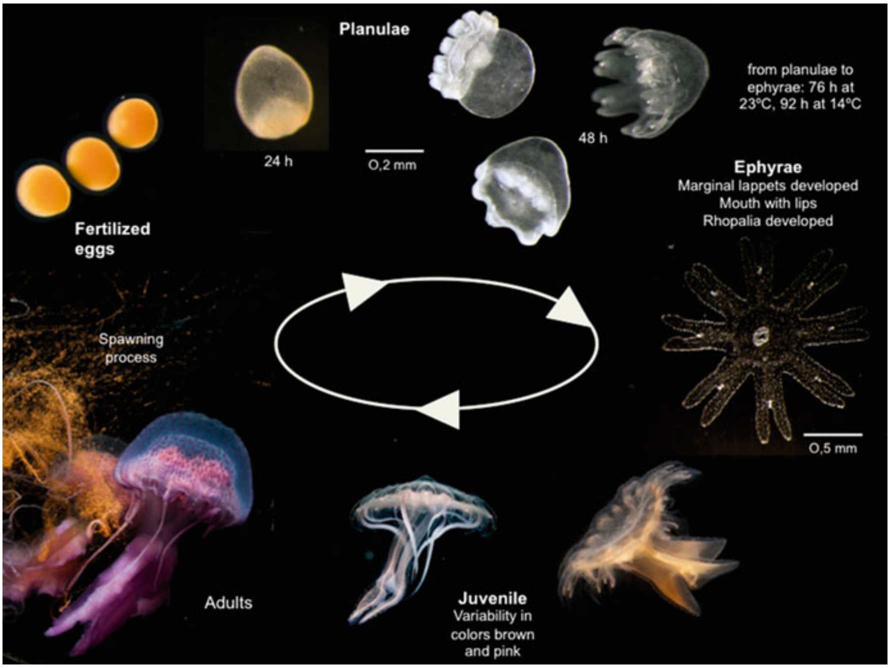

Fig. 11.1 Holoplanktonic life cycle of *Pelagia noctiluca* photographed at the ZAE (Experimental Aquaria Zone at ICM-CSIC in Barcelona) with indications on the sizes and times of developments (Photos Eduardo Obis Alberola)

Mediterranean Sea to the temperate waters of the North Sea (Russell 1970; Graham et al. 2003; Purcell 2005; Licandro et al. 2010) and up to 4° of latitude (Doyle et al. 2008; Bastian et al. 2011).

In pelagic ecosystems *P. noctiluca* has been recorded at a maximum depth of 1,400 m (Franqueville 1971, cited in Mariottini et al. 2008), but it is especially abundant on shelf slopes where concentrations of plankton occur (Sabatés et al. 1989). There, *P. noctiluca* occurs near the surface between 10 and 30 m with the maximum occurrence at 12 m, coinciding with the upper halocline/pycnocline and the layer of maximum current shear, especially at night (Graham et al. 2003; Mariottini et al. 2008). This vertical distribution pattern coincides with the nocturnal migration of zooplankton, their main prey (Malej 1989; Sandrini and Avian 1989; Sabatés et al. 2010).

Pelagia noctiluca is an important nonselective planktonic predator (Larson 1987; Morand et al. 1987; Sandrini and Avian 1989; Giorgi et al. 1991; Daly Yahia et al. 2010; Rosa et al. 2013), feeding on almost all types of zooplankton and ichthyoplankton (Giorgi et al. 1991; Zavodnik 1991; Malej et al. 1993; Sabatés et al. 2010), and may exert top-down control on marine food webs. Gut contents of *P. noctiluca* have shown a great variety of items consumed; Cladocera, Appendicularia, Copepoda, Hydromedusae, Siphonophora, and fish eggs were the most common

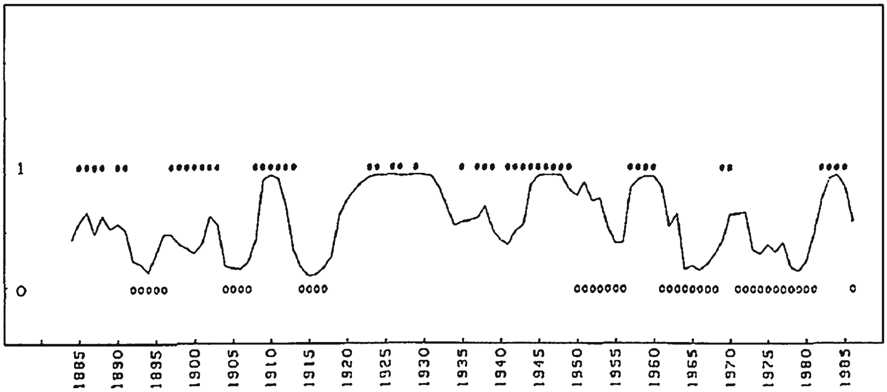

Fig. 11.2 Periodicity of *Pelagia noctiluca* blooms. *Open circles*: years without *P. noctiluca*. *Closed circles*: years with *P. noctiluca*. *Solid line*: probability of *P. noctiluca* blooms (After Goy et al. 1989)

food items of adults (Malej 1989). From analysis of gastric pouches of *P. noctiluca* ephyrae in the NW Mediterranean Sea, Sabatés et al. (2010) found positive selection for chaetognaths and larvae of mollusks during both day and night and for fish larvae during the night only. Recently, feeding experiments have revealed the potential of *P. noctiluca* to act as a control of the invasive ctenophore *Mnemiopsis leidyi* (Tilves et al. 2012).

11.1.2 History of Blooms of **Pelagia noctiluca** *in the Mediterranean Sea*

Intense interest in the dynamics of *Pelagia noctiluca* blooms started in the early 1980s when a massive occurrence of *P. noctiluca* affected the eastern Mediterranean Sea, the Adriatic Sea, and subsequently the western Mediterranean Sea (Malej and Malej 2004; Mariottini et al. 2008). The United Nations Environmental Program (UNEP), through the Mediterranean Action Plan (MAP), launched a project to fund scientific research on jellyfish in the Mediterranean Sea. Research activities culminated in two workshops in 1983 and 1987 (UNEP 1984, 1991). In those and other publications, all available information on *P. noctiluca* blooms in the Mediterranean was assembled.

Trends in jellyfish populations (including *P. noctiluca*) in the Mediterranean have been recently reviewed (e.g., Brotz and Pauly 2012; Condon et al. 2013). The periodic occurrence of *P. noctiluca* in the western Mediterranean was first reported by Goy et al. (1989) who used archival data from the Station Zoologique at Villefranche-sur-Mer and various other sources to reconstruct a time series of the occurrence of *P. noctiluca* dating back to 1775. Blooms of *P. noctiluca* occurred 55 times between 1775 and 1987, with a periodicity of about 12 years (Fig. 11.2), and were related to climatic fluctuations. Analyses of more recent data from the Gulf of Tunis, the Balearic Islands (Daly Yahia et al. 2010), and Ligurian Sea (Bernard et al. 2011), however, indicate that blooms may now be occurring more frequently in the western Mediterranean Sea. The recent potential change in the periodicity of blooms of *P. noctiluca* in the western Mediterranean, however, does not appear to be occurring in the eastern Mediterranean. Kogovšek et al. (2010) reconstructed a 200-year time series of the occurrence of *P. noctiluca* in the northern Adriatic Sea and identified three periods when *P. noctiluca* formed conspicuous blooms, around 1915, during the late 1970s and early 1980s, and from 2004 to 2007, but there was no evidence of a recent change in the periodicity of blooms although other species in the region do appear to have increased. Furthermore, there is limited evidence for a general increase in the periodicity of blooms of *P. noctiluca* in the southern Adriatic or Aegean seas (Daly Yahia et al. 2010).

11.2 Climatic, Oceanographic, and Biological Drivers of Jellyfish Blooms in the Mediterranean Sea

Possible relationships between environmental factors and blooms of *Pelagia noctiluca* have been studied since the establishment of the framework of the Long-Term Programme for Pollution Monitoring and Research in the Mediterranean Sea (MED POL – PHASE II) (UNEP 1984). Nevertheless, few clear associations have been determined, and final conclusions about the environmental variables controlling the distribution of this species are still under study (Kogovšek et al. 2010; Ferraris et al. 2012; Rosa et al. 2013).

The complex occurrence patterns of *P. noctiluca* associated with a lack of precise data on occurrence of blooms and the associated environmental variables make the prediction of *P. noctiluca* blooms difficult (UNEP 1984). We propose that factors that correlate with the occurrence of *P. noctiluca* be classified into the following four different types: physical, physicochemical, biological, and climatic forcing (Table 11.1).

11.2.1 Climatic Forcing

Long-term climate fluctuations have been correlated with jellyfish abundance in Mediterranean waters (Table 11.1). Molinero et al. (2005, 2008) using the most important modes of atmospheric circulation over the Northern Hemisphere (i.e., Northern Annular Mode [AO/NAO], East Atlantic pattern [EA], Gulf Stream/Northern Current Index, East Atlantic Western Russian pattern, and the Northern Hemisphere temperature [NHT]) established the first principal component (accounting for 47 % of the total variance) as a proxy of the Atlantic climate variability. This North Atlantic climate variability is significantly related to long-term changes in zooplankton functional groups, including *Pelagia noctiluca*, in the NW Mediterranean (Molinero et al. 2008). Daly Yahia et al. (2010) showed that abundances of *P. noctiluca* in 2004, 2005, and 2007 were positively associated with variations of the Northern Hemisphere

Table 11.1 Literature review on proposed forcings that explain jellyfish blooms in the Mediterranean Sea

Forcing	Environmental variable	Effect on	Relationship	Location	References
Climatic	Northern hemisphere temperature (NHT)	Abundance	Positive	Mediterranean Sea	Daly Yahia et al. (2010)
		Reproduction	Positive	SW Mediterranean Sea	Gislaso and Gorsky (2010)
	Atmospheric average annual temperature (AAT)	Abundance	Negative	Mediterranean Sea	Daly Yahia et al. (2010)
	Regional atmospheric index (RAI)	Abundance	Negative	Mediterranean Sea	Daly Yahia et al. (2010)
		Reproduction	Negative	SW Mediterranean Sea	Gislaso and Gorsky (2010)
	Rainfall	Co-occurrence	Negative	Mediterranean Sea	Goy et al. (1989)
	North Atlantic Oscillation (NAO)	Abundance	Neutral	Mediterranean Sea	Daly Yahia et al. (2010)
	North Atlantic climate variability	Abundance	Positive	Western Mediterranean Sea	Molinero et al. (2005, 2008)
Physical	Current direction	Accumulation and transport	Positive	Northern Adriatic Sea	Maretić (1984), Zavodnik (1987), Benović (1991), Legović and Benović (1984), Malej and Malej (2004), Kogovšek et al. (2010)
	Wind direction	Accumulation and transport	Positive	Adriatic and Maltese waters	Maretić (1984), Zavodnik (1987), Zavodnik (1991), Axiak et al. (1991), Legović (1991), Malačič et al. 2007
	Water masses	Transport	Positive	Mediterranean Sea	Vučetić (1984)
	Tidal	Accumulation	Positive	Adriatic Sea	Zavodnik (1987)
	Front structure	Accumulation	Positive	NW Mediterranean Sea	Sabatés et al. (2010)

Physicochemical	Dissolved oxygen	Co-occurrence	Negative	Northern Adriatic Sea	Vučetić (1991)
	Light intensity	Activity (pulsation rate)	Negative	Malta (experimental)	Axiak (1984)
	SST	Activity	Negative	Experimental	Malej and Malej (2004), Rosa et al. (2013)
		Co-occurrence	Positive	Strait of Messina (Italy)	Rosa et al. (2013)
		Growth	Negative	Experimental	Rosa et al. (2013)
		Transport	Negative	Adriatic Sea	Benović (1991)
		Co-occurrence	Positive	Mediterranean Sea	Goy et al. (1989), Vučetić (1991)
		Activity (pulsation rate)	Positive	Northern Adriatic Sea	Avian et al. (1991)
		Reproduction	Positive	Adriatic Sea	Legović (1991)
		Survival	Positive	Northern Adriatic Sea	Vučetić (1984)
	Salinity	Co-occurrence	Positive	Northern Adriatic Sea	Vučetić (1991)
		Reproduction	Positive	Mediterranean Sea	Vučetić (1984)
	Eutrophication	Survival	Positive	Northern Adriatic Sea	Legović (1987), Malej and Malej (2004)
	Nutrient load	Survival	Positive	Adriatic Sea	Legović (1991)
	Toxicants	Reproduction	Positive	Mediterranean Sea	Vučetić (1984)
Biological	Competition	Survival	Negative	Adriatic Sea	Legović (1991)
	Productivity (Chla)	Growth	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)
		Reproduction	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)
	Zooplankton (biomass)	Co-occurrence	Positive	Northern Adriatic Sea	Kogovšek et al. (2010)

temperature (NHT) and, conversely, abundances were negatively correlated with the Regional Atmospheric Index (RAI) and the atmospheric Average Annual Temperature (AAT); however, the North Atlantic Oscillation (NAO) index was not significantly related to abundances. These climatic conditions correspond to mild winters, low rainfall, high temperature, and high-atmospheric pressure, which seem to favor *P. noctiluca* reproduction and probably determine optimal conditions for the formation of *P. noctiluca* blooms and their maintenance for several months and even years (Daly Yahia et al. 2010; Rosa et al. 2013). Thus, *P. noctiluca* may be an indicator of climate variability in the Mediterranean Sea.

11.2.2 Physical Forcing

Physical forcing (wind and current direction and velocity, and also tidal effects) was thought to determine the presence of *Pelagia noctiluca* in inshore and offshore waters in the northern Adriatic Sea (Vučetić 1984). Physical forcing has also been responsible for coastal or inshore aggregations in the Adriatic Sea (Maretić 1984; Benović 1991; Legović 1991; Zavodnik 1991; Malej and Malej 2004) and in Maltese waters (Axiak et al. 1991). In these cases in shallow coastal waters wind, currents and tides have been the main drivers, allowing for big (sometime huge) accumulations of medusae (Zavodnik 1987). Some smaller-scale characteristics may explain certain locations for aggregation, such as in embayments, gulfs, islands, and ports.

The first record of *P. noctiluca* in the northern Adriatic Sea was principally due to advection by a strong southeastern Adriatic current (Malej and Malej 2004). Benović (1991) demonstrated that *P. noctiluca* enters into the Adriatic Sea only during the colder seasons with incoming surface currents from the Ionian Sea. A modeling study showed that the pathways of water parcels through the Adriatic Sea depended on the origin of the particles and suggested that this jellyfish enters the Adriatic Sea at the eastern side of the Otranto Strait (Malačič et al. 2007). This suggested connection between Adriatic and Mediterranean metapopulations and is supported by genetic evidence (Ramšak et al. 2007).

11.2.3 Physicochemical Forcing

Relationships between physicochemical forcing variables and the presence, demography, and behavior of *Pelagia noctiluca* have been assessed using field and experimental data. Sea surface temperature and salinity have a positive relationship with the presence of *P. noctiluca*. Survival of *P. noctiluca* increased with increased nutrient concentrations and eutrophication (Legović 1991; Malej and Malej 2004). Conversely, negative associations of the presence of this scyphozoan with dissolved oxygen have been shown (Vučetić 1991). Experiments reveal that temperature affects the activity (pulsation rate) of this species; specifically extreme temperatures, <11 °C and >26 °C, cause decreased activity (Malej and Malej 2004). Light intensity (lux shone on the jellyfish) also has a negative effect on pulsation rate

(Axiak 1984). This result is consistent with the nocturnal migration behavior of this species, where high abundances of large medusae are found only in deep waters (at least 400–600 m) during the daytime and in surface waters at night (Stiasny 1921; Axiak 1984; Ferraris et al. 2012). Vučetić (1984) also showed that survival of *P. noctiluca* was positively related to sea surface temperature (SST). A SST above the winter average enabled *P. noctiluca* to remain in surface waters and, in association with eutrophication and high-nutrient levels, resulted in more food being available and thus increased survival of the species (Table 11.1). Finally, reproduction was positively correlated with SST, salinity, and coastal toxic agents. Vučetić (1984) hypothesized that sublethal contamination levels of North Adriatic coastal waters had boosted *P. noctiluca* proliferations from 1977 onwards through "hormesis" (i.e., the increase of sexual reproduction as well as the stimulation of jellyfish growth rate by exposure to low concentrations of toxicants), as reported for several hydrozoans and other taxa (Loomis 1957; Braverman 1962, 1963; Muller 1965; Stebbing 1980, 1981; Piraino 1991). Temperatures higher than 10 °C in winter and lower than 27 °C in summer and salinities of 35–38 (reflecting low rainfall) are positively associated with good conditions for *P. noctiluca* occurrence (Goy et al. 1989; Purcell et al. 1999; Purcell 2005; Molinero et al. 2005; Licandro et al. 2010).

