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HORIZONS

Beyond the jellyfish joyride and global oscillations: advancing jellyfish research

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There has been debate in the literature recently about increases in jellyfish populations in response to anthropogenic change, and this has attracted widespread media interest. Despite an international collaborative initiative [National Center for Ecological Analysis and Synthesis (NCEAS) working group on jellyfish blooms] to investigate trends in global jellyfish numbers, interpretations from the data remain ambiguous. Although this is perhaps to be expected given the diversity of potential drivers, the debate has not been helped by a general lack of rigorous data and loose definitions. There is a need for the community to refocus its attention on understanding the implications of jellyfish blooms and managing them, because regardless of global trends, jellyfish are a problem in some coastal marine ecosystems. Here, we provide recommendations for advancing jellyfish research. These include directing research toward better managing jellyfish impacts, expanding research into socio-economic consequences to grow the money available for research, building more operational and ecosystem models for tactical and strategic management, filling in the gaps in our biological knowledge for supporting models, improving surveillance using observing systems and making jellyfish research more rigorous. Some vehicles

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to address these recommendations include international standardization of methods, a discipline-specific journal for jellyfish research and an international science program on the global ecology and oceanography of jellyfish.

KEYWORDS: jellyfish; bloom; impacts; management; debate

INTRODUCTION

Copepods play an undeniably important role in the trophic functioning, biogeochemistry and (indirectly) socio-economics of most marine ecosystems, and consequently the number of publications on each has risen year-on-year (Fig. 1). Yet the increase in the number of publications concerning copepods fails to match those for studies on jellyfish, especially in recent times (Fig. 1). And this is a group of animals that is common only in some coastal systems, for some of the time, and which is eaten by few things of any "value" to us.

If publications on jellyfish in the peer-reviewed press are on the exponential increase, the rate of change in jellyfish headlines in the popular and news press has been meteoric (Figure 3 from Condon *et al.*, 2012). Surprising as it is, few people have ever heard of copepods (Fig. 2b), let alone understand the role they and other crustacean zooplankton play in providing us with the fish on our dinner plates. In contrast, everyone has heard of jellyfish (Supplementary data, Fig. S1): we can see them with the naked eye, they are in our folklore and our interactions with them have, for the most part, been direct and negative, particularly in western nations.

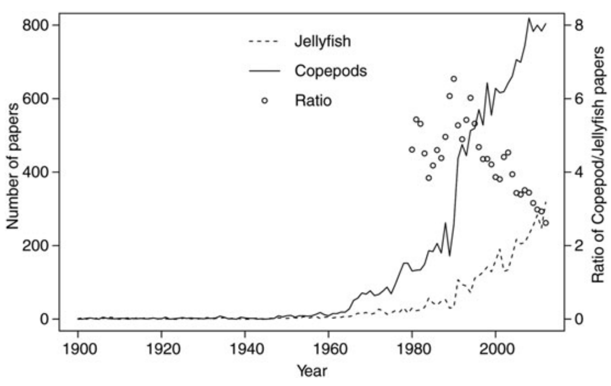

Fig. 1. Numbers of papers published on copepods and jellyfish over the period 1970–2010. The ratio between the two is also shown (spline smoothing: dotted) and it indicates that in the 1970s there were ~15 times as many papers on copepods than jellyfish, now there is only approximately four times more. Data extracted on 21 May 2013 from Web of Science using the Topic search (searching Title, Abstract and Keywords) and the words "copepod* or calanoid* or harpacticoid* or cyclopoid* or poecilostomatoid*" ($N = 17\,507$) and "scyphomedusa* or hydromedusa* or ctenophor* or siphonophor* or cubomedusa*" ($N = 4\,569$).

