Chapter 5
Ecological and Societal Benefits of Jellyfish

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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

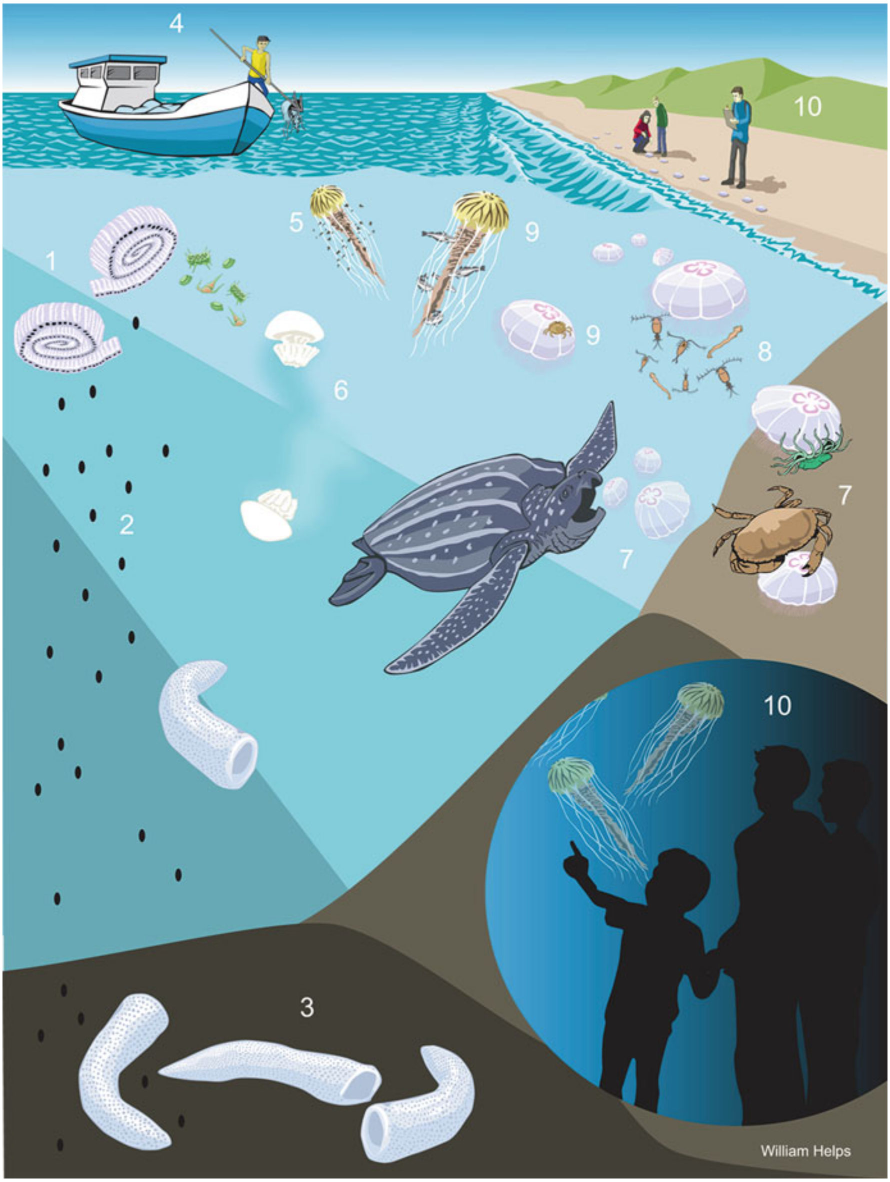

Fig. 5.1 The ecosystem services provided by jellyfish. Regulating services: (*1*) salps consume phytoplankton and transport carbon to the benthos via faecal pellets (*2*). (*3*) Accumulation of jellyfish carcasses (pyrosomes) on the seabed plays an important role in the transfer of carbon from surface 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