11.2.4 Biological Forcing

Although the temporal dynamics of this species seems to be controlled by large-scale factors (Daly Yahia et al. 2010; Kogovšek et al. 2010; Condon et al. 2013) local-scale features promote the retention of *P. noctiluca* medusae for extended periods, thus increasing their local abundance and survival (Legović 1991; Rosa et al. 2013). The local-scale factors relate to high primary production (Chl-*a* levels) increasing the availability of animal prey (zooplankton biomass), individual growth, and reproduction (Kogovšek et al. 2010) and ultimately leading to local *P. noctiluca* blooms. Biological interactions like competition have been suggested (Legović 1991; Brotz and Pauly 2012), but this kind of interaction is difficult to assess.

11.3 Impact of *Pelagia noctiluca* on Human Activities

Pelagia noctiluca is the most important species of scyphozoan in the Mediterranean Sea due to its high abundance, its distribution throughout the Mediterranean Sea, and because of its painful sting (Mariottini et al. 2008). Thus, negative interactions between this species and humans are diverse (Purcell et al. 2007). We classified the impacts of *P. noctiluca* blooms as "direct" or "indirect." Direct impacts have an immediate effect with direct repercussions for humans (and/or human activity); indirect impacts are related to reduction of the profit that humans receive from the activity (Table 11.2). *P. noctiluca* blooms negatively affect five main human activities, here presented in the order of decreasing scientific coverage: tourism, fisheries, aquaculture, energy, and ecosystem functioning.

Table 11.2 Literature review of the impacts of *Pelagia noctiluca* blooms on human activities in the Mediterranean Sea

Human activity	Impact type	Effect	Year	Location	References	Comments
Tourism	Direct	Stinging	1976	Italy	UNEP (1984)	
			1978	Pula, Croatia	Maretić (1984)	±50 % of bathers affected
			1977–1978	Istrian Coast (Yugoslavia)	Malej and Vuković (1984), UNEP (1991), Maretić et al. (1987)	
			1978–1983	Adriatic Sea (Trieste)	Legović (1991)	
			1983	Portoroz (Slovenia)	Malej and Vuković (1984)	
			1991	Yugoslavia	Axiak et al. (1991)	110 (52 %) of bathers affected
			1982	Greece	Axiak et al. (1991)	1,500 affected (2–3 stings per day)
			1981–1983	Athens	Axiak et al. (1991)	240 cases per year (720 total)
				Adriatic Sea	Legović (1991)	
			1984–1987	Monaco	Bernard 1991, Purcell et al. 2007	45,000 people affected
			2007	French Riviera	Purcell et al. (2007)	2,500 people affected
				Spain	Purcell et al. (2007)	More than 14,000 persons affected
			2008	Italy	Mariottini et al. (2008)	
			2010	Adriatic Sea	Nastasi (2010)	Review
			2011	Mediterranean Sea	Bernard et al. (2011)	
Fisheries	Indirect	Predation on fish eggs and larvae	1987	Ligurian Sea	Morand et al. (1987)	
			1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean Sea	CIESM (2001)	Review
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
		Predation on fish larvae	2010	NW Mediterranean Sea	Sabatés et al. (2010)	
		Predation on fish food	1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean Sea	CIESM (2001)	Review
			2004	Adriatic Sea	Malej and Malej (2004)	
			2010	NW Mediterranean	Sabatés et al. (2010)	

	Direct	Stinging	1978	Pula (Croatia)	Maretić (1984)	During 1978
			1977–1980	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980
			1985	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	700 fishermen in 192 days of fishing
			1987	Mediterranean Sea	Maretić et al. (1987)	
			1991	Adriatic Sea	Legović (1991)	Review
			2001	Mediterranean	CIESM (2001)	Review
			2008	Adriatic Sea	Mariottini et al. (2008)	Review
			2010	Adriatic Sea	Nastasi (2010)	Review
		Net clogging	1977	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	
			1978	Pula (Croatia)	Maretić (1984)	
			1983	Portoroz (Slovenia)	Malej and Vuković (1984)	
			1983–1984	Adriatic Sea	Legović (1991), Malej and Malej (2004)	Review
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
			2010	Mediterranean	Nastasi (2010)	Review
		Boat engine clogging	1985	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980
		Bycatch and economic impact	1983	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	Bycatch of 0.5 kgh^{-1} (review)
			2012	Israel Coast	Nakar et al. (2012)	Loss of 8 % “Trawl fish” profit
			2012	Israel Coast	Nakar et al. (2012)	Loss of 46.3 % “Gillnet” profit
		Capture damage	1985	Portoroz (Slovenia)	Malej and Vuković (1984)	Summer of 1983
			1987	Gulf of Trieste (Adriatic Sea)	Axiak et al. (1991)	
			1991	Adriatic Sea	Legović (1991)	Review
Aquaculture	Direct	Stinging	2010	Mediterranean Sea	Nastasi (2010)	Review
		Capture damage	2011	Spanish Coast	Baxter et al. (2011)	
		Fish mortality	1995	Brittany (France)	Merceron et al. (1995)	
			2007	Mediterranean Sea	Purcell et al. (2007)	Review
Energy	Direct	Clog cooling-water intake	1985	Istrian Coast (Yugoslavia)	Malej and Vuković (1984)	From 1977 to 1980

11.3.1 Tourism

Stings from pelagic cnidarians cause discomfort and sometimes medical emergencies for swimmers, primarily in warm marine waters worldwide (Fenner and Williamson 1996). When the jellyfish form blooms, stings can reach epidemic levels (Purcell et al. 2007). *Pelagia noctiluca* stings are usually limited to the skin's surface and cause only topical lesions with localized pain that persists for 1–2 weeks. Systemic complications or cutaneous infections are infrequent (Mariottini et al. 2008). Most people are stung during summer. Mariottini et al. (2008) reviewed the earliest reports of *P. noctiluca* stinging swimmers. The earliest reports originate from the coast of Italy in 1976 (UNEP 1984), followed by the Istrian coast, Yugoslavia, during 1977–1978 (Malej and Vuković 1984; UNEP 1991), the northern Adriatic (Trieste) during 1978–1983 (Legović 1991), and Slovenia (Portoroz) in 1983 (Malej and Vuković 1984).

The negative impacts of *P. noctiluca* have been reviewed over a larger scale from the Levantine to southern Spanish coast and for the whole Mediterranean basin (CIESM 2001; Nastasi 2010; Bernard et al. 2011). Quantitative data on stings are available for the coast of Pula, Croatia, in the summer of 1978, where *P. noctiluca* stung 50 % of the bathers (Maretić 1984). Similarly, 52 % of the bathers were stung during the same season along the coast of Yugoslavia (Maretić et al. 1987). During 1981 and 1983, 720 people were affected on the coast of Athens, with almost 250 people stung each summer (Vlachos and Kontoes 1987, cited in Axiak et al. 1991). During 1982, a total of 1,500 incidents were reported for Greece (Papathanassiou and Anagnostaki 1987, cited in Axiak et al. 1991). During the following years (1984–1987), the French Riviera reported that 2,500 people required treatment, reaching a peak along the coast of Monaco in 2004 with 45,000 people treated for stings (Bernard 1991). Two years later, the east and south coasts of Spain reported that more than 14,000 people were treated (Pingree and Abend 2006, cited in Purcell et al. 2007). These reports include only people who received medical treatment, so the total amount of people stung, but not attended by the first aid services, could be even larger. Mostly tourists were stung and the risk of being stung discouraged people from spending holidays at places where *P. noctiluca* is known to be abundant. Thus beaches affected by blooms of *P. noctiluca* will have less tourist appeal (Purcell et al. 2007).

11.3.2 Fisheries

Fisheries also have been negatively affected by their interaction with *Pelagia noctiluca*. The level of impact depends on the type of fishing gear being used and on the abundance of jellyfish. Fishers are directly affected by *P. noctiluca* when they are stung while removing the jellyfish from the nets (CIESM 2001; Purcell et al. 2007; Mariottini et al. 2008; Nastasi 2010). The first reported case of fishermen being stung comes from the Istrian coast, Yugoslavia during 1977–1980 (Malej and Vuković 1984), followed by a report from Pula, Croatia in 1978 (Maretić 1984).

Kokelj and Scarpa (1987, cited in Axiak et al. 1991) reported that in the Gulf of Trieste, 700 fishers were stung over a period of 192 days of fishing in 1985. Overall, the Adriatic Sea seems to be the most impacted (and/or reported) location for this type of interaction (reviewed in Legović 1991).

Other direct impacts of jellyfish on fisheries include jellyfish clogging the nets and the engines of fishing vessels (CIESM 2001; Purcell 2005; Nastasi 2010). Most reports come from the Adriatic Sea, where the first cases of net and engine clogging were described in 1977 along the Istrian coast, Yugoslavia (Malej and Vuković 1984). Maretić (1984) reported that in 1978 fishing nets became clogged by *P. noctiluca* along the coast of Pula, Croatia, and similar events occurred during the summer of 1983 along the coast of Portoroz, Slovenia (Malej and Vuković 1984). It seems that the clogging of fishing nets by jellyfish, for the period of the 1983 and 1984, was common in the Adriatic Sea (Legović 1991; Malej and Malej 2004). Little information is available for the rest of the Mediterranean basin, but clogging of fishing nets has been described as a recurrent and cyclic phenomenon (Bernard 1991; Purcell et al. 2007). Associated with clogging of nets is damage to the captured fish which reduces the value of the catch and the subsequent cost of cleaning the nets. The economic losses, however, have not yet been quantified. The Adriatic Sea again seems to be the most affected area (Malej and Vuković 1984; Legović 1991). Kokelj and Scarpa (1987, cited in Axiak et al. 1991) reported a total of 0.5 kg h^{-1} of *P. noctiluca* in fishing nets during trawling activities, in the Gulf of Trieste, northern Adriatic Sea, which together with the accumulation of jellyfish (mostly *Rhizostoma pulmo*) reduced the total fish catch and even caused the rupture of fishing nets. Recently, economic valuation models of the impact of jellyfish blooms on local economies have been presented for the Mediterranean Sea (Nakar et al. 2012; Nastav et al. 2013). Nakar et al. (2012) modeled the interaction of jellyfish with different fishery activities and showed annual reductions of 8% in net fishery income for trawl fishing and a 46.3 % reduction in net profit for the trammel and gillnet fisheries for the coast of Israel.

The case of the alien ctenophore *Mnemiopsis leidyi* in the Black Sea demonstrated that this gelatinous plankter can deplete fish populations by direct predation on fish eggs and larvae and indirectly by preying on the crustacean food of juvenile fish. In this way, gelatinous predators affect fisheries by depleting fish populations. This kind of impact, well quantified in the Black Sea for *Mnemiopsis*, has not been evaluated for *P. noctiluca*, but chances are that, due to the features of this species, its impact on fish populations is even greater than that of *Mnemiopsis*.

11.3.3 Aquaculture

Aquaculture activities also suffer from the effects of *Pelagia noctiluca* and are similar to those for fisheries. The main effects are stinging of the aquaculture operators (Purcell et al. 2007, Rutter 2010, cited in Nastasi 2010) and damage to, or mortality of, the fish inside of the pens (Merceron et al. 1995). On the Spanish coast, *P. noctiluca* inflicted gill damage to the marine-farmed fish *Dicentrarchus* *labrax*, resulting in stress to the fish that reduced their growth and even caused their death (Baxter et al. 2011). Impacts of jellyfish on aquaculture activities are summarized by Purcell et al. (2007, 2013) and Nastasi (2010).

11.3.4 Energy

Jellyfish proliferations also affect the energy industry by clogging cooling-water intake screens (CIESM 2001; Purcell et al. 2007). The only documented case of cooling-water intake screens being clogged by *P. noctiluca* in the Mediterranean Sea happened during 1977–1980 along the Istrian coast of Yugoslavia (Malej and Vuković 1984). However, *P. noctiluca* was also reported to have affected the functioning of the cooling systems of Maltese power plants during June 2009 (Schembri P and Deidun A pers. comm.).

11.4 Impacts of *Pelagia noctiluca* and Other Jellyfish Species on Planktonic Communities, Especially Fish Larvae and Eggs

In the Mediterranean, fisheries have existed since ancient times. Fishery resources have been long considered exploited or overexploited, and at present, forage fishes represent around 50 % of the total landings (Lleonart and Maynou 2003). Thus, the reduction of the finfish populations may result in important structural and functional changes in the marine ecosystem (Coll et al. 2008). In the Adriatic Sea, the proliferation of some jellyfish species since the 1980s has occurred in parallel with the decrease of small pelagic fish.

In the Mediterranean Sea, the highest abundance of *P. noctiluca* occurs in spring and summer (Morand et al. 1992; Licandro et al. 2010), when the majority of fish species reproduce. Indeed, spawning of most neritic fish species (families Sparidae, Labridae, Mullidae, Serranidae, Scombridae), as well as the small pelagic fish, anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*), takes place during this period of the year (Sabatés et al. 2007). Thus both ichthyoplankton abundance and diversity are high during spring-summer and coincide with large populations of jellyfish. As a consequence, the predation pressure of *P. noctiluca* on fish eggs and larvae can be high. In fact, Sabatés et al. (2010) reported that *Pelagia noctiluca* ephyrae would be an important predator on summer ichthyoplankton because fish larvae represented up to 12 % of the total prey captured by young jellyfish.

Gelatinous zooplankton can aggregate at hydrodynamic discontinuities (e.g., Arai 1976; Gili et al. 1988; Graham et al. 2001), and in the NW Mediterranean Sea, the most dense populations of gelatinous zooplankton and fish larvae have been associated with the northern current, along the shelf break, and its associated front (Sabatés et al. 2010; Ferraris et al. 2012). The particular hydrodynamic conditions of that area enhance and maintain high levels of biological production (Estrada and Margalef 1988; Sabatés et al. 2004; Stemmann et al. 2008), providing ideal conditions for feeding, growth, and reproduction of the jellyfish. Indeed, Sabatés et al. (2010) reported that predation on anchovy larvae by *P. noctiluca* ephyrae was higher in the frontal area than in the surrounding waters. Furthermore, during the night, when both groups of organisms co-occur in surface waters, *P. noctiluca* exhibited a positive selection for fish larvae. Thus, the temporal and spatial overlapping of *P. noctiluca* with early life stages of fish suggests that it may be an important predator of summer ichthyoplankton and potentially affect fish recruitment. Recently, Purcell et al. (2012) used a combination of data of jellyfish and fish larvae abundances, in situ jellyfish gut contents, experimentally measured digestion rates, and temperature and estimated that between 18 % and 32 % of the available fish larvae were consumed daily by *P. noctiluca* ephyrae.

Positive interactions between jellyfish and fish also exist. A large variety of fish associate with jellyfish among which, Carangidae are often the most abundant. Some benefits of these associations include predator avoidance, provisioning of food, and shelter for juvenile fish (Arai 1988; Purcell and Arai 2001; Masuda 2009). Associations between *P. noctiluca* and jack mackerel *Trachurus* spp. have been observed in the Mediterranean waters. Nevertheless, there are few systematic, quantitative data on the frequencies or durations of these positive associations, and their effect on the survival and recruitment of these fish species is not known.

Finally, it must be considered that natural predators of jellyfish, i.e., turtles, birds, and large carnivorous fish, have dramatically decreased due to overfishing, ingestion of floating plastics, and loss of essential habitats, therefore decreasing the control they perhaps once exerted over the jellyfish populations (Purcell et al. 2007). *P. noctiluca* has been identified as prey of a number of apex Mediterranean predators, including tuna, swordfish, sunfish, and loggerhead turtles (Cardona et al. 2012). If stocks of these predators were not depleted, they could potentially control the abundance of gelatinous zooplankton across the Mediterranean (Cardona et al. 2012).