JELLYFISH AS HEADLINES

When they are abundant, jellyfish can cause a multitude of problems for fishing and aquaculture: they clog and damage fishing nets; they can spoil catches and alter fishing efficiencies; they are an important occupational safety issue in some fisheries; they can kill cultured fish; they can interfere with the accurate hydro-acoustic assessment of stock sizes; and they can even capsize small vessels during fishing operations. Jellyfish can also obstruct the screens in cooling intakes of, and so temporarily cripple, both large vessels at sea as well as coastal plants for (frequently nuclear) power generation and desalination. We probably encounter jellyfish most when they spoil our enjoyment of a day at the beach. And there is no doubt that as the human population continues to rise, and as our use of the maritime environment increases, so the potential for interaction with jellyfish will increase irrespective of any changes in their

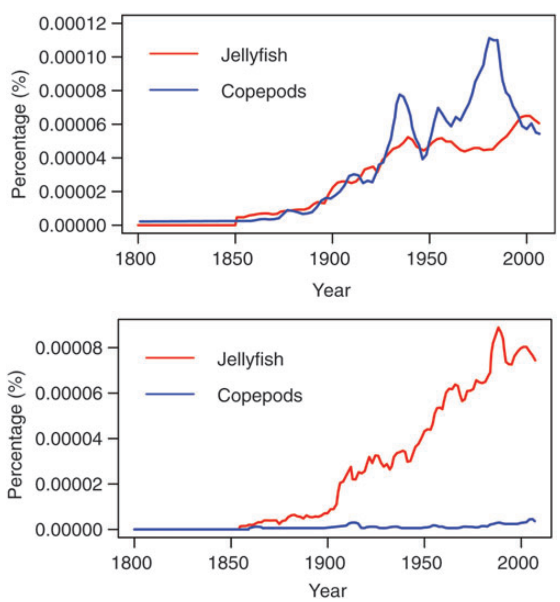

Fig. 2. Changes in the usage of the words jellyfish (jellyfish + Jellyfish + jellyfishes + Jellyfishes) and copepod (copepod + Copepod + copepods + Copepods) in more than 20 million English language books from 1800–2010 (see http://books.google.com/ngrams; Michel et al., 2010). (**a**) All fiction and non-fiction, (**b**) fiction books only. Data extracted on 27 February 2013.

abundance. All of these are worthy headlines, of course, but much of the media hype of late has arisen out of "science" and not spectacle, and is linked to a perception that numbers of some species of jellyfish have increased (Schrope, 2012). This potential increase has been variously attributed to human-mediated environmental change in the Anthropocene: fishing, ocean warming, hypoxia, habitat modification and coastal development, eutrophication and accompanied in some instances by alien introductions (Purcell *et al.*, 2007; Richardson *et al.*, 2009; Purcell, 2012). And it reflects the fact that jellyfish (medusae and polyps) certainly have the potential to respond to these anthropogenic drivers individually (and they could act synergistically) in a way that would lead to increases in population size.

By jellyfish here we refer to those zooplankton in the phyla Cnidaria and Ctenophora, and we deliberately exclude the Thaliacea that are frequently lumped with them as gelatinous zooplankton. The superficial resemblance of thaliaceans is limited to their transparency, high water content and attendant metabolic implications as well as their tendency to form blooms (Table I). We thus propose that only pelagic Medusozoa and Ctenophora be considered "jellyfish" as they are more similar in their nervous and digestive systems, have a generally common habitat (coastal and shelf), their impacts on humans are generally shared and their likely responses to anthropogenic drivers are convergent.

Several authors have written extensively about the attributes of jellyfish that could allow them to increase

Table I: Although Medusozoa, Ctenophora and Thaliacea all have a high water content and are certainly gelatinous zooplankton, they should not all be considered together as jellyfish