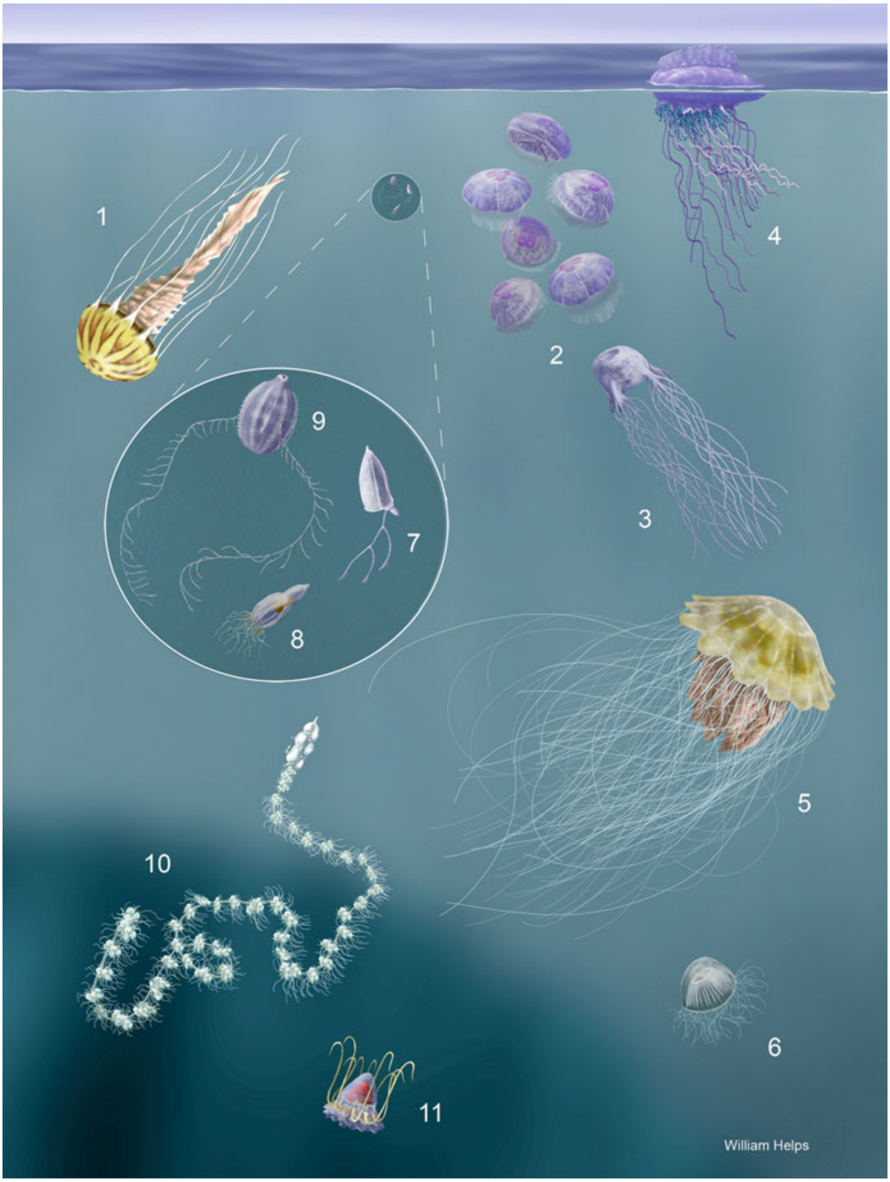

Fig. 5.2 The diversity and relative size of jellyfish within one functional group – the tentaculate predators. Figure illustrates the great variation in jellyfish morphology (e.g. bell shape, colonial structure) and tentacle length, number and type (i.e. nematocyst or colloblast bearing). (1) *Chrysaora 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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References

Addad S, Exposito J-Y, Faye C, Ricard-Blum S, Lethias C (2011) Isolation, characterization and biological evaluation of jellyfish collagen for use in biomedical applications. Mar Drugs 9:967–983

Alldredge AL (1976) Discarded appendicularian houses as sources of food, surface habitats and particulate organic matter in planktonic environments. Limnol Oceanogr 21:14–23

Andersen V (1998) Salp and pyrosomid blooms and their importance in biogeochemical cycles. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, pp 125–137

Anonymous (2005) Millennium ecosystem assessment. Ecosystems and human well-being: biodiversity synthesis. Ecol Manage Restor 6:226–227, World Resources Institute, Washington, DC