11.5 *Pelagia noctiluca* Along the Catalan Coast (NW Mediterranean)

11.5.1 The Medusa Project

In 2007, the Catalan Water Agency (ACA, Agència Catalana de l'Aigua), in collaboration with the Marine Science Institute of Barcelona (ICM-CSIC), underwrote the "Medusa Project," which constituted a network of organizations that contribute information about jellyfish observations. The aim of the Medusa Project was to monitor the presence of jellyfish along the entire Catalan coast. The ACA recorded the presence of jellyfish daily at more than 240 beaches, covering the 69 Municipalities of Catalonia during the summer season. Inspectors recorded the presence of stranded jellyfish on beaches, in nearshore water, and at 200 m offshore by means of a boat. The project also involves participation of Emergency Services from 26 Municipalities

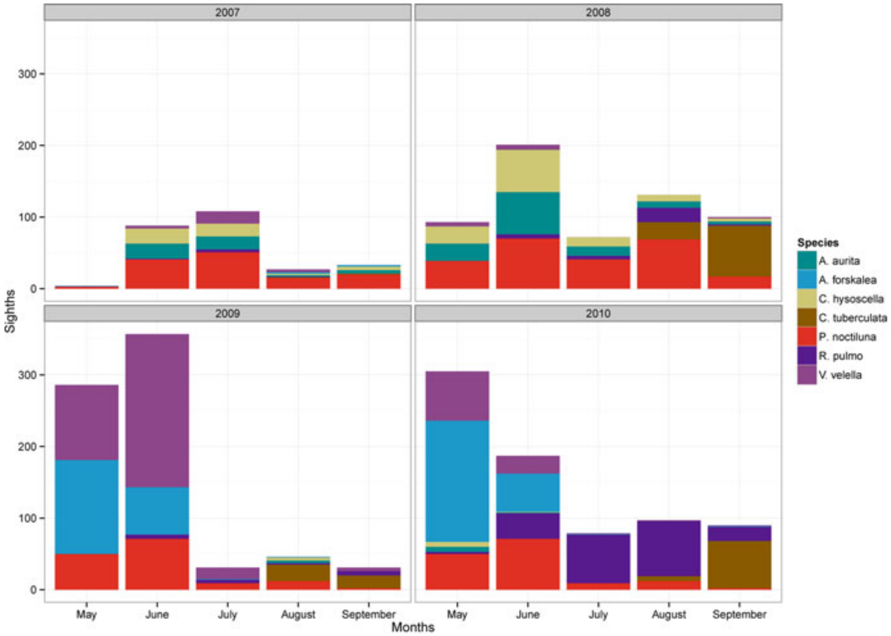

Fig. 11.3 Temporal variability of conspicuous jellyfish species stranded along the Catalan coasts, for the period 2007–2010. *Pelagia noctiluca* is shown in *red* at the base of the bars

and the Fisherman Associations of Catalonia, which report the presence of jellyfish daily. All of the information is summarized on the ACA web page (http://www.gencat.cat/aca/). Technical descriptions of the results and conclusions are presented in Gili et al. (2010).

11.5.2 *Preliminary Results on Spatiotemporal Variability of* **Pelagia noctiluca**

Data on stranded *Pelagia noctiluca* at 243 beaches along the Catalan coast were collected by beach inspectors daily from May to September, 2007–2010. Stranding records were grouped into three abundance categories: **"1"**< 10 medusae per beach (85 % of the reports), **"2"**< 1 medusa m^{-2} (12%), and **"3"**> 1 medusa m^{-2} (only 3.3 %). This last category is recognized as a "bloom" situation. Spatiotemporal variability is presented as the number of reports of stranded *P. noctiluca* medusae along the coast.

Six species of jellyfish were frequently observed on Catalan beaches (Fig. 11.3). Characteristic species observed during spring (May and June) were *Chrysaora hysoscella*, *Aurelia aurita*, *Aequorea forskalea*, and *Velella velella*. Interestingly, in 2007 and 2008, spring records were dominated by *C. hysoscella* and *A. aurita*, but in 2009 and 2010 the hydrozoans *A. forskalea* and *V. velella* were most commonly observed. The summer season (July and August) was characterized by the overlap of some

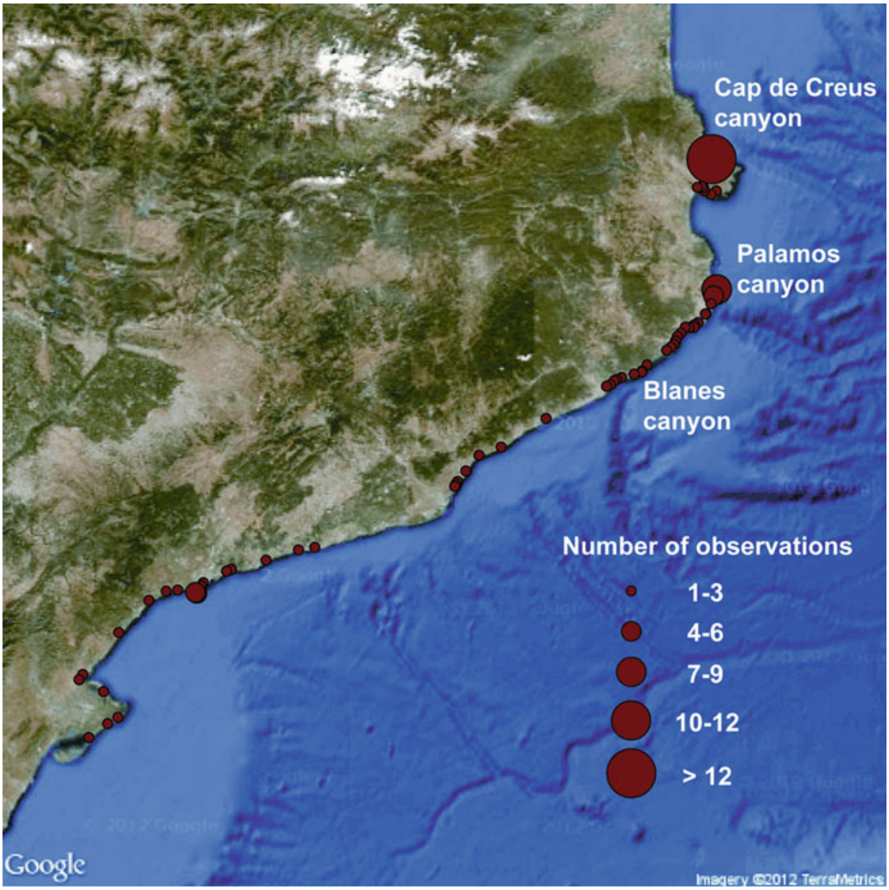

Fig. 11.4 Observations of stranded individuals of *Pelagia noctiluca* along the Catalan coast. Data represents mean annual values (2007–2010)

individuals of the spring species with the scyphozoan *Rhizostoma pulmo*, whose occurrence seemed to increase over time, especially in 2011 and 2012 (Fuentes et al. 2011). Finally, in late summer (September), the scyphozoan *Cotylorhiza tuberculata* appears. Stranded individuals of *Pelagia noctiluca* appear throughout the sampling period (May–September). In 2007, 2009, and 2010, stranded *P. noctiluca* were more abundant during June and July, with fewer reports during August, and September 2008 was an unusual year with high numbers of strandings for the entire study period. Even though the life cycle of *P. noctiluca* could lead to it occurring throughout the year, a clear pattern occurred in the stranded individuals, with the most strandings occurring during the spring-summer seasons, which may reflect its response to spring warming, increasing production, and local wind patterns.

Stranded *P. noctiluca* are widespread along the Catalan coast, but the highest concentrations of observations are along the northern Catalan coast every year (Fig. 11.4). Stranded jellyfish appear to occur most frequently on beaches close to marine canyons, particularly “Palamós” and “Cap de Creus” canyons. The association

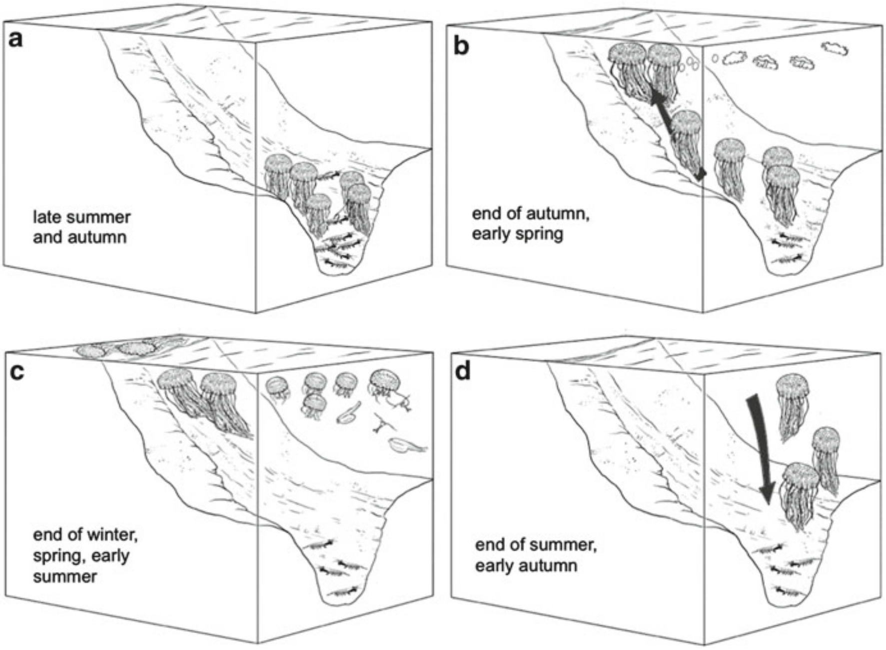

Fig. 11.5 (**a**–**d**) Hypothesis for seasonal vertical migration of *Pelagia noctiluca*. (**a**) Jellyfish overcome the warmer months at colder, mid-water levels; (**b**) by mid-autumn or early winter, jellyfish migrate upward for sexual reproduction; (**c**) throughout spring to early summer, at shallow levels jellyfish feed on the seasonal spring plankton bloom, with rapid somatic growth; (**d**) by the end of summer, jellyfish migrate downward to escape shortage of plankton food and warmer temperatures (Art: Alberto Gennari, concepts: Ferdinando Boero)

between stranding events and proximity to marine canyons along the Catalan coast is corroborated by similar findings along the Italian coasts. Analysis of data from a citizen science program from 2009 to 2012 (*Occhio alla Medusa*, F Boero unpublished data) and from experimental sampling campaigns in the Ionian, Tyrrhenian, and Ligurian seas revealed coastal outbreaks of *P. noctiluca* recurring in the proximity of canyons and upwelling areas, such as the Strait of Messina (NE Sicily) (Rosa et al. 2013). Marine canyons are known as "superhighways" because of the high-speed circulation of water masses, sediments, and organisms during active or passive movements from shallow to deeper waters and vice versa (Palanques et al. 2005; Würtz 2012). *P. noctiluca* is a mid-water jellyfish, and its life cycle may incorporate extensive vertical migration. Indeed, canyons may act as circulation pumps favoring the seasonal zonation of *P. noctiluca* from mid-water levels to surface waters and vice versa (Fig. 11.5). In summer, warm temperatures and the reduction of zooplankton prey make surface waters unfavorable to *P. noctiluca*, and records of *P. noctiluca* along shorelines become increasingly rare. Boero (in Sacchetti 2012) hypothesized that, during summer, jellyfish migrate down to cooler mid-water depths, possibly along canyon corridors (Fig. 11.5a).

Fig. 11.6 Formation of individual pairs during *Pelagia noctiluca* swarms: a behavior to enhance the success of sexual reproduction (Photo: Alejandro Olariaga. Galicia, Spain, summer 2010)

Mid-waters may also provide alternative, abundant crustacean resources (e.g., euphausiid shrimps) to *P. noctiluca*. Thus, this jellyfish may spend the warmer months at deeper habitats along the continental slope with abundant food sources and invest more energy towards future sexual reproduction by germ cell differentiation and gonad maturation (Fig. 11.5b). After surface waters have cooled by the late autumn or early winter, massive outbreaks of *P. noctiluca* occur at localities along the coastline nearest to the upper margins of marine canyons and upwelling areas, such as around the Aeolian Islands archipelago and the Strait of Messina, NE Sicily, the Island of Elba, Tuscany, and the continental platform of the Ligurian Sea. At this time of the year, large *P. noctiluca* can be found in surface waters even in daytime, where they also exhibit an uncommon swimming behavior, with frequent formation of couples (Fig. 11.6).

In late autumn-winter, outbreaks of *P. noctiluca* at the surface may be associated with sexual reproduction, leading to formation of a new cohort of planulae and ephyrae (Fig. 11.5c), followed by rapid somatic growth (Giacomo Milisenda, unpublished data). Indeed, swarms of juvenile jellyfish are encountered throughout winter. During the following months, the juvenile medusae will feed in surface waters on the spring zooplankton and ichthyoplankton (Fig. 11.5d). A new round of sexual reproduction may occur in late spring or early summer. Following the increase of sea surface temperatures and the formation of water mass stratification, *P. noctiluca* will leave the surface waters, starting a new annual migratory cycle (Fig. 11.5a).

11.5.3 Association with Physical Variables

Pelagia noctiluca medusae along the Catalonian coast are associated with particular oceanographic features. Sabatés et al. (2010) examined the role of a front associated with the shelf-slope in aggregating *P. noctiluca*. The front runs from north to south along the continental slope of the northwestern Mediterranean and reaches a depth of ~400 m. The increased primary and secondary productivity in the frontal area could contribute to the high abundances reported for *P. noctiluca* in the region. Jellyfish and other plankton also could be concentrated in the convergence associated with the front (e.g., Graham et al. 2001). Oceanographic conditions associated with the variability of this front were analyzed by Rubio and Muñoz (1997), who developed the first predictive model from physical variables for the arrival of *P. noctiluca* to the coastline of Barcelona. Their model indicated that the following conditions lead to a coastal bloom of *P. noctiluca*. First, if there is little or no rain at the beginning of winter and high solar radiation maximizes primary productivity in offshore waters of the Catalan Sea, an "offshore bloom" of *P. noctiluca* occurs at the front. If the wind fetch is perpendicular to the coastline of Barcelona during the early spring, the first individuals arrive at the coast at the beginning of April. High temperature and low precipitation at the start of summer then provide the ideal conditions for maximum dispersion, because the front is weak and allows transport of the accumulated medusae to the coastal area. These conditions thus cause a "coastal bloom" of *P. noctiluca* (Fig. 11.7) (Rubio and Muñoz 1997). Once the medusae reach the coast, their fate depends on other variables, such as the availability of zooplankton that will allow *P. noctiluca* medusae to increase its survival. Finally, wind and surface currents distribute the individuals to the shore. Thus, the study of stranded jellyfish is important to elucidate patterns of seasonality and population dynamics of jellyfish species (Houghton et al. 2007).

The association between jellyfish strandings and the prevailing wind direction and speed were analyzed from May to September, 2007–2010. Weekly averages of the number of strandings recorded were calculated to elucidate any quantitative pattern. Wind direction and velocity data were obtained from the meteorological service of Catalonia (http://www.meteo.cat). The meteorological stations were often located away from the beaches surveyed for stranding events. To correct for this, different portions of the coast were integrated to match the wind data resolution. This step was critical because coastlines that have different orientations and morphologies will be affected differently by any given wind direction. The relationship between stranded jellyfish and wind direction was analyzed using Generalized Additive Models (GAMs). Results showed a general pattern of stranding events associated with southerly winds. Low stranding category "1" and "2" showed a flattened kernel density distribution associated with winds (Fig. 11.8a upper and central panel). The first general pattern shown by the kernel density function was that more stranding events coincided with wind directions between 100° and 250° (east southeast to west southwest); the second, less obvious group of observations

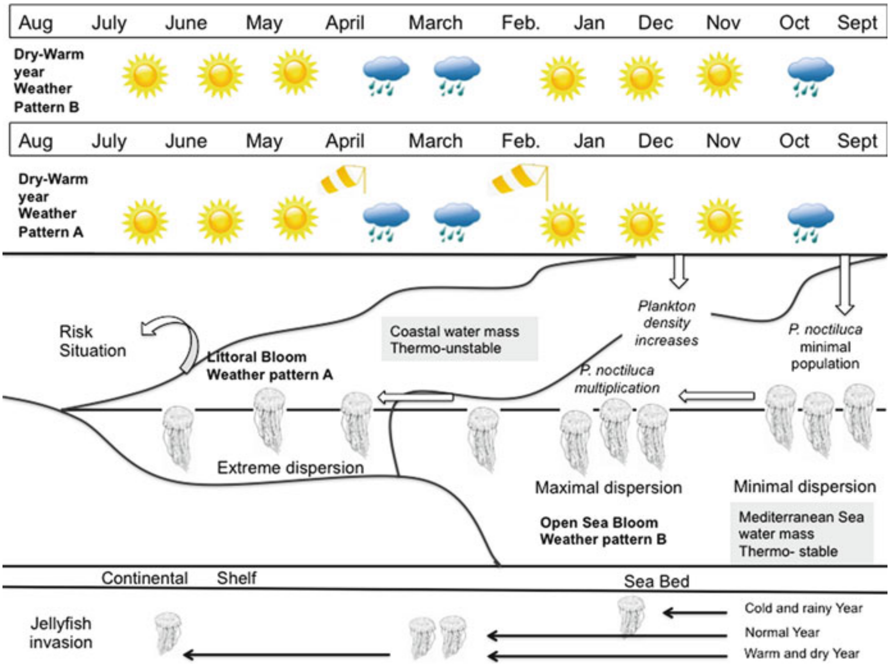

Fig. 11.7 Scheme of the proposed model by Rubio and Muñoz (1997), showing the different conditions leading a coastal bloom of *Pelagia noctiluca* (see text for interpretation)

coincide with northerly winds (0°–20°). For the jellyfish bloom category "3," more stranding events were only associated with southeast to south southwest (140°–200°) winds as seen from the kernel density distribution (Fig. 11.8a). In this category there were fewer observations because such large stranding events happened only occasionally (3.3 % of all records).