	Taxon		
	Medusozoa e.g. *Pelagia, Nemopilema, Chironex, Aequorea*	Ctenophora[a] e.g. *Mnemiopsis*	Thaliacea e.g. *Salpa, Pyrosoma*
Environment	Meroplanktic[b]	Holoplanktic	Holoplanktic
Habitat where they form blooms	Coastal and shelf	Coastal and shelf	Shelf and oceanic
Reproduction	Benthic polyp, asexual; pelagic medusa sexual	Sexual; hermaphroditic	Alternating sexual and asexual zooids
Nervous system	Simple	Simple	Complex
Closed digestive system	No	No	Simple
Diet	Protists—vertebrates	Protists—vertebrates	Bacteria—protists
Impacts			
Coastal plant	Yes	Yes	No
Vessels at sea	Yes	?	Yes
Fishing operations	Yes	?	No
Fish populations	Yes: directly and indirectly	Yes: directly and indirectly	?: indirectly
Fish kills	Yes	No	No
Tourism	Yes	?	No
Health	Yes	No	No
Anthropogenic drivers			
Sprawl	Yes: polyps	No	No
Invasives	Yes: e.g. *Phyllorhiza punctata*	Yes: e.g. *Mnemiopsis leidyi*	No
Fishing	Yes: reduction in predation and competition release niche space	Yes: reduction in predation and competition release niche space	Unknown but unlikely: reduction in predation; not known competitors with fish
Eutrophication	Yes: change in size structure of food web, increase in prey base; increase in turbidity	Yes: change in size structure of food web, increase in prey base; increase in turbidity	No: increased prey base irreversibly clogs gills, leading to "starvation"
Ocean warming	Yes: stratification reduces size structure of food base; warming encourages polyp proliferation and faster medusa growth rates	Yes: stratification reduces size structure of food base; warming leads to faster individual, and likely population, growth rates	Yes: stratification reduces size structure of food base; warming leads to faster individual and population growth rates
Hypoxia	Yes: polyps and medusae tolerant to some hypoxia; polyps can encyst	Yes: ctenophores tolerate, and continue to feed; but growth rates reduced	Unlikely: high oxygen demand as zooids move and feed near constantly

This is because they differ in a number of fundamental ways, including their environment, physiology, biology and ecology, their impacts on humans and potential anthropogenic drivers. We thus propose that only pelagic Medusozoa and Ctenophora be considered "jellyfish" as they are more similar in their nervous and digestive systems, have a generally common habitat (coastal and shelf), their impacts on humans are generally shared and their likely responses to anthropogenic drivers are convergent.

[a]Excluding Platyctenida.

[b]Most Scyphozoa and Cubozoa, some Hydrozoa; ?, unknown.

rapidly in numbers in response to anthropogenic drivers and implications for ecosystems and society [see Parsons and Lalli (Parsons and Lalli, 2002), Purcell *et al.* (Purcell *et al.*, 2007), Richardson *et al.* (Richardson *et al.*, 2009) and Purcell (Purcell, 2012) for more details]. Save to say that jellyfish certainly have the potential to increase in abundance in our rapidly changing world, having likely been through it all before (several times) since the Cambrian.

CRYING WOLF?

It is this potential to respond positively in a highly modified ocean that some researchers are concerned about and which the media have picked up. And it is this potential that has led to much of the present debate in the community. Are jellyfish actually increasing or are we crying wolf?

The debate was initiated by a handful of conversational and intriguing papers in the 1970s and 1980s (Greve and Parsons, 1977; Parsons, 1979; Banse, 1990), was fuelled by reviews of the 2000s (Parsons and Lalli, 2002; Mills, 2001; Purcell *et al.*, 2007; Richardson *et al.*, 2009) and has been followed up with some more quantitative analyses more recently (Brotz *et al.*, 2012; Condon *et al.*, 2012). Whilst Brotz *et al.* (Brotz *et al.*, 2012) have suggested that increases may in fact be near-global across the Large Marine Ecosystems, the paradigm highlighted by Pandolfi *et al.* (Pandolfi *et al.*, 2005) that our global oceans are on a "slippery slope to slime" has not consistently been supported by outputs of the US National Center for Ecological Analysis and Synthesis (NCEAS) working group convened specifically to look at the issue ("Global expansion of jellyfish blooms: magnitude, causes and consequences"). Indeed, outputs from this jellyfish blooms working group are inconclusive: in one study they suggest that there is no increase (Condon *et al.*, 2012), in another they imply there is (Duarte *et al.*, 2012) and then in yet another they suggest modern increases in jellyfish numbers reflect the upward phase of a bigger natural oscillation in global populations (Condon *et al.*, 2013). It is clear that we currently do not have sufficient data to answer conclusively whether there are global increases in jellyfish, and this is probably an ill-posed question anyway.