Arai MN (1988) Interactions of fish and pelagic coelenterates. Can J Zool 66:1913–1927

Arai MN (2005) Predation on pelagic coelenterates: a review. J Mar Biol Assoc UK 85:523–536

Arai MN, Welch DW, Dunsmuir AL, Jacobs MC, Ladouceur AR (2003) Digestion of pelagic Ctenophora and Cnidaria by fish. Can J Fish Aquat Sci 60:825–829

Ates RML (1988) Medusivorous fishes a review. Zoologische Mededelingen (Leiden) 62:29–42

Berline L, Stemmann L, Vichi M, Lombard F, Gorsky G (2011) Impact of appendicularians on detritus and export fluxes: a model approach at DyFAMed site. J Plankton Res 33:855–872

Billett DSM, Bett BJ, Jacobs CL, Rouse IP, Wigham BD (2006) Mass deposition of jellyfish in the deep Arabian Sea. Limnol Oceanogr 51:2077–2083

Bishop RE, Geiger SP (2006) Phronima energetics: Is there a bonus to the barrel? Crustaceana 79:1059–1070

Boero F (2002) Gelatinous zooplankton: here today and gone tomorrow, but ignored at our peril. Ocean Challenge 12(1):24–27

Boero F, Bouillon J, Gravili C, Miglietta MP, Parsons T, Piraino S (2008) Gelatinous plankton: irregularities rule the world (sometimes). Mar Ecol Prog Ser 356:299–310

Bonnet X, Shine R, Lourdais O (2002) Taxonomic chauvinism. Trends Ecol Evol 17:1–3

Breitburg DL, Crump BC, Dabiri JO, Gallegos CL (2010) Ecosystem engineers in the pelagic realm: alteration of habitat by species ranging from microbes to jellyfish. Integr Comp Biol 50:188–200

Brodeur RD (1998) In situ observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. Mar Ecol Prog Ser 163:11–20

Brodeur RD, Sugisaki H, Hunt GL (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar Ecol Prog Ser 233:89–103

Buesseler KO, Lamborg CH, Boyd PW, Lam PJ, Trull TW, Bidigare RR et al (2007) Revisiting carbon flux through the ocean's twilight zone. Science 316:567–570

Castro JJ, Santiago JA, Santana-Ortega AT (2001) A general theory on fish aggregation to floating objects: an alternative to the meeting point hypothesis. Rev Fish Biol Fisher 11:255–277

Chalfie M, Kain SR (2006) Green fluorescent protein. Properties, applications, and protocols, 2nd edn. Wiley, Hoboken, 443 pp

Chudakov DM, Matz MV, Lukyanov S, Lukyanov KA (2010) Fluorescent proteins and their applications in imaging living cells and tissues. Physiol Rev 90:1103–1163

Colin SP, Costello JH, Graham WM, Higgins J (2005) Omnivory by the small cosmopolitan hydromedusa *Aglaura hemistoma*. Limnol Oceanogr 50:1264–1268

Condon RH, Steinberg DK, del Giorgio PA, Bouvier TC, Bronk DA, Graham WM, Ducklow HW (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc Natl Acad Sci U S A 108:10225–10230

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Naeem S, Limburg K, Paruelo J, O'Neill RV, Raskin R, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Costello JH, Colin SP (1994) Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar Biol 121:327–334

Costello JH, Colin SP (1995) Flow and feeding by swimming scyphomedusae. Mar Biol 124:399–406

Costello JH, Colin SP (2002) Prey resource use by coexistent hydromedusae from Friday Harbor, Washington. Limnol Oceanogr 47:934–942

Costello JH, Colin SP, Dabiri JO (2008) Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. Invertebr Biol 127:265–290

Curtis DE (2001) "The Lion's Mane": a topical review. The Baker Street J 56(4):15–19

Dawson MN, Hamner WM (2003) Geographic variation and behavioral evolution in marine plankton: the case of *Mastigias* (Scyphozoa, Rhizostomeae). Mar Biol 143:1161–1174

Dawson MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451:131–144

Díaz S, Tilman D, Fargione J, Chapin F, Dirzo R (2005) Biodiversity regulation of ecosystem services. In: Hassan R, Scholes R, Ash N (eds) Ecosystems and human wellbeing: current state and trends: findings of the condition and trends Working Group, Chapter 11. Island Press, Washington, DC, pp 297–329