Weekly stranding events also revealed the variability in the association with southeastern winds (Fig. 11.9); the different magnitude axis on each circular plot illustrates the temporal variation of the stranding events. For all years, weeks with low abundances of jellyfish had a wider spread of wind direction (Fig. 11.9). Conversely, high weekly average abundances of jellyfish and blooms were particularly restricted to the southeastern winds.

The association between jellyfish strandings and wind speed needs to be interpreted with care, because jellyfish also can be "washed ashore" by waves generated by strong winds. Figure 11.8b shows the relationship between the stranding events according to abundance categories and wind speed. For all categories, stranding events increased with slow winds up to five knots, and then stranding events decreased at higher wind velocities.

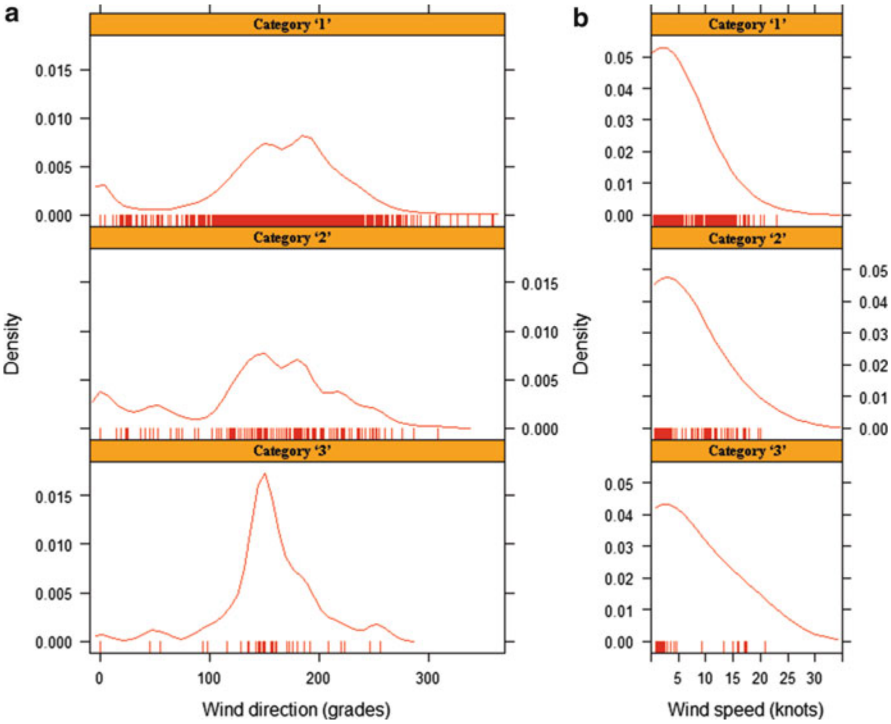

Fig. 11.8 (**a**–**b**) Relationship between stranded jellyfish species along the Catalonian coast with (**a**) wind direction and (**b**) speed. *Vertical lines* above the x-axis represent the raw stranded data. *Continuous line* represents the kernel density function used to model the relationship between stranded individuals and environmental factors

In summary, jellyfish strandings are associated with southeastern winds, which, due to the coastal orientation, are winds that blow mostly shoreward and push the water and the jellyfish to the coast. Nevertheless, the arrival of medusae to the coast will be ultimately limited by their presence along the coastal waters of Catalonia.

11.5.4 Effects on Human Activities

Along the Catalan coast one of the most important economic activities is beach-associated tourism. Nearly four million people visit Catalonia and use its beaches every year. During the summer season, *Pelagia noctiluca*, *Rhizostoma pulmo*, *Olindias phosphorica*, and *Carybdea marsupialis* (in decreasing order of importance based on their abundance) are responsible for stings that require first aid attention. Reports of the number of people affected by jellyfish stings recorded by the Red Cross service have provided useful data to understand the temporal patterns

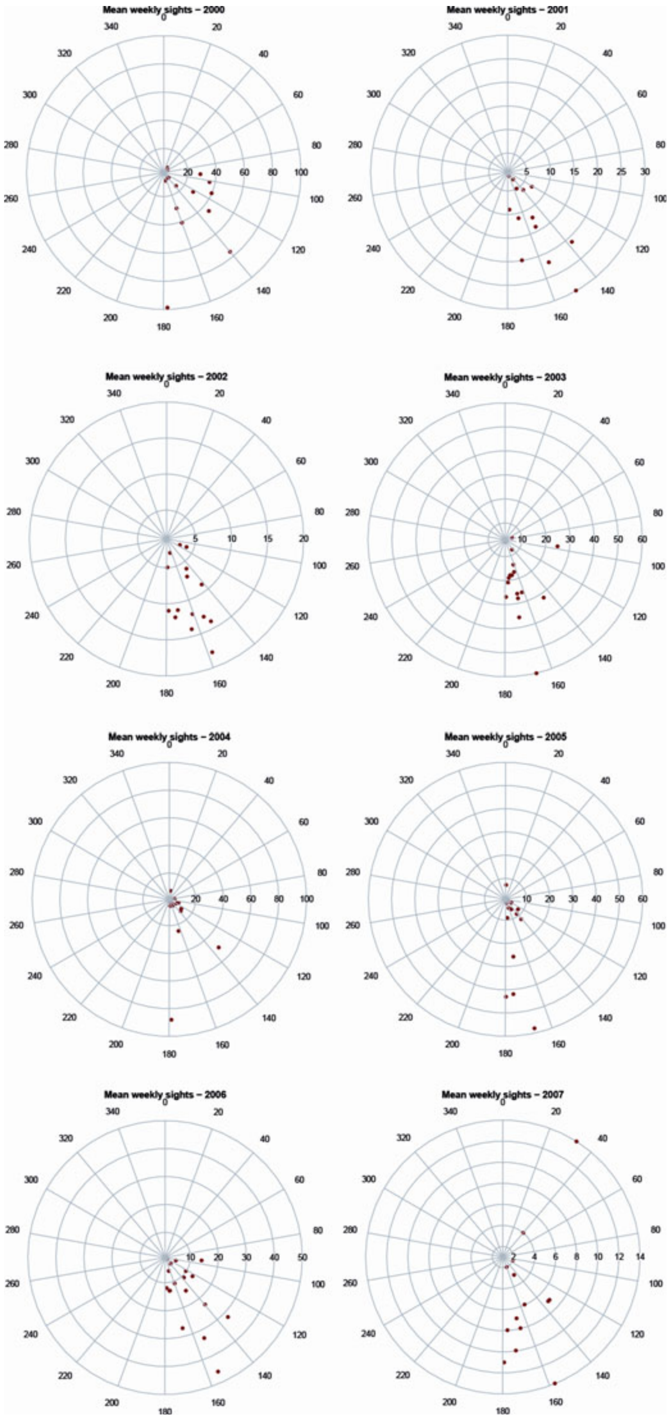

Fig. 11.9 Average weekly stranded jellyfish during May–Oct 2001–2007. *Degrees* represent compass directions, with north = 0°. Different magnitude scales in each year reflects differences in the total records

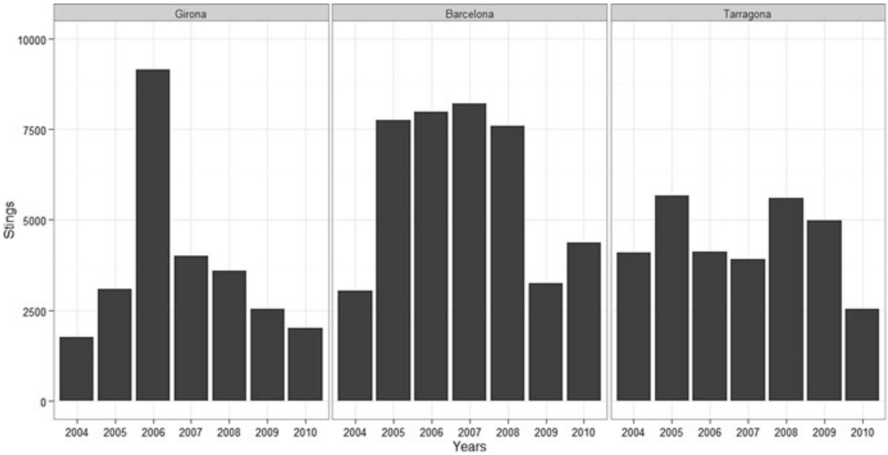

Fig. 11.10 Temporal distribution of people stung by jellyfish in the three provinces along the Catalan coast. Data showed the maximum number of assistances

and the magnitude of the stinging events. The information collected by the Red Cross for 2004–2010 was divided among the three provinces of Catalonia, from north to south: Girona, Barcelona, and Tarragona.

In the northern province of Girona, the number of people stung showed a strong peak during 2006, when 9,155 cases were registered (Fig. 11.10). The Barcelona province had a more extended peak, with an average of 7,880 cases recorded annually from 2005 to 2008 (Fig. 11.10). The southern province of Tarragona showed no clear pattern with two small peaks during the years 2005 and 2008 when 5,661 and 5,605 cases were registered, respectively (Fig. 11.10).

For the Catalan coast, jellyfish stings represent about 60% of all the requests for assistance from the Red Cross service. Reports of jellyfish stings included no information about the species responsible, and bathers usually do not know which species have stung them. Identification of the species that has stung a patient is very difficult and can be achieved only for a few species and within a few minutes of the patient being stung (Mariottini et al. 2008). Thus, to try to determine which species of jellyfish was responsible for most stings, in Barcelona province we correlated abundances of each species of jellyfish (as reported by the ACA beach inspectors) with the numbers of stings (as reported by the Red Cross). Among all recorded stinging jellyfish species, *P. noctiluca* was the only species with a significant correlation between abundance and first aid attention (Fig. 11.11).

The Medusa Project in Catalonia is an attempt to understand the spatiotemporal dynamics of the jellyfish populations along the Catalan coast. With a high temporal and spatial coverage, this project is a useful tool for elucidating answers to many of the questions surrounding jellyfish. *Pelagia noctiluca* is the most important jellyfish

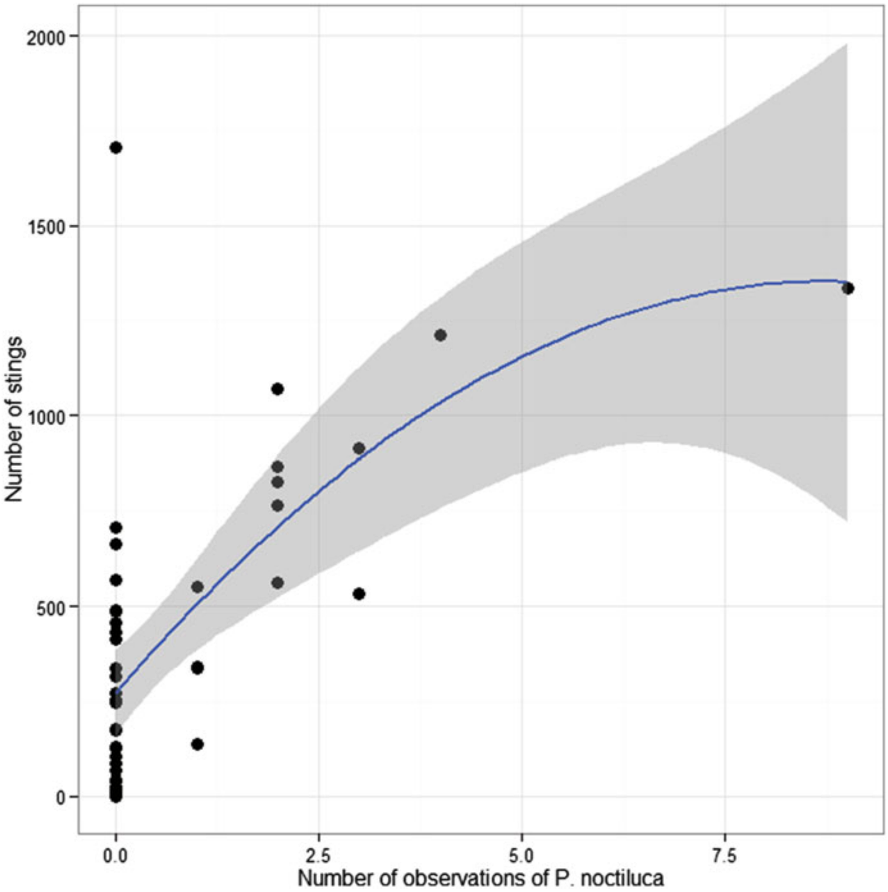

Fig. 11.11 Relationship between number of stings and strandings of *Pelagia noctiluca* along the coast of Barcelona (Catalonia)

species due to its distribution, abundance, and ecological role and also because it is the main species responsible for the negative interaction with humans. Finally, we recommend that similar efforts should be undertaken elsewhere to expand our knowledge about blooming patterns of dangerous jellyfish species.

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Chapter 12
The Ecology of Box Jellyfishes (Cubozoa)

Michael J. Kingsford and Christopher J. Mooney

Abstract The Cubozoa are poorly known compared to their scyphozoan relatives. This has partly been due to a limited knowledge of taxonomy, the rarity of some taxa as well as extreme temporal and spatial variation in abundance of medusae. The latter may reflect the small spatial scales of many populations. Although cubozoan medusae vary greatly in size, they are all excellent swimmers and have strong orientation behaviour. This, combined with resting on the bottom for extended periods of the day in some taxa (e.g. *Copula sivickisi*), suggests that dispersal may be limited. Despite this, some taxa, such as *Tripedalia cystophora*, have broad pantropical distributions suggesting a successful phenotype and a long geologic history. Statoliths allow medusae to be aged and provide unique opportunities to obtain accurate estimates of growth and to test ecological hypotheses. The life histories of few taxa have been studied, and until recently only the life cycle of *Tripedalia cystophora* had been fully described. The ability to rear species is critical for experimentation. Further, knowledge of the ecology of cubozoans is important for understanding population dynamics and predicting risk to swimmers and prey. With the exception of worldwide occurrences, population units have not been determined using well-known tools such as comparative morphology, genetics and elemental chemistry, and this is overdue. New technology is offering exciting ways to study these elusive creatures. This, combined with experimentation, will provide a better understanding of the physical and biological factors influencing the distribution and abundance of cubozoans within and among populations, both now and under climate change.

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Keywords Cubozoa • Irukandji • Carybdeids • Chirodropids • Life histories • Population dynamics • Statoliths • Age of jellyfish • Cubomedusae eyes • Predatory impact • Climate warming • Ocean acidification

12.1 Introduction

There has been great interest in the Cubozoa for their unique characteristics such as the complex eyes (e.g. Coates and Theobald 2003; Nilsson et al. 2005), powerful venom (Chung et al. 2001; Kintner et al. 2005), and strong swimming and orientation behaviour (Gordon and Seymour 2009; Garm et al. 2012). However, the basic biology and fundamental demographic parameters required for population studies are poorly described for most of the known 40–50 species of recorded cubozoans; 41 of which are considered true species. Since 2002, 5–12 papers have been published per year on the Cubozoa, and few of these are on ecology (Web of Science ISI). By necessity a primary focus has been on taxonomy (Bentlage et al. 2010), and a major impediment to progress on obtaining ecological data has been the rarity of many taxa and short-term availability due to great variation in abundance of medusae both temporally and spatially (Kingsford et al. 2012).