The debate has not been helped by loose language. For example, if the question is framed as "are jellyfish increasing globally", does this mean that "all jellyfish everywhere are increasing", "some species are increasing globally" or "some species are increasing in some areas"? If, as has been suggested, humans are contributing to the "increase", then it is reasonable to expect that areas heavily impacted by people will be most affected, and biologically it is reasonable to expect that only some of the many species of jellyfish would respond. Our language needs to be tightened to avoid misconceptions and to focus discussions and analyses.

Unfortunately, much of the historical information on jellyfish is anecdotal and one of the great advances engendered by the debate has been the bringing together of available information (Brotz *et al.*, 2012; Condon *et al.*, 2012). While this exercise has highlighted the paucity of data globally, it has hopefully also provided a renewed impetus for the collection of time series information. Regardless, there are certainly some systems in which jellyfish have increased in abundance (Richardson *et al.*, 2012) and where they are proving to be a problem (see references in Condon *et al.*, 2013).

A key issue for jellyfish research is where to from here? In the remainder of our article, we outline a series of measures that we believe will take jellyfish research forward.

ADVANCING JELLYFISH RESEARCH

Manage bloom impacts

Interestingly, this same debate about potential increases and their causes raged in the harmful algal bloom (HAB) literature during the 1990s (e.g. Hallegraeff, 1993 and references therein). As for jellyfish, the debate about potential increases in HABs was hamstrung by the few long time series available and by the difficulty of disentangling the effect of greater awareness, surveillance and use of the coastal zone.

Although jellyfish and HABs are very different, there is more similarity between these groups, their drivers and human impacts than might at first appear, suggesting jellyfish researchers might learn from the larger HAB research community. Both HABs and jellyfish can cause severe medical symptoms and even death; they are problematic to aquaculture and bathers in the coastal zone; they form large yet ephemeral blooms; they have complex lifecycles (HABs: cysts and cells; jellyfish: polyps and medusae) that provide research and management challenges; long-term changes are poorly known because time series are lacking; their numbers could be controlled by predators (shellfish for HABs; possibly small pelagic fish for jellyfish); human impacts such as eutrophication have been implicated in bloom formation; introduced species have become invasive; and warming could cause range expansion of problem tropical species. The debate about whether HABs are on the increase remains unresolved, but there is now a realization that problems with HABs are undoubtedly increasing because of increasing human use of the coast. This has resulted in a shift of research effort and resources toward research supporting management of HABs. We believe that such a shift in jellyfish research focus is needed.

Whether jellyfish increases are global or not, cyclical or not, or not changing is an academic debate, and one that might take several decades of improved data collection and refined hypotheses to answer. It is an interesting question, but unfortunately the answer does little to help manage current problems associated with jellyfish blooms. Marine systems and their resources are generally managed at the local and regional level, where the full suite of potential drivers are best understood. And in the case of jellyfish, with the exception perhaps of fishing, different drivers are likely to be more or less important in different systems. Nevertheless, problems associated with jellyfish blooms are undoubtedly increasing because of greater beach use, more recreational fishing in the coastal zone and more coastal infrastructure. Our research resources need to be focused on better managing problems associated with impacts happening now.

There are many existing strategies for managing effects of jellyfish blooms, including predicting blooms, avoidance by bathers, beach closures, use of protective clothing and nets, more effective sting treatment, design of fishing nets to minimize jellyfish capture, avoidance of blooms by fishers, bubble curtains and modified management for aquaculture farms and shutting down of coastal water intakes. There is a need to optimize existing prevention and mitigation strategies and develop new more effective measures.