Dong J, Jiang L-X, Tan K-F, Liu H-Y, Purcell JE, Li P-J, Ye C-C (2009) Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review. Hydrobiologia 616:113–118

Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays GC (2007) The energy density of jellyfish: estimates from bomb-calorimetry and proximate-composition. J Exp Mar Biol Ecol 343:239–252

Fanelli D (2010) Do pressures to publish increase scientists' bias? An empirical support from US States data. PLoS One 5(4):e10271

Fautin DG (2009) Structural diversity, systematics, and evolution of cnidae. Toxicon 54:1054–1064

Fenaux R (1998) The classification of Appendicularians. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, NY, pp 295–306

Fleming NEC, Houghton JDR, Magill CL, Harrod C (2011) Preservation methods alter stable isotope values in gelatinous zooplankton: implications for interpreting trophic ecology. Mar Biol 158:2141–2146

Garm A, Oskarsson M, Nilsson D-E (2011) Box jellyfish use terrestrial visual cues for navigation. Curr Biol 21:798–803

Gasca R, Haddock SHD (2004) Associations between gelatinous zooplankton and hyperiid amphipods (Crustacea: Peracarida) in the Gulf of California. Hydrobiologia 530:529–535

Godeaux J (1998) The relationships and systematics of the Thaliacea, with keys for identification. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, NY, pp 273–294

Gorsky G, Fenaux R (1998) The role of appendicularia in marine food webs. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, NY, pp 161–169

Graham CT, Harrod C (2009) Implications of climate change for the fishes of the British Isles. J Fish Biol 74:1143–1205

Graham WM, Kroutil RM (2001) Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. J Plankton Res 23:67–74

Greene HW (2005) Organisms in nature as a central focus for biology. Trends Ecol Evol 20:23–27

Haddock SHD (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. Hydrobiologia 530:549–556

Haddock SHD (2007) Comparative feeding behavior of planktonic ctenophores. Int Comput Biol 47:847–853

Hardy AC (1956) The open sea: the world of plankton. Collins, London

Harrod C, Grey J, McCarthy TK, Morrissey M (2005) Stable isotope analyses provide new insights into ecological plasticity in a mixohaline population of European eel. Oecologia 144:673–683

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, padee NG, Sims DW (2012) High activity and Levy searches: jellyfish can search the water column like fish. Proc Roy Soc Ser B Lon 279:465–473

Heaslip SG, Iverson SJ, Bowen WD, James MC (2012) Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. PLoS One 7(3):e33259

Hodgson WC, Isbister GK (2009) The application of toxins and venoms to cardiovascular drug discovery. Curr Opin Pharmacol 9:173–176

Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. Ecol Econ 29:253–268

Hong J, He-Qin C, Hai-Gen X, Arrequin-Sanchez F, Zetina-Rejon MJ, Luna PDM, Le Quesne WJF (2008) Trophic controls of jellyfish blooms and links with fisheries in the East China Sea. Ecol Model 212:492–503

Houghton JDR, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87:1967–1972

Hsieh YHP, Leong FM, Rudloe J (2001) Jellyfish as food. Hydrobiologia 451:11–17

Katija K, Dabiri JO (2009) A viscosity-enhanced mechanism for biogenic ocean mixing. Nature 460:624–626

Kideys AE (2002) Fall and rise of the Black Sea ecosystem. Science 297:1482–1484

Kingsford MJ, Choat JH (1989) Horizontal distribution patterns of presettlement reef fish – are they influenced by the proximity of reefs. Mar Biol 101:285–297

Kingsford MJ, Pitt KA, Gillanders BM (2000) Management of jellyfish fisheries, with special reference to the order Rhizostomeae. Oceanogr Mar Biol Annu Rev 38:85–156

Knowlton N (2004) Multiple “stable” states and the conservation of marine ecosystems. Prog Oceanogr 60:387–396

Kotler BP, Brown JS, Slotow RH, Goodfriend WL, Strauss M (1993) The influence of snakes on the foraging behavior of gerbils. Oikos 67:309–316