A major driver for greater knowledge of cubozoans has been to reduce risk from highly toxic species such the 'Irukandji' jellyfishes (9–10 species) and *Chironex fleckeri* ('Stingers') to swimmers and other users of the marine environment. On the Great Barrier Reef, cubozoans are considered one of the greatest threats to tourism (Association of Marine Park and Tourist operators; AMPTO). In other parts of the world, stinging jellyfishes are also a threat to major tourism trades (Fenner and Lippmann 2009). For accurate risk assessment, information is required on identification, seasonality, spatial patterns, the source of medusae and physical factors that have a major influence on abundance are critical.

Although we have some knowledge of cubozoan life histories (e.g. Straehler-Pohl and Jarms 2011), detailed descriptions are not available for most taxa. In contrast to their scyphozoan relatives (Arai 1997; Kingsford et al. 2000; Brodeur et al. 2002; Lynam et al. 2006), critical information on temporal and spatial variation in abundance, reproductive output, larval distribution, age, growth, recruitment, mortality and the influence of physical forcing on population dynamics are rare for cubozoans. We have only found two papers that have quantitative data on abundance (Bordehore et al. 2011; Kingsford et al. 2012). Some studies have used envenomation of swimmers as a proxy for abundance (Thomas et al. 2001) or back calculation of dates of metamorphosis based on daily rings in statoliths (Gordon and Seymour 2012). As for many species, valuable data are hidden in grey literature, including books from small publishing enterprises (e.g. Brown 1973).

Critical to understanding temporal and spatial variation in abundance is the determination of how populations are structured. A spatial articulation of population units (e.g. Hastings and Harrison 1994) is a useful construct to review what we know about cubozoan ecology (Fig. 12.1). At small spatial scales, box jellyfishes

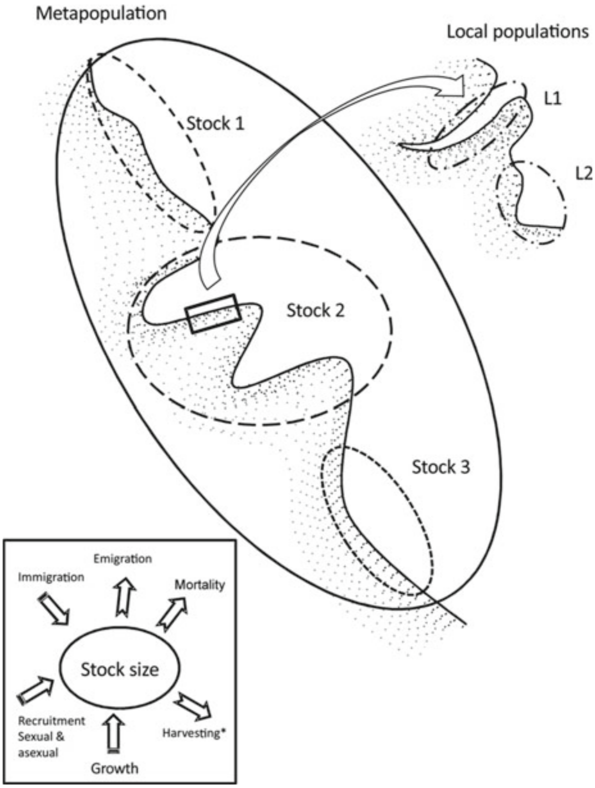

Fig. 12.1 A diagrammatic representation of the nested nature of population units. For example, local populations metres to kilometres; stocks 10s of kilometres to hundreds of kilometres; mesopopulation, hundreds to thousands of kilometres. *L1* local population 1, *L2* local population 2 (Adapted from Hastings and Harrison 1994; Kingsford and Battershill 1998). The *line* represents an idealised coastline. The *inset* represents the gains and losses from a stock; recruitment can be from asexual benthic products and sexual products from medusae. The stock size can be measured as number of animals or more typically for fisheries as weight. *Unlikely for cubozoans

may be found along a beach or in a bay ('local population'), and there could be considerable exchange among local populations that extend along a stretch of coastline; for example, around an island or some other geographic entity. At some spatial scales immigration from, and emigration to, a group of local populations will be minimal, and this equals a 'mesopopulation' or in fisheries terms a 'stock'. Ideally, a stock is a self-contained unit where reproductive output, recruitment and growth determine population size (Sinclair 1988). A 'metapopulation' is a collection of mesopopulations, and this often corresponds to the biogeographic range of a species.

The objective of this chapter is to review what is known about the ecology of cubozoans and provide some focus to resolve the gaps in our knowledge. Our approach is to summarise all that is known about the global distributions of cubozoans so that hot spots of cubozoan diversity can be identified and mesopopulations predicted. The morphology of jellyfish is briefly described as this gives some insight to the biomechanics of cubozoans that influence local distributions, orientation, movements and predator prey interactions. Reproduction, life history, age and growth are covered as key components of population ecology. Spatial and temporal variations in distribution patterns are reviewed, and the methods that have been used to elucidate them are also covered. Physical forcing affects many marine populations, and cubozoans, especially those that are near shore, are likely to be affected by riverine runoff (Grimes and Kingsford 1996), temperature and changing currents. This is well known for scyphozoans (e.g. Lu et al. 1989; Purcell et al. 1999), and recent data suggest this is also likely for cubozoans. Cubozoans are strong swimmers, and recent data from tagged individuals has revealed complex behaviour and movement from hundreds of metres to kilometres within a day (Gordon and Seymour 2009). Potential impacts on prey are discussed, and finally we address concerns about the likely responses of cubozoan populations to a warming planet, low pH seas and increasing regions of ocean that are anoxic (Brierley and Kingsford 2009).

12.2 Taxonomy, Morphology and Occurrence

Cubozoans are a class within the phylum Cnidaria. Several characteristics set cubomedusae apart from all other jellyfishes (Fig. 12.2). They have a distinctively cuboidal bell, for which they are named. All Cubozoa possess four rhopalia (one on every side of the bell; each of which has up to six eyes) connected via a nerve ring and pedalium from each corner of the bell from which contractile tentacles hang. All box jellyfishes are grouped into two orders, the Carybdeida and Chirodropida, based largely on their gross morphology. Carybdeids typically have only a single tentacle per pedalium. Further, they have nematocysts present both on their tentacles and on their bell. In contrast, chirodropids have multiple tentacles per pedalium (some species have up to 15 tentacles per pedalium); each tentacle can extend up to 3 m (e.g. *Chironex fleckeri*; Kinsey 1986), and nematocysts are usually only found on their tentacles. Due to the gelatinous nature and rarity of cubomedusae, the taxonomy of this class is regularly updated (Gershwin 2005a; Bentlage et al. 2010). According to the World Register of Marine Species (WoRMS; Appeltans et al. 2012), there are currently 41 accepted species of Cubozoa, 31 carybdeids and 10 chirodropids (Table 12.1); this total is expected to increase.

Cubozoans are primarily tropical jellyfishes with few species found outside of tropical latitudes (including ‘accepted’ and ‘not accepted’ species). However, a few taxa have been recorded at higher latitudes, to 42°N and 42°S (Table 12.1; Fig. 12.3). The highest diversity of species is found in the high biodiversity region of the Indo-West Pacific (12 accepted species) and Coral Sea (10 accepted species). Several species have been documented from the Philippine Sea (6), Caribbean Sea (6), Gulf of Mexico (4) and both the east (4) and west (4) boundaries of the Atlantic Ocean. Cubozoans are not only restricted to continental coastlines; they have also been

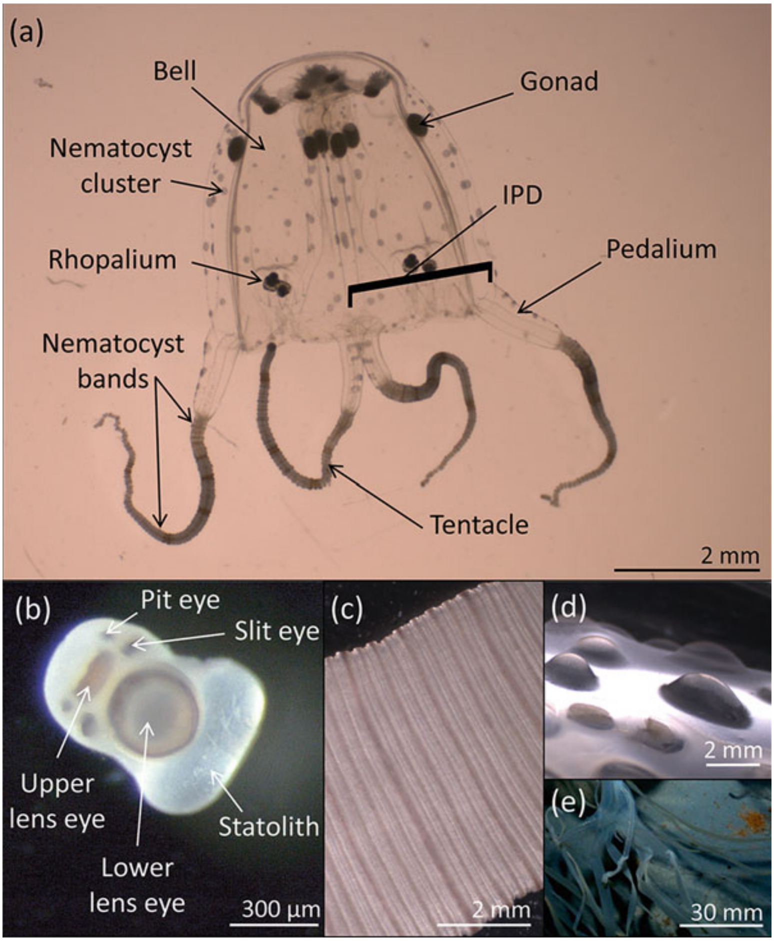

Fig. 12.2 Cubozoan morphology; (**a**) gross morphology of carybdeid *Copula sivickisi* medusa, (**b**) *Chironex fleckeri* rhopalium (preserved in ethanol), (**c**) nematocyst banding on tentacle of *Morbakka* sp., (**d**) nematocyst clusters/bell warts on exumbrella of bell of *Morbakka* sp., and (**e**) multiple tentacles per pedalium of chirodropid *Chironex fleckeri*

found in waters of islands, some isolated by nearly 4,000 km of oceanic waters, including Hawaii (4 species), Samoa (1), Society Islands (1) and New Zealand (1) in the Pacific basin as well as Bermuda (1) and Saint Helena (1) in the Atlantic basin. Box jellyfishes, therefore, are almost pantropical in distribution.

The distributions of most species appear to be somewhat localised (Table 12.1). For example, *Carybdea arborifera* is only found in Hawaii, and *Chirodropus palmatus* is only found in Saint Helena. A few species, however, have widespread distributions. Both *Carybdea rastonii* and *Copula sivickisi* are found throughout the Pacific Ocean (Table 12.1), and this suggests a long geologic history as well as good

Table 12.1 Accepted cubomedusae according to WoRMS (Appeltans et al. 2012), distribution, maximum latitude, recognition as pest and bell height

Order	Species	Description	Alternate representation	Countries/ regions	Maximum latitude (° from equator)	Recognised pest	BH (cm)	Reference
Carybdeida	*Alatina alata*	Reynaud (1830)	*Carybdea alata*	Red Sea, South Atlantic, North Carolina (USA)	35°N, 30°S	Y	25	Gershwin (2005a), Calder (2009)
	Alatina grandis	Agassiz and Mayer (1902)		Society Islands (Pacific Ocean)	17°S		23	Gershwin (2005a)
	Alatina madraspatana	Menon (1930)		North Indian Ocean (Madras)	13°N		11	Gershwin (2005a)
	Alatina moseri	Mayer (1906)	*Alatina mordens*	Hawaii, Osprey Reef, GBR	20°N, 17°S	Y	10	Chung et al. (2001) – As *Carybdea alata;* Bentlage et al. (2010)
	Alatina pyramis	Haeckel (1880)		West Indies	20°N		3	Kramp (1961), Gershwin (2005a)
	Alatina rainensis	Gershwin (2005a)		GBR (Australia)	11°S		16	Gershwin (2005a)
	Alatina tetraptera	Haeckel (1880)		?			3	Gershwin (2005a)
	Manokia stiasnyi	Bigelow (1938)	*Carybdea stiasnyi*	Indonesia	1°S		2	Gershwin (2005a)
	Carukia barnesi	Southcott (1967)		QLD (Australia), Indo-Pacific	20°S	Y	3.5	Underwood and Seymour (2007)
	Carukia shinju	Gershwin (2005b)		WA-80 mile beach (Australia)	19°S	Y	2	Gershwin (2005b)
	Gerongia rifkinae	Gershwin and Alderslade (2005)		NT/QLD-Gulf of Carpentaria (Australia)	17°S	Y	6	Gershwin and Alderslade (2005)
	Malo filipina	Bentlage and Lewis (2012)		Philippines	14°N		4	Bentlage and Lewis (2012)
	Malo kingi	Gershwin (2007)		QLD (Australia)	21°S	Y	3	Gershwin (2007)

Malo maxima	Gershwin (2005b)		WA (Australia)	19°S	Y	5	Gershwin (2005b)
Morbakka fenneri	Gershwin (2008)		NSW/QLD (Australia)	34°S	Y	15	Gershwin (2008)
Morbakka virulenta	Kishinouye (1910)	*Tamoya virulenta*	Japan	35°N			Kramp (1961)
Carybdea alata var. Grandis	Reynaud (1830)		Gulf of Mexico, Guam	29°N		20	Gershwin (2003), Segura-Puertas et al. (2009)
Carybdea arborifera	Maas (1897)		Hawaii	20°N			Bentlage et al. (2010)
Carybdea branchi	Gershwin and Gibbons (2009)		South Africa	34°S	Y	8	Gershwin and Gibbons (2009)
Carybdea brevipedalia	Kishinouye (1891)		Japan	35°N			Bentlage et al. (2010)
Carybdea marsupialis	Linnaeus (1758)		Mediterranean	42°N	Y	6	Bordehore et al. (2011)
Carybdea morandinii	Straehler-Pohl and Jarms (2011)		(Polyps from German Zoo to Laboratory)- thought to originate from somewhere in East Asia				Straehler-Pohl and Jarms (2011)
Carybdea murrayana	Haeckel (1880)		West Africa	0°		6	Gershwin and Gibbons (2009)
Carybdea rastonii	Haacke (1886)		SA/TAS/NSW (Australia), Japan, California (USA), Hawaii, Philippines, Pacific Ocean, Taiwan, Guam	37°N, 42°S	Y(Japan, Aus(SA))	6	Matsumoto (1995), Nagai et al. (2000), Edgar (2008)

(continued)

Table 12.1 (continued)

Order	Species	Description	Alternate representation	Countries/ regions	Maximum latitude (° from equator)	Recognised pest	BH (cm)	Reference
	Carybdea xaymacana	Conant (1897)		WA/QLD (Australia), Panama, Central Indo-Pacific, Jamaica, Bermuda, Gulf of Mexico, Tropical waters of West Atlantic, Caribbean Sea, California (USA)	32°N, 32°S	Y	4	Larson (1990), Kramp (1961), Bailey et al. (2005)
	Tamoya gargantua	Haeckel (1880)		Indo-West Pacific, Samoa Islands, Indonesia	14°S		22	Kramp (1961)
	Tamoya haplonema	Müller (1859)		The Netherlands Antilles, Gulf of Mexico, Long Island (USA), Brazil, West Africa, Argentina	41°N, 39°S	Y	9	Pastorino (2001), Segura-Puertas et al. (2009)
	Tamoya ohboya	Collins et al. (2011)		The Netherlands Antilles, Lesser Antilles, Honduras, Mexico	12°N	Y	6	Collins et al. (2011)
	Copula sivickisi	Stiasny (1926)	*Carybdea sivickisi*	QLD (Australia), Japan, New Zealand, Guam, Hawaii, Philippines, Vietnam, Thailand	36°N, 40°S		1	Hartwick (1991b), Matsumoto et al. (2002)
	Tripedalia binata	Moore (1988)		NT (Australia), India	20°N, 12°S		1	Moore (1988)
	Tripedalia cystophora	Conant (1897)		Indonesia, Caribbean Sea, Brazil, Florida (USA)	26°N, 3°S		1	Orellana and Collins (2011)