Socio-economic consequences

Jellyfish research has been hampered by the relatively small amount of money available. To grow the total pool of money for jellyfish research, the first step is to quantify the magnitude of socio-economic impacts of blooms. This should be a research priority because it contextualizes jellyfish problems, encourages industry and government funding and participation in research and allows for the prioritization of research questions. Obtaining this information requires innovative collaborations with economists and social scientists. It also requires the use of unconventional data sources, including questionnaires to key stakeholder groups to ascertain problems and costs, meta-analyses of newspaper articles to estimate the range of sectors affected and analysis of hospitalization records to estimate health costs. Cost-benefit analysis of different mitigation options will be needed to identify the best management practices economically and environmentally.

Currently, estimates of the cost of jellyfish to coastal economies are sparse and qualitative, although there are some robust estimates of impacts. For example, Kawahara *et al.* (Kawahara *et al.*, 2006) calculated that the giant schyphomedusa *Nemopilema nomurai* cost at least $US20M in loss of fish catch and net damage. Graham *et al.* (Graham *et al.*, 2003) estimated that the invasive jellyfish *Phyllorhiza punctata* cost $US10M in losses to the shrimp fishery in the Gulf of Mexico by reducing shrimp harvest and fouling gear. More recently, Quinones *et al.* (Quiñones *et al.*, 2013) showed that the scyphomedusa *Chrysaora plocamia* cost $US200K in losses from 17% of the Peruvian anchovy fishermen over 35 days in 2008/2009 when jellyfish were not particularly abundant. There are also a few estimates of the estimates of the costs to tourism of venomous jellyfish. These can be huge and need to be better quantified. For example, an estimate of losses to the tourism industry in North Queensland, Australia, due to negative publicity around Irukandji stings in 2002 was estimated at $Aus65 million (Williams, 2004 in Gershwin *et al.*, 2009). Economic impacts are probably best estimated using simple input–output models to calculate the direct and indirect effects of jellyfish on different sectors (Hoagland and Scatasta, 2006).

These studies have usually been of direct effects of financial impacts of jellyfish from once-off events. They do not consider indirect and induced impacts associated with negative public perception and long-term behavioural changes (e.g. people not taking beachside vacations when major sting events are reported in the media), and effects on the community of reductions in regional incomes.

Operational and ecosystem models for tactical and strategic management

Ecosystem models are useful for learning about the role that jellyfish play in the trophic functioning of ecosystems (Pauly *et al.*, 2009) and for testing the efficacy of longer-term strategic decision making. For example, ecosystem modelling studies in the Northern Benguela (Roux *et al.*, 2013) and in the Northern California Current (Brodeur *et al.*, 2011) explore how fishing can affect foodweb structure and promote jellyfish numbers, and how energy cycles through foodwebs, with jellyfish having a top-down control on their zooplankton prey but with little energy from jellyfish reaching higher trophic levels. Ecosystem models can also provide insight into the primary drivers of changes in jellyfish populations in different areas (e.g. fishing or eutrophication). Ecosystem models allow us to test alternate management regimes (e.g. different fishing scenarios; alternative future climate scenarios) and see how these affect jellyfish and ecosystem goods and services. Finally, the stable state between jellyfish and fish that has been hypothesized, where fish keep jellyfish in check until they are overfished and jellyfish then keep fish numbers down (Pauly *et al.*, 2009;

Richardson *et al.*, 2009) can best be tested using ecosystem models.