Last JM (1978) The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Mar Biol 45:359–368

Lebrato M, Jones DOB (2009) Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). Limnol Oceanogr 54:1197–1209

Lebrato M, Pitt KA, Sweetman AK, Jones DOB, Cartes JE, Oschlies A, Condon RH, Molinero JC, Adler L, Gaillard C, Lloris D, Billett BSM (2012) Jelly-falls historic and recent observations: a review to drive future research directions. Hydrobiologia 690:227–245

Link JS, Ford MD (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. Mar Ecol Prog Ser 320:153–159

Lynam CP, Brierley AS (2007) Enhanced survival of 0-group gadoid fish under jellyfish umbrellas. Mar Biol 150:1397–1401

Lynam CP, Heath MR, Hay SJ, Brierley AS (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. Mar Ecol Prog Ser 298:157–167

Lynam CP, Gibbons MJ, Axelsen BE, Sparks CAJ, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. Curr Biol 16:492–493

Mackie GO (2002) What's new in cnidarian biology? Can J Zool 80:1649–1653

Mackie GO, Pugh PR, Purcell JE (1987) Siphonophore biology. Adv Mar Biol 24:97–262

Madin LP (1982) Production, composition and sedimentation of salp fecal pellets in oceanic waters. Mar Biol 67:39–45

Madin LR, Deibel D (1998) Feeding and energetics of Thaliacea. In: Bone Q (ed) The biology of pelagic tunicates. Oxford University Press, Oxford, NY, pp 81–103

Mansueti R (1963) Symbiotic behavior between small fishes and jellyfishes, with new data on that between the Stromateid, *Peprilus alepidotus*, and the Scyphomedusa, *Chrysaora quinquecirrha*. Copeia 1:40–48

Mapstone GM (2003) Redescriptions of two physonect siphonophores, *Apolemia uvaria* (Lesueur, 1815) and *Tottonia contorta* Margulis, 1976, with comments on a third species *Ramosia vitiazi* Stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae). Syst Biodivers 1:181–212

Marc P, Canard A, Ysnel F (1999) Spiders (Araneae) useful for pest limitation and bioindication. Agr Ecosyst Environ 74:229–273

Martorelli SR (2001) Digenea parasites of jellyfish and ctenophores of the southern Atlantic. Hydrobiologia 451:305–310

Masuda A, Baba T, Dohmae N, Yamamura M, Wada H, Ushida K (2007) Mucin (Qniumucin), a glycoprotein from jellyfish, and determination of its main chain structure. J Nat Prod 70:1089–1092

Mochioka N, Iwamizu M (1996) Diet of anguilloid larvae: Leptocephali feed selectively on larvacean houses and fecal pellets. Mar Biol 125:447–452

Monterey Bay Aquarium (2004) Jellies: living art. Summative evaluation. Monterey Bay Aquarium, New York, 49 pp

Moss AG, Estes AM, Muellner LA, Morgan DD (2001) Protistan epibionts of the ctenophore *Mnemiopsis mccradyi* Mayer. Hydrobiologia 451:295–304

Ohta N, Sato M, Ushida K, Kokubo M, Baba T, Taniguchi K, Urai M, Kihirak K, Mochida J (2009) Jellyfish mucin may have potential disease-modifying effects on osteoarthritis. BMC Biotechnol 9:98

Olson MH (1996) Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77:179–190

Omori M, Nakano E (2001) Jellyfish fisheries in Southeast Asia. Hydrobiologia 451:19–26

Pagès F (2000) Biological associations between barnacles and jellyfish with emphasis on the ectoparasitism of *Alepas pacifica* (Lepadomorpha) on *Diplulmaris malayensis* (Scyphozoa). J Nat Hist 34:2045–2056

Pagès F, Corbera J, Lindsay D (2007) Piggybacking pycnogonids and parasitic narcomedusae on *Pandea rubra* (Anthomedusae, Pandeidae). Plankt Benth Res 2:83–90

Pauly D, Graham W, Libralato S, Morissette L, Palomares MLD (2009) Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia 616:67–85