Chirodropida	*Chirodectes maculatus*	Cornelius et al. (2005)		GBR (Australia)	16°S		15	Cornelius et al. (2005)
	Chirodropus gorilla	Haeckel (1880)		Ghana, W Africa, South Africa	5°N, 31°S		15	Kramp (1961)
	Chirodropus palmatus	Haeckel (1880)		Saint Helena	15°S		10	Kramp (1961)
	Chironex fleckeri	Southcott (1956)		WA/NT/QLD (Australia), Indonesia, PNG	24°S	Y(fatal)	32.5	Kinsey (1986), Coughlan et al. (2006)
	Chironex yamaguchii	Lewis and Bentlage (2009)		Japan, Philippines	27°N	Y(fatal)	11	Lewis and Bentlage (2009)
	Chiropsalmus alipes	Gershwin (2006)		West coast Mexico	17°N		11.5	Gershwin (2006)
	Chiropsalmus quadrumanus	Müller (1859)	*Tamoya quadrumanus*	Gulf of Mexico, North Carolina (USA), Brazil	35°N, 23°S	Y(fatal)	10	Calder and Peters (1975), Segura-Puertas et al. (2009)
	Chiropsella bart	Gershwin and Alderslade (2006)		NT (Australia)	12°S		5	Gershwin and Alderslade (2006)
	Chiropsella bronzie	Gershwin (2006)		QLD (Australia)	19°S		10.5	Carrette et al. (2002), Gershwin (2006)
	Chiropsoides buitendijki	Horst (1907)	*Chiropsalmus buitendijki*	Indonesia, Sri Lanka, Malaysia, India, Pakistan	25°N		7	Tahera and Kazmi (2006), Bentlage et al. (2009)
***Nomen dubium*/species inquirenda/unaccepted**								
	Alatina obeliscus	Haeckel (1880)						
	Alatina philippina	Haeckel (1880)						
	Alatina turricula	Haeckel (1880)						
	Carybdea aurifera	Mayer (1900)						

(continued)

Table 12.1 (continued)

Order	Species	Description	Alternate representation	Countries/ regions	Maximum latitude (° from equator)	Recognised pest	BH (cm)	Reference
	Carybdea latigenitalia	Kishinouye (1891)						
	Carybdea mora	Kishinouye (1910)	Accepted as *Carybdea brevipedalia*					
	Tamoya bursaria	Haeckel (1880)						
	Tamoya prismatica	Haeckel (1880)	Accepted as T*amoya haplonema*					
	Chiropsalmus quadrigatus	Haeckel (1880)	Accepted as *Chiropsoides quadrigatus*					
	Chiropsalmus zygonema	Haeckel (1880)						
	Chiropsoides quadrigatus	Haeckel (1880)						

GBR Great Barrier Reef, *NSW* New South Wales, *NT* Northern Territory, *PNG* Papua New Guinea, *QLD* Queensland, *SA* South Australia, *TAS* Tasmania, *WA* Western Australia

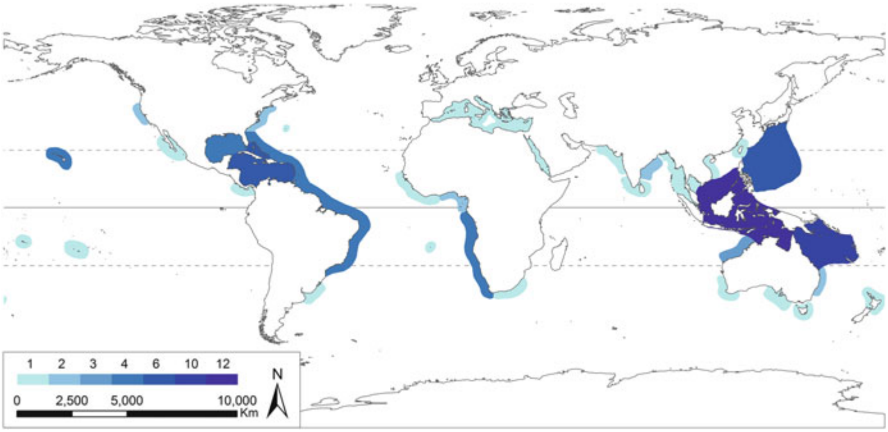

Fig. 12.3 Published occurrences of accepted cubozoan species around the world. *Colour* indicates number of accepted species for region. The width of regional patches is for presentation only; the majority of taxa were caught close to shore. For detail of species occurrence see Table 12.1

dispersal abilities. Although some taxa, such as *Carybdea marsupialis*, are recorded with worldwide distributions, the taxonomic robustness of these species has been questioned (Bentlage et al. 2010); it is however unlikely that taxa such as *Copula sivickisi* have been mistakenly identified. Despite taxonomic issues some carybdeids seem to be more widespread than chirodropids. Erroneous identification of chirodropids is unlikely as they are much larger and easier to identify.

12.3 Reproduction and Life History

Cubozoans have a polymorphic life history that is typical for many pelagic cnidarians. There are differences, however, particularly in the development of medusae from polyps. Rhizostome jellyfishes generally have monodisc polypoid strobila, while most of the semaeostomes release multiple ephyrae from each scyphistoma by transverse fission during the process of strobilation (Arai 1997). The scyphistoma regenerates during the last phase of strobilation. Cubozoan polyps, however, do not strobilate and, instead, polyps metamorphose completely into a single medusa (see generalised life history Fig. 12.4). Adult medusae are gonochoristic, and in some cases sexual dimorphism is obvious based on the shape of gonads (e.g. *Carybdea sivickisi*; Lewis and Long 2005, now *Copula sivickisi* Fig. 12.5, *Tripedalia cystophora*, Conant; Werner 1973, 1976). Although the complete life cycle has been described for only one species, a large proportion of the life histories have been described for several taxa (Werner et al. 1971; Cutress and Studebaker 1973; Arneson and Cutress 1976; Laska-Mehnert 1985; Stewart 1996; Stangl et al. 2002; Straehler-Pohl and Jarms 2005, 2011). As for other cnidarians, planulae must result from fertilised embryos. The planulae of many scyphozoans are brooded prior to

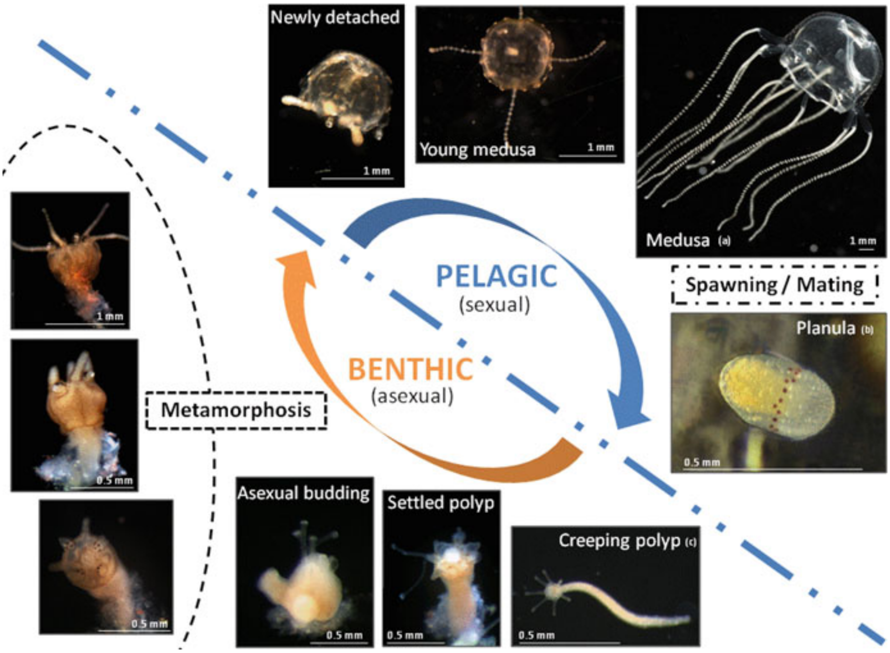

Fig. 12.4 Typified cubozoan life cycle showing sexual pelagic and asexual benthic phases, example of carybdeid *Tripedalia cystophora*. (**a**) *T. cystophora* medusa; Image: J. Bielecki, (**b**) *Copula sivickisi* planula (Image: D. Nilsson), and (**c**) *Carybdea* sp. Creeping polyp (Images: I. Straehler-Pohl) (except if otherwise noted)

Fig. 12.5 Sexual dimorphism of a mature carybdeid, *Copula sivickisi* – *left* three sexually mature females; *right* two sexually mature males. *GP* – gastric pockets, *G* – gonads

release, as found in scyphozoans such as *Aurelia* (Arai 1997); this is also found in cubozoan species such as *Tripedalia cystophora* (Conant 1898; Werner 1973; Stewart 1996), *Carybdea rastonii* (Okada 1927) and *Copula sivickisi*. Embryo strands have been reported in *Copula sivickisi* (Hartwick 1991a; Lewis and Long 2005), and the eggs in these probably develop into planulae before the embryo strands are released. Once a planula has settled, it transforms into a two- to three-tentacled, crawling primary polyp which stays mobile until a suitable substratum is found on which to settle and to grow into a multi-tentacled polyp.

Asexual budding is likely to be an important process in population expansion. Polyps bud creeping polyps (Fig. 12.4), a mobile phase to form new individuals (e.g. *Carybdea morandinii*, Straehler-Pohl and Jarms 2011) and which presumably is important for the choice of microhabitats to which late stage polyps can attach, so asexual reproduction is an important form of population expansion as for other cnidarians (Arai 1997). The process of budding was observed in detail in *Carybdea* sp. (formerly *Carybdea marsupialis* from Puerto Rico) by Fischer and Hofmann (2004). If conditions become unfavourable, polyps can contract into balls and become encapsulated in a layer of mucus which hardens to form a cyst. The cyst is, in the case of *Carybdea morandinii* (Straehler-Pohl and Jarms 2011) and *Carybdea* sp. (Straehler-Pohl 2001, 2009), capable of dispersing before reattaching and giving rise to the former polyp within a week.

The sequence of the metamorphosis of *Carybdea morandinii* from polyp to detached medusa is so comprehensive that the newly released medusa takes the base disk of the polyp with it (for detailed illustration, see Straehler-Pohl and Jarms 2011). The process of metamorphosis takes 3–7 days, and metamorphosis appears to depend on temperature and light in combination (varying water temperature and introducing potassium iodide had little effect); complete metamorphosis also occurs in *Tripedalia cystophora* (Werner et al. 1971; Laska-Mehnert 1985) and *Carybdea marsupialis* (Stangl et al. 2002; Straehler-Pohl and Jarms 2005). Once in the plankton, the medusae presumably grow quickly, but only the one study on *Tripedalia cystophora* (Werner 1973, 1976) reared medusae successfully to reproduction.

Reproduction has been observed in *Copula sivickisi* that were caught in the wild (Lewis and Long 2005; Lewis et al. 2008). Pairs of jellyfish were allowed to mate in the laboratory, and this took place shortly after males and females were put in the same container. As for *T. cystophora* (Werner 1973, 1976; Stewart 1996), mating involved the passing of a spermatophore. Lewis and Long (2005) found that *C. sivickisi* females accepted spermatophores from multiple males but only produced one strand of embryos.

Ecologically, a combination of benthic and pelagic forms of life history increases the complexity of understanding processes that influence population size (Kingsford et al. 2000). Key issues include understanding the cues (proximate factors) for metamorphosis of medusae from polyps and biological processes that influence survival (ultimate factors, *sensu* Giese and Pearse 1974). The distribution of benthic phases is also crucial and may have a strong role in determining the distribution and size of many population units. However, polyps have only been found twice in the wild – *Chironex* in Australia (Hartwick 1991b) and *C. marsupialis* in Puerto Rico (Cutress and Studebaker 1973).

12.4 Age and Growth

An understanding of age and growth is critical for population studies. An advantage that cubozoans have over scyphozoans (Sötje et al. 2011) for ecological studies is they have statoliths with clear sequential increments. Although the statoliths are made of calcium sulphate hemihydrate (bassanite; Tiemann et al. 2006), rather than the calcium carbonate (usually aragonite) of fish otoliths, they are analogous in function and utility. Fine increments were found in the statoliths of *Carybdea rastonii* (Ueno et al. 1995) and were inferred to be daily. Increments were subsequently used for estimates of growth, age, and age to maturity, based on the assumption that they were daily (e.g. *Chiropsella bronzie*, vice *Chiropsalmus* sp., Gordon et al. 2004). In this study it was concluded that medusae 3–71 mm BD grew up to 7 mm/week, and they reached sexual maturity in 70 days. Modal progression of age classes was used to validate the daily aging technique.

Daily rings were also assumed in a study on *Chironex fleckeri* by Gordon and Seymour (2012). They concluded that jellyfish were increasing their interpedalia distance (IPD; a common unit of measurement of size in cubozoans; Fig. 12.2) at about 3 mm d^{-1} and that the sexes could be differentiated at about 50 mm IPD and at ages of 45–50 days. Based on a Gompertz equation, asymptotic size was estimated to be 190 mm IPD after about 140 days, but the maximum age of any specimen collected was about 88 days and IPD of size of ~155 mm. As the use of the daily aging technique expands to multiple taxa, the field needs to carry out more validation experiments to conclusively determine that increments are deposited daily.

Other ecological questions that have been addressed with statoliths include testing for synchronisation of detachment post-metamorphosis by aging medusae (Ueno et al. 1995), determining temporal variation in the onset of the medusae season for *Chironex fleckeri* (Gordon and Seymour 2012) and measuring elemental changes in the use of different water masses from detachment in *C. fleckeri* (Mooney and Kingsford 2012). Information from statoliths and limited data on size versus time of year (Brown 1973) indicates that growth of jellyfish is rapid and they have the potential to bloom as for other types of medusae.

12.5 Sampling Cubozoans

Cubozoans have generally been sampled for taxonomic studies, and on rare occasions, quantitative estimates of abundance have been obtained. Techniques used to sample cubozoans have included the following: scoop buckets, dip-netting medusae that were observed from boats, towing nets or pushing nets, visual observations and quantitative counts in transects or using the photopositive response of cubozoans to collect them around lights or attract them to a digital camera system (Table 12.2). Problems that are encountered with sampling largely tropical cubozoans have included difficulty of detection because they are rare and, when present, are often most abundant in very shallow water. Near-shore waters have many obstacles, are often highly turbid and in some regions crocodiles and bull sharks can pose a risk to sampling.

Bordehore et al. (2011) used a hand net that was pushed over a fixed distance to obtain estimates of *Carybdea marsupialis* density in shallow water. The 30.9 × 30.9 cm net (5 mm mesh) was pushed over 100 m at depths that ranged from 0.5 to 1.2 m. A maximum mean density of 265.9 jellyfish per 100 m^2 was caught using this method. Beam trawls (1.5 m wide and 0.5 m deep, squeezed mesh 8 mm) were used by Kingsford et al. (2012) in shallow water. Sampling was stratified as shallow (<2 m) and deep (4–6 m) water to allow for potential movements of cubozoans with phase of the tide. To test a hypothesis that numbers of jellyfishes would be higher near estuaries, sampling was also done near to estuaries and a kilometre or more away from them at three sites. Despite high sampling effort, only two cubozoans were collected. Plankton nets have also been used to collect *Carybdea rastonii* (Lai 2010), *Copula sivickisi* (Lewis and Long 2005), *Tamoya haplonema* and *Chiropsalmus quadrumanus* (Kraeuter and Setzler 1975). Brown (1973) used plankton nets to collect very small *Chironex* that were difficult to observe by eye. Although nets have been used in other studies (e.g. Yamada et al. 2010), sampling details are few.

Surface transects can be used, as for Pitt and Kingsford (2000a) with the rhizostome *Catostylus mosaicus*. In this study the observer sat on the bow of a small boat, counted jellyfish to a depth of 1 m and used a pole to measure transect width. Transect length (500 m) was determined with GPS by travelling at a fixed speed. Kingsford (1993) towed a rope of a known length, past an object dropped in the water, to determine transect length. Surface transects can only be done accurately if sea conditions are carefully prescribed (i.e. define the minimum visibility and maximum chop in which counts are made).

Night lights are effective in attracting cubozoans, but this method is most effective in waters of low turbidity. In a 3-year study at multiple locations over the Great Barrier Reef, Kingsford et al. (2012) collected 263 cubozoans. Lights (1,000 W) were held just below the surface and were fished for a minimum of 1 h (and sometimes longer if extra specimens were being collected). From this study, and additional sampling that we have done, maximum catches of up to 50 medusae per hour have been collected using swimming pool nets. All sampling was done in waters from 3 to 15 m deep, and the most abundant taxa captured were *Carukia barnesi* and *Copula sivickisi.*

Visual counts while diving are possible, but come with risks in tropical waters. Brown (1973) used SCUBA to cover distances of several kilometres in shallow waters around Magnetic Island, North Queensland, to determine broad-scale patterns of abundance. In this case, the visibility would generally have exceeded a metre, but in tropical near-shore waters, the visibility is often less than 1 m.