Operational models provide short-term predictions to support tactical management: when and where jellyfish blooms might occur, for how long might they persist and what species could be present? Most operational ocean forecasts are physical in nature, but there is increasing interest in biological predictions from coupled biophysical models. As jellyfish blooms are often controlled by wind and currents, hydrodynamic models are starting to be used for prediction (e.g. Berline *et al.*, 2013). Such models can provide real-time forecasts. The Chesapeake Bay Ecological Prediction System uses a regional ocean model to generate daily nowcasts and 3-day forecasts of several environmental variables, including sea surface temperature, salinity, nutrient and chl-a concentrations (Brown *et al.*, 2012; http://chesapeakebay.noaa.gov/forecasting-sea-nettles/). These environmental predictions then drive species distribution models for HABs and the sea nettle *Chrysaora quinquecirrha*. Such forecast models can provide environmental managers with estimates of bloom movements and potential impacts a few days into the future, providing a window of opportunity for managers to take precautionary actions prior to potential impacts. Coupled biophysical models have also been used to identify the possible location of polyp beds of problem blooms (Johnson *et al.*, 2001). Early warning systems based on forecast models would be valuable for identifying problematic jellyfish that are venomous to bathers, kill farmed fish or compromise fisheries operations and cause blockage of water intakes. These models will become more sophisticated in the future: partially through an ever-finer grid for the physical system, but mainly through improved dynamic population models of jellyfish.

Biological information supporting models

Dynamic population models can be improved through realistic biological parameterization of lifecycle complexity (polyp and medusa), bentho-pelagic coupling, behaviour, physiological rate processes and trophic interactions. Models demand data on production and ingestion, which are largely missing for most systems. While production may be obtained in the first instance from generalized metabolic relationships (e.g. Purcell, 2010), in the absence of a specific enzyme (e.g. chitobiase in copepods), production is practically studied through dedicated, short-term, repeated, local studies focusing on changes in the size structure of populations (e.g. Palomares and Pauly, 2009). And in the case of ingestion, there is a need for more detailed studies on diet and feeding. Traditional gut contents analyses have proven useful in identifying the varied diet of jellyfish, although there are obvious limitations and biases. Newer methods such as fatty acid and stable isotope analyses provide some new insights into pathways (Pitt *et al.*, 2009), but they may often be incapable of identifying prey considering the broad diet of many jellyfish and will thus fail to capture prey dynamics. Models of jellyfish feeding (Costello and Colin, 2002; Acuña *et al.*, 2011) could be usefully developed in a size-dependent way alongside diet studies to further our understanding of the trophic relationships of jellyfish and their possible (changing) impacts on prey populations. Jellyfish abundance is not only influenced by hydrographic processes, but by the interplay among species-specific physiological and behavioural relationships with the environment, and competitive and trophic (with predators, prey and disease) interactions.

Models of jellyfish also need to consider behaviour, as they migrate vertically in response to light (Schuyler and Sullivan, 1997) and food (Hays *et al.*, 2012) and so vary their susceptibility to different horizontal currents (Moriarty *et al.*, 2012). An understanding of senescence and processes leading to population declines and its impacts on biogeochemistry is as important as those leading to blooms. We do not know, for most taxa, how long they can live. In the case of some temperate species, adult medusae may die over winter, but off Namibia we now know from laboratory studies that they can live for >18 months, and there is evidence from Japan that "formerly" annual species are surviving through the present warmer winters (Uye and Ueta, 2004). Lebrato *et al.* (Lebrato *et al.*, 2012) have recently reviewed our (scant) understanding of jelly-falls, concluding that the role of jellyfish in exporting surface production downwards will increase as the sinking of phytodetritus declines as diatoms are replaced by picoplankton in a warming ocean. Although these authors make some useful recommendations for monitoring jelly-falls, we should be cautious in extrapolating experimental results on bacterial decomposition in mesocosms or in shallow water to deeper and/or hypoxic environments with different microbial communities.

It has been suggested that populations of medusae are driven more by the processes affecting the polyp on the benthos, when present, than processes in the plankton (Hernroth and Grondahl, 1985), and these processes are rarely included in current models. The polyp stage is certainly one of the "irregularities" (Boero *et al.*, 2008) that make these metagenic taxa challenging to understand, and different from holoplankton. While important advances are being made in our understanding of polyp ecology, and the various factors that induce proliferation, podocyst formation and strobilation (Lucas *et al.*, 2012), these data have largely been derived from laboratory experiments on *Aurelia* and hard links between these with field data on polyps/ephyrae/medusae is often missing. Polyps are difficult to locate in the field owing to their minute size, which makes any validation of laboratory findings difficult, but routinely collected plankton samples in coastal waters should reveal the presence of ephyrae, which would help make the links to the location of polyps and timing of ephyrae production.