Perissinotto R, Pakhomov EA (1997) Feeding association of the copepod *Rhincalanus gigas* with the tunicate salp *Salpa thompsoni* in the southern ocean. Mar Biol 127:479–483

Piraino S, Boero F, Aeschbach B, Schmid V (1996) Reversing the life cycle: Medusae transforming into polyps and cell transdifferentiation in *Turritopsis nutricula* (Cnidaria, Hydrozoa). Biol Bull 190:302–312

Piraino S, Fanelli G, Boero F (2002) Variability of species' roles in marine communities: change of paradigms for conservation priorities. Mar Biol 140:1067–1074

Pitt KA, Koop K, Rissik D (2005) Contrasting contributions to inorganic nutrient recycling by the co-occurring jellyfishes, *Catostylus mosaicus* and *Phyllorhiza punctata* (Scyphozoa, Rhizostomeae). J Exp Mar Biol Ecol 315:71–86

Pitt KA, Welsh DT, Condon RH (2009) Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616:133–149

Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar Biol 65:83–90

Purcell JE (1984) Predation on fish larvae by *Physalia physalis*, the Portuguese man of war. Mar Ecol Prog Ser 19:189–191

Purcell JE (1989) Predation on fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. Can J Fish Aquat Sci 46:1415–1427

Purcell JE (1991) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216:335–342

Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Annales de l'Instit Oceanogr 73:125–137

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:27–44

Purcell JE, Grover JJ (1990) Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. Mar Ecol Prog Ser 59:55–61

Purcell JE, Uye S-I, Lo W-T (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Purcell JE, Clarkin E, Doyle TK (2012) Foods of *Velella velella* (Cnidaria: Hydrozoa) in algal rafts and its distribution in Irish seas. Hydrobiologia 690:47–55

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Riisgard HU, Larsen PS (2010) Particle capture mechanisms in suspension-feeding invertebrates. Mar Ecol Prog Ser 418:255–293

Robison BH (2004) Deep pelagic biology. J Exp Mar Bio Ecol 300:253–272

Runge JA, Pepin P, Silvert W (1987) Feeding behavior of the Atlantic mackerel *Scomber scombrus* on the hydromedusa *Aglantha digitale*. Mar Biol 94:329–333

Sato R, Tanaka Y, Ishimaru T (2001) House production by *Oikopleura dioica* (Tunicata, Appendicularia) under laboratory conditions. J Plankton Res 23:415–423

Silvertown J (2009) A new dawn for citizen science. Trends Ecol Evol 24:467–471

Smith S, Ward V, House A (2011) 'Impact' in the proposals for the UK's Research Excellence Framework: shifting the boundaries of academic autonomy. Res Policy 40:1369–1379

Sørnes TA, Hosia A, Båmstedt U, Aksnes DL (2008) Swimming and feeding in *Periphylla periphylla* (Scyphozoa, Coronatae). Mar Biol 153:653–659

Steinberg DK, Silver MW, Pilskaln CH, Coale SL, Paduan JB (1994) Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. Limnol Oceanogr 39:1606–1620

Towanda T, Thuesen EV (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. Mar Ecol Prog Ser 315:221–236

Tsien RY (1998) The green fluorescent protein. Annu Rev Biochem 67:509–544

Turner JT (2002) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. Aquat Microb Ecol 27:57–102

Welsh DT, Dunn RJK, Meziane T (2009) Oxygen and nutrient dynamics of the upside down jellyfish (*Cassiopea* sp.) and its influence on benthic nutrient exchanges and primary production. Hydrobiologia 635:351–362

West EJ, Pitt KA, Welsh DT, Koop K, Rissik D (2009) Top-down and bottom-up influences of jellyfish on primary productivity and planktonic assemblages. Limnol Oceanogr 54:2058–2071

Wiebe PH, Madin LP, Haury LR, Harbison GR, Philbin LM (1979) Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. Mar Biol 53:249–255

You K, Ma C, Gao H, Li F, Zhang M, Qiu Y, Wang B (2007) Research on the jellyfish (*Rhopilema esculentum* Kishinouye) and associated aquaculture techniques in China: current status. Aquac Int 15:479–488

Zimmer M (2009) GFP: from jellyfish to the Nobel prize and beyond. Chem Soc Rev 38:2823–2832