Table 12.2 Examples of temporal variation in abundance, densities, methods of collection and habitat for accepted cubomedusae

Species	Season present	Country	Density	Method of collection	Habitat	Reference
Alatina moseri	Regularly observed on leeward Hawaiian beaches 8–10 d post full moon	Hawaii	ND	Shallow nets	ND	Chung et al. (2001)
	Large predictable spawning aggregations near Osprey Reef 8–10 d post full moon	Coral Sea	ND	ND	ND	Courtney (2010)
	Can be encountered any time of year	GBR	ND	ND	ND	Gershwin (2005a)
Carukia barnesi	ND	Australia	ND	Night lighting	Near granite islands	Kingsford et al. (2012)
Gerongia rifkinae	ND	Australia	ND	Dip netting at high tide	Mangrove vicinity	Gershwin and Alderslade (2005)
Malo kingi	Found throughout year in very low numbers, most commonly found washed up on beach late summer/early winter	Australia	ND	Trawling, night lighting	ND	Gershwin (2007)
Malo maxima	Collected May–July (common post cyclone)	Australia	ND	Night lighting	Offshore	Gershwin (2005b)
Carybdea alata var. Grandis	ND	Gulf of Mexico	ND	ND	Neritic, depth (0–20 m)	Segura-Puertas et al. (2009)

Carybdea marsupialis	All year round	Caribbean Sea	ND	ND	Bays, harbours and mangrove channels	Cutress and Studebaker (1973)
	Late summer/fall – into January	California, USA	Usually 1–2/9 m^2, reports of 30–50/m^3	ND	Shallow waters (~4 m) in nearshore part of kelp beds known as sand channels, sunny areas	Martin (2004)
	August–November	Spain	5.4 ± 3.8 ind/100 m^2 (end of September)/record highest abundances 0–265 ind/100 m^2	100 m transect with hand net (0.3 m^2) 5 cm off bottom 0.5–1.2 m depth	Shallow sandy beaches with gentle slope	Bordehore et al. (2011)
Carybdea rastonii	Late summer–early autumn	Japan	ND	ND	ND	Nagai et al. (2000)
	Peak during February–April, but can be found throughout the year in predictable locations	Australia	Patches of several 100, Marino Rocks population = 200–300 in 3.5 m (95 % initially observed within 1 m of bottom)	Individually in plastic jars	Sandy patches in shallow subtidal	Matsumoto (1995)
	October–November	California, USA	ND	ND	ND	Matsumoto (1995)
Tamoya haplonema	September–March and June	North Atlantic	1–2 medusae per collection	Trawl	Neritic, depth (0–21 m)	Calder (2009)
	Summer/fall	Brazil	ND	ND	ND	Nogueira et al. (2010)
	ND	Gulf of Mexico	ND	ND	Neritic, depth (0–85 m)	Segura-Puertas et al. (2009)

(continued)

Table 12.2 (continued)

Species	Season present	Country	Density	Method of collection	Habitat	Reference
Tamoya ohboya	Majority of sightings July–September, seen all months of year	Caribbean Sea	ND	ND	Shallow <10 m, near-shore waters	Collins et al. (2011)
Copula sivickisi	ND	Japan	ND	Scoop buckets	ND	Straehler-Pohl (2011)
Tripedalia binata	Collected March, April, June	Australia	ND	ND	Mangroves at high tide	Moore (1988)
Tripedalia cystophora	Summer months, seldom seen during late fall/winter months	Puerto Rico	ND	ND	Among mangrove roots but never in open mangrove channels, usually within 10 cm of surface during day	Coates et al. (2006), Stewart (1996)
Chirodectes maculatus	May (post cyclone)	GBR	One found	ND	Outer reef, within 5 m of surface	Cornelius et al. (2005)
Chironex fleckeri	Summer months (November–May)	Australia	ND	Trawling	Restricted to nearshore waters, estuarine areas, mainland beaches	Kingsford et al. (2012), Hartwick (1991a)
Chironex yamaguchii	Summer (July–September)	Japan	ND	ND	Sandy beaches	Lewis and Bentlage (2009)

Chiropsalmus quadrumanus	June–October	North Atlantic	1–7 medusae per collection	Dipnet, trawl	Neritic	Calder (2009)
	Summer/fall (appears late Spring, disappears end of summer) – July/August	Gulf of Mexico	ND	ND	Estuarine, neritic, depth (0–85 m), soft mud bottom barren of attached vegetation	Segura-Puertas et al. (2009), Guest (1959), Kraeuter and Setzler (1975)
	Summer and winter (August–September and December)	Gulf of Mexico	ND	ND	ND	Phillips and Burke (1970)
Chiropsella bart	May– October (outside NT stinger season: October–June)	Australia	Can swarm in 100 s or 1,000 s	Routine netting by Surf Life Saving Club	Shallow waters, sandy beaches	Currie et al. (2002), Gershwin and Alderslade (2006)
Chiropsella bronzie (as *Chiropsalmus* sp.)	Summer months, ~14 d post rainfall event, 4 cohorts in a season	Australia	ND	Drag net	Coastal marine waters, sandy beaches	Carrette et al. (2002), Gordon et al. (2004)
Chiropsoides buitendijki	Summer monsoon	Pakistan	ND	ND	Sandy bottoms and shallow waters	Tahera and Kazmi (2006)

ND no available data, *GBR* Great Barrier Reef, *NT* Northern Territory

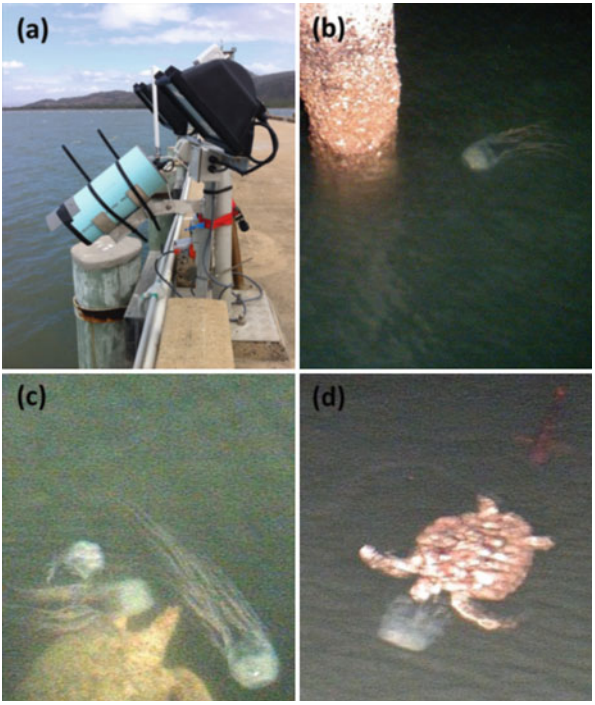

Fig. 12.6 (**a**) Digital monitoring camera setup with floodlights facing water surface, (**b**) obstacle avoidance under pier by *Chironex fleckeri* – image caught by monitoring camera, (**c**–**d**) predation on *Chironex fleckeri* by green turtle *Chelonia myda* – image caught by monitoring camera

Remotely operated vehicles (ROVs) are a possibility for underwater transects, and image recognition software may speed up the process of analysis.

Digital cameras combined with strong lighting is proving to be a useful monitoring tool to detect the presence of cubozoans, and loggers assist to determine the conditions jellyfish experience. We are trialling a camera/light combination with our collaborator (Lyndon Llewellyn, AIMS) that takes multiple images at a predetermined interval and sends the images via Wi-Fi or a mobile network (Fig. 12.6a, b). Where estimates of abundance are required, static cameras that are in the same position over months have problems with repeat counts. MaxN can be used as a metric as for baited remote underwater video (BRUVS; Cappo and Brown 1994) as long as the data can be considered independent among times. A combination of loggers and cameras, however, can provide detailed information on water conditions that jellyfishes can tolerate, and data of this type are very difficult to obtain using time and person intensive traditional observational methods.

12.6 Temporal and Spatial Patterns of Medusae Abundance

It is well recognised that temporal variation in the abundance of scyphozoan jellyfishes is great, and the sexually mature medusae are generally shorter lived than the polyps (reviews: Arai 1997; Kingsford et al. 2000). Quantitative data are rare, but discrete seasons in abundance are well known for cubozoans (e.g. *Chironex fleckeri*; Brown 1973; Gordon and Seymour 2012). Although *Alatina moseri* is recorded year round in Hawaii (Chung et al. 2001) envenomations by this species show strong seasonality (*Carybdea alata*=*Alatina moseri*; Thomas et al. 2001). *Carybdea marsupialis* (=*Carybdea xaymacana*) is also recorded year round in the Caribbean (Cutress and Studebaker 1973), but abundance probably varies considerably with time of year as for the same species in California and the Mediterranean (Table 12.2).

There are some data that indicate variation in abundance within a season, and these patterns may be due to physical forcing caused by factors such as rainfall (see Sect. 12.7). Moreover, the metamorphosis of polyps or the reproductive behaviour of some taxa may vary according to lunar phase. This has been demonstrated in Hawaii where seasonal abundance of *Alatina moseri* medusae increases 8–10 days after the full moon (http://www.808jellyfish.com/), probably due to spawning behaviour (Angel Yanagihara pers. com.). Patterns for other taxa, such as *Copula sivickisi* and *Carukia barnesi* (Kingsford et al. 2012), indicate that this may be restricted to a few species. *Alatina*, for example, may be distributed in deep water and only come to the surface to reproduce.

Data on spatial patterns of populations and local populations (i.e. Fig. 12.1) are few for cubozoans. Information has been summarised on the occurrence of species over many years and from different studies (Fig. 12.3). These data suggest that for some cosmopolitan species (e.g. *Copula sivickisi*), metapopulations are found on different continents and other isolated landmasses. Within these metapopulations are likely to be robust 'stocks' that are ecologically (e.g. Pitt and Kingsford 2000a, b) and in some cases genetically well separated as for some scyphozoan species (Dawson 2005).

Structured sampling designs that compare variation in abundance at multiple spatial scales are rare, but anecdotal accounts suggest that great patchiness at small spatial scales (i.e. less than 1 km) is common. Kingsford et al. (2012) found that abundance of *Carukia barnesi* varied greatly across the continental shelf of the Great Barrier Reef, where jellyfish were most abundant around islands and reefs at inner and mid-distances across the shelf. Distance from shore explained some variation in abundance (measured as variance components, 7.8 %), but within distances from shore, great variation was explained between sites separated by hundreds of metres to kilometres (41 %) and between replicates separated by tens of metres (51 %). Kingsford et al. (2012) suggested that this variation was due to localised sources of polyps and restricted distributions due to the strong swimming abilities of medusae. There was also evidence that the medusae of some species were most abundant near granite islands, and the authors suggested this may provide the best habitat for polyps.

Brown (1973) completed a 4-year study at Magnetic Island, North Queensland, Australia. The island is about 40 km in circumference and has one large bay (Horseshoe Bay) with a small (~3,800 m^2) estuarine area. Brown counted medusae around the entire island multiple times each season and concluded that recruit and small *Chironex fleckeri* were only found in Horseshoe Bay and within ~1 km of the estuarine area. Furthermore, he concluded that adults swam around the island in response to the wind. When conditions were choppy, large medusae moved to the leeward side of the island.

There is a clear lack of data on stock structure for all species of cubozoans because standard tools of stock discrimination have not been applied (e.g. genetics, morphology, chemistry). Given cubozoans are commonly found in areas of complex geography (e.g. estuaries, near-shore waters and coral reefs), we predict that standard approaches will reveal that population units may be surprisingly small.

Spatial patterns of distribution for some cubozoans are thought to be influenced by the proximity of estuaries and freshwater input. For example, Hartwick (1991b) proposed that *Chironex fleckeri* metamorphose from a polyp into a medusa in estuarine environments and may swim to adjacent coastal waters. Furthermore, there was strong evidence from Brown's 1973 study at Magnetic Island that indicated a small estuary was the primary source of juvenile medusae for the entire island. Near-shore distributions of high abundance in waters of mixed salinities have also been found for other chirodropids (e.g. *Chiropsalmus quadrumanus*; Kraeuter and Setzler 1975). Mooney and Kingsford (2012) used elemental chemistry of the statoliths to test the prediction that the source of *C. fleckeri* is from lower salinity estuarine environments. They examined the core (near time of metamorphosis) and edge of statoliths from *C. fleckeri* specimens collected at many locations in tropical waters of Australia and established that medusae had originated from waters ranging from normal sea water (~ salinity 34) to lower salinity waters. Accordingly, it was concluded that suitable habitat for polyps may be greater than previously thought (i.e. not just in estuaries).

12.7 Processes Influencing Abundance

Physical forcing, through variation in climatic conditions, has a strong influence on terrestrial (e.g. Holmgren et al. 2006) and marine ecosystems (e.g. Lehodey et al. 1997; Attrill and Power 2002). Correlations between physical processes and population size have focused on phenomena at large spatial scales of thousands of kilometres (e.g. North Atlantic Oscillation Index, NAOI, scyphomedusae; Lynam et al. 2005a, 2011) to localised conditions (e.g. salinity in a river, scyphozoa; Rippingale and Kelly 1995). Localised conditions, of course, are strongly influenced by broad scale meteorological forcing such as El Niño Southern Oscillation

(ENSO), but local feedback loops will generate variance relevant to natural processes (e.g. local rainfall).

It is well established through correlation and experimentation that physical factors are cues to trigger events (proximate factors) in the life history stages of scyphozoans and that the timing of these events has consequences for survival (ultimate factors) which in turn will determine how population sizes vary. Proximate factors that influence scyphozoans include temperature, salinity, light and abundance of food (reviews: Kingsford et al. 2000; Purcell et al. 2007).

The life history stage of scyphozoans that is generally most affected by physical factors is the timing and success of strobilation, though the growth and mortality of ephyrae and medusae can also be affected (review Kingsford et al. 2000; Holst and Jarms 2010). It would be reasonable to hypothesise that the closely related cubozoans would be affected in similar ways. There are clear patterns of seasonality in abundance of some cubozoans. However, among years the duration of the season may vary, and jellyfish abundance may also change (Brown 1973; Gordon and Seymour 2012; Kingsford et al. 2012).

Abundance of juvenile and adult *Chironex fleckeri* and *Chiropsella bronzie* varies within and among years (e.g. Brown 1973; Gordon et al. 2004). There is strong evidence that freshwater runoff affects populations of these species (Kingsford et al. 2012). Freshwater can affect jellyfishes indirectly or directly. Indirect effects are usually changes caused by freshwater input altering nutrient regimes and the related primary and secondary production. Direct effects include a proximate factor for metamorphosis from polyp to medusa and a loss of condition, or death, in salinities that are too low. Kingsford et al. (2012) provided evidence that medusae largely disappeared from coastal waters over a broad stretch of coastline (~200 km) during periods of heavy runoff into coastal waters. There is an irony in that freshwater may be a proximate factor for metamorphosis, but too much water may kill different life history stages at some critical level. Experiments are required to determine the role of physical factors as a cue for metamorphosis and critical physical conditions for survival.

It is not only physical factors that can influence abundance of gelatinous zooplankton. Key factors could include abundance of predators and prey as well as competition. For example, abundance of the ctenophore *Mnemiopsis* has decreased greatly in the Black Sea since it was introduced and a contributing factor is likely to be that the introduced predatory ctenophore *Beroe* was a causal factor (Shiganova et al. 2001). It has been concluded for some jellyfishes that they may compete for planktonic prey and compromise the survival of other plankton such as fish larvae (Lynam et al. 2005b). Predation is not a prerequisite for variation in prey abundance, as the latter can be influenced by other factors (e.g. temperature; Beaugrand et al. 2003). Interactions between cubozoans, their prey and potential competitors are unknown at scales ranging from local populations to stocks.

12.8 Movements and Behaviour

It is critical to understand an organism's movement and behaviour if interrelationships between it and the environment are to be determined. There are few data on the movements and behaviour of the largely cryptic cubomedusae when compared to scyphozoans (e.g. Hamner and Hauri 1981; Shanks and Graham 1987; Hamner et al. 1994). Cubozoans inhabit environments of varying structural complexity, and this has a strong influence on their behaviour. For example, *Carybdea marsupialis*, *Carybdea rastonii*, *Chiropsella bronzie* and *Chiropsoides buitendijki* utilise shallow sandy patches (Matsumoto 1995; Gordon et al. 2004; Tahera and Kazmi 2006; Bordehore et al. 2011), while *Chironex fleckeri*, *Gerongia rifkinae*, *Tripedalia binata* and *Tripedalia cystophora* can be found in estuaries and often with strong currents and close proximity to mangroves (pers. obs.; Moore 1988; Stewart 1996; Gershwin and Alderslade 2005). In contrast, *Alatina* spp., *Chirodectes maculatus* and *Copula sivickisi* can be found in association with coral reefs (Hartwick 1991a; Cornelius et al. 2005; Gershwin 2005a; Kingsford et al. 2012). *Alatina* probably have vertical migration from deep water as suggested by their periodic appearance in the shallows during spawning. Cubomedusae possess several characteristics which enable orientation and movement that facilitates vertical movement and survival in structurally complex habitats.