Recently, the elegant application of population genetic tools has established the origin of jellyfish in blooms. Lee *et al.* (Lee *et al.*, 2013) have noted that *Rhizostoma octopus* in the Irish Sea are derived from both resident and expatriate polyp beds. Although this significantly complicates our understanding of bloom dynamics because different drivers may be acting on the resident and immigrant components of a population, we need to consider ways of factoring this information into coupled biophysical models in advective environments.

Improved surveillance using observing systems

Humans impact environments and ecosystems faster than we become aware of it (Pitcher, 2012). Ocean observing systems provide the dynamic baselines needed to identify these changes. Global ocean observing systems are moving more into the biological realm and jellyfish could be a key component. Jellyfish could be incorporated into such observing systems to provide baselines for ecosystem monitoring because of their importance to people, their rapid response to environment conditions and their suggested role as indicators of disturbed systems. Such data sets would help expand our jellyfish time series, an essential component for expanding our knowledge of key drivers of jellyfish blooms. In the future, ocean observing systems could provide data for assimilation into coupled biophysical operational models.

There are many ways of collecting data on jellyfish abundance. Net sampling has been used to provide some of the best evidence for long-term changes in jellyfish abundance, particularly as part of fisheries surveys where trawl nets are deployed over large spatial scales which helps circumvent problems of patchy distribution (e.g. Lynam *et al.*, 2011). Net sampling also underpins global analysis of patterns of jellyfish abundance, which highlights how the largest biomass tends to be found in coastal sites (Lilley *et al.*, 2011). Trawl net sampling is appropriate for large, firmer-bodied individuals such as many scyphomedusae, a few hydromedusae and some ctenophores. However, trawl net sampling (and indeed some plankton net sampling) is poor for fragile species that break-up in nets and it will fail to collect small animals. Although net tows could be augmented with visual observations onboard ship (as, e.g. Sparks *et al.*, 2001; Doyle *et al.*, 2007) or from the air (Houghton *et al.*, 2006), this requires an understanding of the relationship between the observable and the hidden distribution of animals deeper in the water column, as well as effects of weather on observability. Although dual-frequency identification sonar shows much promise for the remote quantification of jellyfish populations in (very) shallow water, measures of abundance cannot at this stage be automated (Han and Uye, 2009; Makabe *et al.*, 2012). And this presents a problem for estimating the abundance of jellyfish in large blooms over the shelf. Perhaps the best way of obtaining routine, real-time data on abundance/biomass is to use multi-frequency hydro-acoustic methods as were first explored by Mutlu (Mutlu, 1996) and as have been used off Namibia by Brierley *et al.* (Brierley *et al.*, 2001, 2004, 2005) and Lynam *et al.* (Lynam *et al.*, 2006), though the task of developing and validating algorithms for separating jellyfish from other plankton and finfish is challenging. Often data on jellyfish exist, particularly on larger species in fisheries surveys and often over decades, but they have not yet been analysed and are not in the public domain (Lilley *et al.*, 2011; Lynam *et al.*, 2011). There needs to be an effort to identify and publish these existing datasets. Citizen scientists around our coastlines could also assist with semi-quantitative abundance estimates for common species (e.g. http://www.jellywatch.org), although we have to temper our enthusiasm with pragmatism (Silvertown, 2009).

A particularly powerful approach employed in HAB research is molecular probes for identification of problem species and their toxins (e.g. Bovee *et al.*, 2011). These can be deployed on automated buoys that can relay back to a ground station in near real time. Such integrated molecular and remote buoy technology could be developed for jellyfish that are particularly hazardous to human health (e.g. irukandji, box jellies). For problems where abundance is the issue (e.g. water intakes) then simpler monitoring solutions are possible—imaging systems on buoys.

