REVIEW

Successes and challenges in jellyfish ecology: examples from *Aequorea* spp.

Jennifer E. Purcell[*]

Biology Department, Western Washington University, 516 High St., Bellingham, WA 98225, USA

ABSTRACT: Historically, jellyfish have been little studied relative to fishes, and they have been considered to be nuisances to humans and of little ecological importance. Research in the last 3 decades on *Aequorea* spp. hydromedusae highlights how important jellyfish are, how little is known, and the many needs and opportunities for studies on jellyfish. The family Aequoreidae contains about 30 recognized species worldwide; however, discrimination among those species is difficult and needs clarification by molecular genetics. As for most cnidarians with a swimming medusa stage, *Aequorea* spp. also have an attached stage that probably is key to bloom formation but whose extent and ecology are not known. Because of their large sizes, they are reported from citizen science programs and caught in fishing trawls; therefore, abundance data for *Aequorea* spp. exist from commercial fishing areas. Dietary data for *Aequorea victoria* show it is an important predator of fish eggs, fish larvae, and crustacean zooplankton, indicating that the medusae are potentially important as predators and competitors of fish. Although their potential importance seems obvious, *Aequorea* spp. have been understudied globally. New chemical methods may increase knowledge about feeding by *Aequorea* spp. and other species. Large-scale feeding effects could be estimated from metabolic and biomass data, which is important for ecosystem models and fisheries management. As pelagic cnidarians and ctenophores and opportunities to study them increase, new technology and methods will provide new insights into their biology.

KEY WORDS: Review · Bloom · Fish · Aquaculture · Gelatinous · Trophic · Predation · Reproduction · Zooplankton

INTRODUCTION

Many recent reviews about jellyfish have similar conclusions; specifically, that jellyfish seem to be increasing, possibly due to deteriorating conditions in the oceans through a combination of human activities (overfishing, eutrophication, transport of invasive alien species, marine construction, and global warming), and causing more problems for humans (e.g. Purcell 2012 and references therein). Some scientists request caution in interpreting the reported jellification of the oceans because of the cyclic long-term temporal patterns of blooms and the paucity of data from most of the oceans (e.g. Purcell 2005, 2012, Condon et al. 2013). Here, I review research on *Aequorea* spp. to highlight what is known and not known to suggest fruitful research opportunities for the increasing number of scientists studying jellyfish.

I feature *Aequorea* spp. jellyfish for several reasons. Foremost is that they illustrate many important research directions for pelagic cnidarian and ctenophore species, the predaceous groups of gelatinous zooplankton. Because of their large sizes and abundance, their distributions can be documented from fishery trawls and citizen science programs. The few regions where data are available show that the spe-

cies occur in unusually high abundances (blooms) in some years. *Aequorea victoria* is important in the ecosystem as a predator of fish eggs, fish larvae, zooplankton, and other pelagic cnidarians and ctenophores. Therefore, I suggest that because they are large, abundant, and predators and competitors of fish, *Aequorea* spp. are of special interest to humans in marine ecosystems. Despite the fact that the family and genus are globally distributed, what is known about these jellyfish is only from a few locations. Therefore, I also update past methods with new techniques that can further the study of *Aequorea* spp. and other pelagic cnidarians and ctenophores.

AEQUOREA SPP. IDENTIFICATION

The family Aequoreidae in the order Hydrozoa is comprised of about 30 recognized species. The inconspicuous attached hydroids are known for only 2 *Aequorea* species; therefore, the species in the genus are distinguished based on characteristics of the medusae, which are distinctive among hydromedusae due to their large sizes, numerous radial canals (10s up to 100), and large mouths (Fig. 1). The medusae are very large (up to 40 cm) relative to most of the other 800+ species of hydromedusae, which generally are 1 cm or less in swimming bell width or height (Bouillon & Boero 2000). The 5 recognized genera (*Aequorea*, *Aldersladia*, *Gangliostoma*, *Rhacostoma*, and *Zygocanna*) are distinguished by only microscopic differences of the radial canals (Bouillon
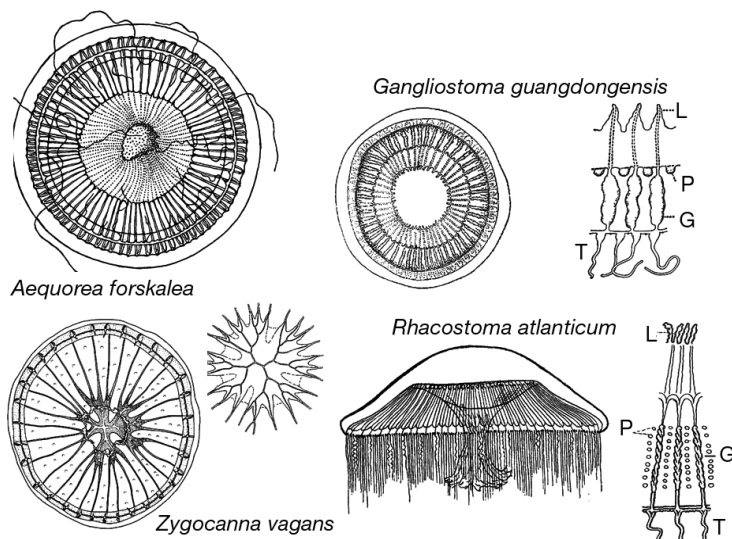

Fig. 1. Representatives from genera in the family Aequoreidae. G: gonad; L: lip; P: papilla; T: tentacle. Assembled from Bouillon et al. (2006) and reprinted with permission from ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris

et al. 2006, Gershwin 2006; Fig. 1), suggesting that even less-conspicuous features are required for discrimination among species.