Orientation using eyes is a distinctive characteristic of cubomedusae when compared to scyphozoans. Each rhopalium (Fig. 12.2b) typically holds six eyes equating to 24 eyes per medusa. These six eyes consist of two camera-type lens eyes similar to cephalopod and vertebrate eyes [the upper (ULE) and lower lens eyes (LLE)], a pair of pit eyes and a pair of slit eyes, the latter two of which appear to act purely as photoreceptors (Garm et al. 2008). The statoliths allow orientation, and the rhopalium hangs from a stalk in a cavity within the sidewall of the bell so that it faces a proximal direction towards the centre of the bell and the ULE peers up through Snell's window (a 97° circular window through which an entire 180° of terrestrial world can be observed from underwater compressed by refraction as light passes through the water's surface), and LLE surveys the waters below (Garm et al. 2007a, 2011). The ULE and LLE differ in neural circuitry supporting the idea that these eyes play different functional roles in visual detection (Gray et al. 2009). An example of this has been seen in *Chiropsella bronzie* where the LLE detects only large structures at short range, but the ULE is involved in detecting solar/lunar position, possibly detecting direction to or from the beach or keeping a course while swimming (O'Connor et al. 2009). Although all cubomedusae possess these eye types, the time it takes for the eyes to respond to a stimulus differs between species (Garm et al. 2007a). Garm et al. (2007a) suggested these differences may correlate with differences in habitat or behaviour. For example, faster responding eyes are seen in *T. cystophora* inhabiting the complex mangrove roots compared to the slower responding eyes of *C. bronzie* which inhabits the relatively homogeneous sandy beaches.

Cubozoan rhopalia also act as swim pacemakers. Locomotion itself is a result of jet propulsion following contraction of the bell and expulsion of water through the velarium (sub-umbrella tissue that constricts the opening of the bell; Shorten et al. 2005, for a detailed description of cubozoan musculature, see Satterlie et al. 2005). Interspecific differences in locomotion vary with body size as larger individuals swim faster with a lower pulse frequency than smaller individuals. Furthermore, smaller animals tend to swim faster relative to their bell size (Shorten et al. 2005). While medusae have the ability to move independent of currents, as seen in *Chironex fleckeri*, they do so only until a current reaches a critical velocity (Gordon and Seymour 2009). Cubozoans are capable of strong directional swimming combined with rapid turns which can be up to 180° in two bell contractions (Garm et al. 2007b). Satterlie and Nolen (2001) suggested that the turning behaviour of *C. marsupialis* was due to asymmetric contractions in the velarium which create a ‘nozzle’ effect increasing the velocity of ejected water. More recently investigations on *T. cystophora* have found that turning is a result of not only an asymmetrical contraction of the velarium but also an asymmetrical contraction of the bell and that this predictable response can be a direct effect of changes in light, suggesting these to be the mechanics behind obstacle avoidance (Petie et al. 2011).

Obstacle avoidance has been documented in several cubozoan species (Fig. 12.6b), where orientation is through strong photosensitive behaviour. Daytime field observations on *Carybdea rastonii* found that medusae reacted to the presence of divers by swimming away. They also avoided seagrass beds and other dark objects, and in the laboratory, they avoided dark standpipes of 1 cm diameter (Matsumoto 1995). During tank experiments Ueno et al. (2000) trialled different coloured walls and found that *C. rastonii* continuously struck the wall coloured grey. It was speculated that grey looked like a horizontal extension of sea water, while black or white walls were rarely struck and probably emulate the colours associated with obstacles. Hamner et al. (1995) observed *Chironex fleckeri* to swim around pier pilings without touching them (also captured by digital monitoring cameras, Fig. 12.6b) and in the laboratory found *C. fleckeri* would swim away from black and towards white. They also showed a clear reaction to 1 cm black bars to a distance of 50 cm and manoeuvred around them. An obstacle avoidance study showed that *Chiropsella bronzie* also responds most strongly to black obstacles. In contrast, *Tripedalia cystophora* responded most strongly to objects with intermediate contrast (red obstacles; Garm et al. 2007b).

In an ecological context, cubozoan photosensitivity has been best demonstrated in *Tripedalia cystophora*. Field and laboratory observations have found that *T. cystophora* is capable of rapid, laterally directed swimming towards vertical light shafts among mangrove prop roots and once within a shaft will modify its swimming behaviour to increase the time spent within the light shaft where it can forage on copepod swarms (Buskey 2003). *T. cystophora* has also recently been found capable of using terrestrial visual cues for navigation (Garm et al. 2011). Garm et al. (2011) found that the size of the visual field of the ULE of *T. cystophora* agrees closely with Snell’s window and that if displaced from their habitat at the edge of lagoons medusae would rapidly swim back to the lagoon edge by seeing the edge of the mangrove canopy, and this was independent of compass orientation.

Recent studies have investigated whether the cubozoan visual system is capable of colour vision. Ekström et al. (2008) established that the lens eyes of *Carybdea marsupialis* utilise a single opsin (protein constituent) and are thus colour-blind. Coates et al. (2006) also found a single opsin in the lens eyes of *Tripedalia cystophora* and that the peak spectral sensitivity falls toward blue-green light. This supported earlier findings that *T. cystophora* medusae are attracted to blue or green light but not red (Coates 2005). This development of a single opsin may help improve contrast in *T. cystophora*'s surrounding habitat of a predominantly green world (ULE sees green canopy of mangroves, LLE sees algae and organic material; Coates et al. 2006).

Medium scale movements (metres to kilometres) and diurnal activity have been observed in cubomedusae. Medusae of *Carybdea rastonii* have been observed resting on the bottom during the day and were found at the surface at night (Matsumoto 1995). This pattern was also seen in *Copula sivickisi,* which are inactive and attached to the substratum during the day and actively mate and forage at night (Garm et al. 2012). Inversely, all complex behaviour of *Tripedalia cystophora* is carried out in day time, and they are less active on the bottom at night (Garm et al. 2012). Seymour et al. (2004) suggested that *Chironex fleckeri* 'sleep' at night, resting motionless on the sandy bottom conserving energy. However, further acoustic telemetry tracking found that resting at night was dependent on the medusa's location. Some *C. fleckeri* medusae in coastal zones with low tidal current rested at night, but medusae in estuarine zones with stronger tidal currents moved more at night than in the day (Gordon and Seymour 2009). The same acoustic tracking study found that *C. fleckeri* medusae tagged in coastal habitats remained in coastal habitat (maximum time tracked = 38 h) and those tagged in estuarine habitat remained in estuarine habitat. An exception was one large medusa (180 mm IPD) which was tracked moving ~10 km up and down a beach front and in and out of an estuary over a 26 h period (Gordon and Seymour 2009). It has been suggested that cubomedusae movement/activity patterns have developed according to their preferred prey (Matsumoto 1995; Gordon and Seymour 2009; Garm et al. 2012). More tagging and observations of behaviour are required as the robustness of some conclusions is weak due to low sample sizes.

12.9 Prey, Predatory Impacts and Consumers of Cubozoans

Cubozoans are voracious predators, preying on a variety of both invertebrate and vertebrate prey. Species and age-specific toxins and injection mechanisms are thought to have evolved to target specific types of prey (Carrette et al. 2002; Underwood and Seymour 2007). The toxins from some species are so potent that they can be fatal to humans (e.g. *Chironex fleckeri* and *Chironex yamaguchii*). Not surprisingly a cubozoan's prey will depend on the medusa's size with most small cubomedusae preying primarily on planktonic crustaceans while larger, or more mature, individuals prey on fish. An ontogenetic shift in preferred prey has been documented from gut content analyses of at least four species including the carybdeids *Carukia barnesi* (Underwood and Seymour 2007) and *Carybdea rastonii* (Lai 2010) and the chirodropids *Chironex fleckeri* (Carrette et al. 2002) and *Chiropsalmus quadrumanus* (Nogueira and Haddad 2008). The ontogentic shift noted in *C. fleckeri* moved from a predominant prey of prawns (*Acetes australis*) to fish (including juvenile trevally, *Caranx* sp.; pony fish, *Leiognathus* sp.; perchlets, *Ambassis* sp., and mullet, *Mugil cephalus*; Hamner et al. 1995); this change occurred at a size of ~60–100 mm IPD (Carrette et al. 2002). Gordon and Seymour (2012) recently suggested that this size range of medusae would be reached after ~50–65 d of growth, and this is when *C. fleckeri* venom becomes more lethal to swimmers.

Cubomedusae are entangling predators and capture prey by envenomation via nematocysts on their tentacles (Carrette et al. 2002; Buskey 2003). Most species exhibit a feeding or foraging behaviour typical to cubomedusae. With tentacles extended a medusa will increase swimming speed vertically upwards for a short period, perform a 180° turn then stop bell pulsation. The negatively buoyant medusa drifts down apex first with tentacles extended. When prey is entangled in tentacles, the pedalia fold inwards, and the tentacles with attached prey are moved into the bell where the manubrium locates and removes the prey from the tentacles (Larson 1976; Kinsey 1986; Hamner et al. 1995; Matsumoto 1995). An exception to this is *Carukia barnesi*. Underwood and Seymour (2007) noted that mature *C. barnesi* would swim through the water with tentacles extended and would periodically contract and extend a tentacle. This jerking motion of tentacles was thought to attract small fish.

The primary prey of box jellyfishes is planktonic crustaceans. *Tripedalia cystophora* fed almost exclusively on the copepod *Dioithona oculata* in the field (Buskey 2003), and predation behaviour has been studied (Sect. 12.8). *Chiropsella bronzie* fed almost exclusively on the prawn *Acetes australis* (Carrette et al. 2002). *Carybdea marsupialis* has been noted to feed on both mysids and fish hatchlings in California, USA, (Martin 2004) but mostly the copepod *Acartia* and also polychaete *Ceratonereis* and herring (*Jenkinsia* sp.) in Puerto Rico (Larson 1976). Small *Copula sivickisi* feed most frequently on copepods, cumaceans and zoea larvae (Garm et al. 2012) and also on amphipods and polychaetes (Hartwick 1991a). Gut content analyses of freshly caught *Carybdea rastonii* demonstrated that crab zoea and shrimp larvae were ~50 % of prey, and copepods, arthropods and fish larvae were also common prey (Lai 2010). *Chiropsalmus quadrumanus* was also found to prey predominantly on crustaceans with >20 % of gut contents consisting of sergestid pelagic shrimps and another ~20 % consisting of brachyuran larvae and penaeid shrimp (Nogueira and Haddad 2008).

Jellyfishes can have an impact on abundance of plankton, and they have been identified as key organisms for direct predation on fish larvae (Frank and Leggett 1982; Möller 1984). Further, abundance of small plankton can be reduced and that in turn can affect the survival of other plankters (Lynam et al. 2005b). Predatory impacts can be at small (e.g. tens to hundreds of metres) or large spatial scales (tens to hundreds of kilometres), but existing studies on jellyfishes have been restricted to scyphozoans (e.g. Möller 1984). In the case of cubozoans, envenomation and death is clearly relevant to the prey, but how scalable is this predatory effect from small to larger spatial scales? Here we have adapted the construct used by Weldon and Slauson in 1986 for competition. Predation can be ‘intense’ (i.e. rapid predation that depletes prey at small spatial scales) and ‘important’ for determining population size of prey (i.e. at spatial scales of local, meso or metapopulations, e.g. Möller 1984; Lynam et al. 2005a). Quantitative data on abundance of cubozoans are few (see Sect. 12.6), but these combined with anecdotal accounts suggest that high concentrations of cubozoans are rare and aggregations/blooms are usually found at small spatial scales. Predation therefore, is likely to be intense, but unimportant in affecting the population dynamics of prey.

Literature on the predators of cubozoans is sparse and what is available is largely anecdotal. Predators have only been documented for *Chironex fleckeri* in Australia. Several fish species such as small tailor, bream, small Spanish mackerel, queenfish, toadfish and parrotfish have been noted as predators of *C. fleckeri* (Kinsey 1986). Perhaps a more important predator of cubomedusae is the green turtle *Chelonia myda*, which has been observed actively feeding on *C. fleckeri* (Hamner et al. 1995, pers. obs.), and feeding observations have also been recorded by digital monitoring cameras (Fig 12.6c, d). There are no data on predator-related mortality of polyps, but nudibranchs probably consume them, as for syphozoans (Hoover et al. 2012), and grazers may dislodge them.

12.10 The Potential Impacts of Climate Change

Climate change is already affecting marine assemblages (review Brierley and Kingsford 2009) and given the rapid response times for planktonic organisms (Beaugrand et al. 2003), as for scyphozoans (e.g. Lynam et al. 2005a), cubozoans will be affected. There will be changes in physical factors (temperature, salinity, pH and sea level height) and biotic factors including abundance of prey, predators and competitors (Sect. 12.9). Although there is broad acknowledgment that there will be changes to marine ecosystems, the direction of change is difficult to determine. For example, jellyfish abundance may increase and have a great influence on other taxa in a pelagic assemblage (Lynam et al. 2011) or the direction of change could vary greatly by location and species (e.g. Lynam et al. 2005b). Because the species diversity of cubozoans is greatest in tropical waters (Sect. 12.2) and few are found beyond the tropics (i.e. ~23°30′ Latitude) north and south, it would be reasonable to predict range extensions as sea water temperature increases (Orellana and Collins 2011).

In some parts of the world, range extensions may happen at a faster rate due to high rates of localised warming. For example, the average temperature of the East Australian Current has warmed by 2.2 °C since 1960, and the current now extends over 350 km further south (Ridgway 2007). A sensible prediction would be that medusae could be dispersed further south, and if suitable conditions prevailed, then planulae could settle to give rise to new and more southern local populations.

The alteration of critical physical factors through climate change could affect the population dynamics of cubozoans. Warmer water could extend the season in which medusae are found and when they are most abundant. Furthermore, increased evaporation due to warmer waters could increase local rainfall which would change salinity and local secondary production (Grimes and Kingsford 1996). It is known for *Chironex fleckeri* and *Chiropsella bronzie* that salinity may be a proximate and ultimate factor affecting populations (Sect. 12.7). The duration, intensity and frequency of rainfall are also likely to be important. There are a number of plausible outcomes to increased rainfall: higher metamorphosis rates and subsequent recruitment of juveniles to the population of medusae and mortality of different life history stages as low salinities exceed the tolerances of individuals. Variation in secondary production could affect all life history stages, while variation in sedimentation rates could affect polyps.

There is a predictable relationship between an increase in CO_2 in the atmosphere and a decrease in pH (Caldeira and Wickett 2003). A decrease in pH will have greatest impact on organisms with calcium carbonate skeletons including coccolithophores and pelagic molluscs (Brierley and Kingsford 2009). Cubozoans do not have a calcium carbonate skeleton, but they do have calcium sulphate statoliths that are the basis of their ability to balance (Garm et al. 2007b), orientate and have complex behaviour (Sect. 12.9). Moreover, decreased pH can affect non-calcifying taxa by causing acidosis of the tissues. One recent study has examined the interactive effects of ocean warming and acidification on the asexual budding of polyps of the Irukandji jellyfish *Alatina* nr *mordens* (Klein 2012). Klein (2012) found that although warming moderately enhanced rates of budding, reducing pH from 7.9 to 7.6 (as predicted for 2100 International Panel on Climate Change) had an overwhelmingly negative effect on rates of budding and caused a 24 % reduction in the width of statoliths of newly metamorphosed medusae. It is unclear, however, whether the reduction in the width of the statoliths compromised their functioning. A loss of orientation can compromise survival to recruitment of presettlement fishes (Munday et al. 2010) and potentially the ability of marine taxa to feed. Average predictions of climate change (e.g. increases in temperature) are of limited value because in some regions changes are more than twice that of global averages (Brierley and Kingsford 2009), while in other areas the changes are below average. It is clear, however, that the climate is changing and that will alter the ecology of cubozoans worldwide. There is an urgent need to get baseline data on the distribution and abundance of populations of different species. Furthermore, we need to determine their physiological limits through a combination of monitoring and manipulative experiments. However, a key issue concerning experiments on the impact of chemical and physical environmental factors is the degree of intergenerational adaptation in gradually changing conditions.

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