Along with (hopefully) increased observations for jellyfish, appropriate data-basing of information is needed. Regional and global databases will support future efforts for understanding drivers of bloom events and prediction. The JEDI database (Condon *et al.*, 2012) has started this process and it is hoped that this database is continually updated into the future.

Rigorous jellyfish research

The field of jellyfish biology must be considered to be in its infancy and it is data-poor by comparison with that of other zooplankton taxa such as copepods. Much of our understanding of jellyfish biology and ecology comes from taxa that are readily available and easy to keep in culture, hence the plethora of work on *Aurelia* (Supplementary data, Fig. S2), largely from boreal labs. Yet, *Aurelia* is as poor a model for *Chrysaora* as it is for *Cyanea*, and to pool all data to generate empirical tools that can be applied to other systems is to compromise our understanding.

Perhaps part of the reason for jellyfish scientists to uncritically accept and use existing data could be our collective understanding of how difficult it is to work on jellyfish. Their size poses problems for experimentation; their lack of a closed digestive system means that collecting animals for otherwise standard diet studies from anywhere but the surface become a blue-water operation with the accompanying expense; their watery character means that estimates of population biomass, abundance and size structure are of relative value only, as they are so dependent upon the vagaries sampling at sea.

As a research community, we should strive to be more rigorous with our science. The NCEAS working group on investigating jellyfish blooms is a good example where quantitative methods have been applied to a global database of jellyfish time series (Condon *et al.*, 2013). Unfortunately, not all efforts by the jellyfish community are similarly rigorous. For example, of the 18 studies of jellyfish gut contents that have been published in the past 30 years, where the data have been based on individually dip-netted specimens, fewer than 12% have reported on the actual mesh size of the dip-nets used (Supplementary data, Table SI). And equally interesting is that of the 10 studies where individual jellyfish have been collected using a solid sampler (jar, bucket etc.), only 40% have reported on the mesh size subsequently used to screen gut contents (Supplementary data, Table SI). And yet we know that jellyfish can eat anything from protists to chordates. And we seem to be all too happy to accept, for example, results from unrepeated, once-off (especially field) studies. If we were working on fish, copepods, krill or even chaetognaths, we would not be able to get away with some of the work we are currently publishing and there is a pressing need for us to make our science more rigorous.

We therefore propose that the community motivate for an ICES/SCOR working group, with the aim of standardizing and increasing rigour in jellyfish methodology. This could culminate in a Jellyfish Methods Manual, similar to the ICES Zooplankton Methods Manual (Harris *et al.*, 2000). Such a manual would be a valuable addition to the field of jellyfish research.

Stimulating jellyfish research

The HAB research community can provide some lessons for promoting jellyfish research. The journal Harmful Algae is now 12 years old, has an impact factor of 4.28 (2011) and is a showcase for world-class HAB research. We call on the jellyfish research community to consider initiating a journal focused on jellyfish research, which would build on the regular special issues from jellyfish conferences. This could dramatically raise the profile of jellyfish research, although a journal devoted to jellyfish research might limit the number of non-jellyfish researchers who might view the papers.

The HAB research community has also established the international science program GEOHAB (Global Ecology and Oceanography of HABs), endorsed by SCOR (Scientific Committee on Oceanographic Research) and the IOC (Intergovernmental Oceanographic Commission). It has detailed Implementation and Science plans that support local science (see http://www.geohab.info). Its mission is to "foster international co-operative research on HABs in ecosystem types sharing common features, comparing the key species involved and the oceanographic processes that influence their population dynamics." The program encourages combined and innovative experimental, observational and modelling approaches, supports a global synthesis of scientific results and provides a way to help lever money from national and regional funding agencies. There would be similar benefits to establishing an international science program on the Global Ecology and Oceanography of Jellyfish (our own GEOJelly?). This is already happening on a regional scale, with the North Pacific Marine Science Organization (PICES) establishing a working group to address jellyfish issues in the North Pacific and propose solutions to minimize risk in the member nations.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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