Because differentiation among *Aequorea* spp. is difficult for non-experts, correct identification of the medusae has been uncertain. For example, *Aequorea forskalea* (formerly *A. aequorea*) has been reported from all over the world (e.g. Bering Sea, northeastern Pacific, Mediterranean Sea, South Africa), but that name may have been applied without correct identification (e.g. Purcell 2003). Molecular genetics of *Aequorea* spp. has been used in phylogenetic analyses (Collins et al. 2006, Maronna et al. 2016) and species identification (Zheng et al. 2008). Molecular genetics has great promise to elucidate the various species in the Aequoreidae and their distributions globally.

AEQUOREA SPP. POPULATION DYNAMICS

Reproduction

The life cycles of many medusae, including *Aequorea* spp., alternate between a swimming medusa stage and an attached polyp stage: hydroids of hydromedusae, scyphistomae of scyphomedusae, cubopolyps of cubomedusae. Mature medusae of all jellyfish are sexually reproductive, yet little is known about how sexual reproduction contributes to population size. Only 2 scyphozoan species, Siphonophorae (>176 species) and Trachylinae (>101 species) hydrozoan species, and pelagic ctenophores (>190 species) are known to have direct development in the water (Jarms et al. 1999, Bouillon & Boero 2000, Collins et al. 2006). In other scyphozoans (>200 species), cubozoans (>37 species), and most hydromedusans (>900 species), the fertilized eggs develop into planulae that attach to hard surfaces (Bouillon et al. 2006, Bentlage et al. 2010). In those species, the many factors affecting survival between sexual reproduction and the next medusa generation make determining the importance of sexual reproduction extremely difficult.

Light may coordinate the sexual biology of pelagic cnidarians and ctenophores, but little information exists. Ovulation and sperm release in some hydromedusae are stimulated by light (e.g. Genzano & Kubota 2003 and references therein), as

observed for *Aequorea forskalea* (V. L. Fuentes pers. comm.). Although *A. victoria* medusae do not have ocelli or any other conventional photoreceptors, they appear at the surface near dawn in the Salish Sea (semi-enclosed coastal waters of northwestern Washington, USA, and southwestern British Columbia, Canada) and spawned about 4 h after dawn in the laboratory (Mills 1983). Thus, *A. victoria* medusae were concentrated near the surface when spawning, which could increase fertilization success.

Larson (1986a) measured daily ova production in 6 species of hydromedusae in the Salish Sea. Unfed *A. victoria* medusae produced 300 to 8600 eggs d^{-1} medusa^{-1} daily for 7 d (3% of medusa dry weight d^{-1}). Egg production for the 6 species ranged from 1 to 16% of medusa dry weight d^{-1}. The dry weights of gonads relative to the swimming bell of mature medusae of 8 species ranged from 9 to 50%, excluding *A. victoria* with its narrow gonads on numerous radial canals (Larson 1986a), which was comparable to that (31%) of another hydromedusa, *Olindias sambaquiensis*, near shore in Argentina (Chiaverano et al. 2004).

Although huge numbers of sexual products typically are produced by pelagic cnidarians, few studies have examined the mortality rates of eggs or larvae. Pennington (1990) found that *Phialidium gregarium* (*Clytia gregaria*) hydromedusae ate *A. victoria* embryos and planula larvae, but neither species fed on *C. gregaria* or conspecific embryos or larvae.

Recruitment of conspicuous hydroids in nature is relatively well studied (e.g. Migotto et al. 2001, Wintzer et al. 2011, Martell et al. 2017) compared to recruitment of scyphozoans or cubozoans, for which virtually no information exists *in situ*. Concern about damage to fish in aquaculture pens recently has spurred studies on hydroid biofouling (Guenther et al. 2009, Bosch-Belmar 2016).

The role of asexual reproduction in contributing to blooms is poorly studied in hydromedusae. The hydroid stage is known for about half of the described hydromedusae species (Bouillon & Boero 2000). The hydroids of *Aequorea* spp. are very small (~1 mm), cryptic, and seldom reported in nature (e.g. Mills 1981, Migotto et al. 2001). Only a few studies estimate the extents or reproductive capacities of hydroid populations in nature that would contribute to jellyfish blooms (e.g. Genzano et al. 2008, Bosch-Belmar 2016). The hydromedusae also reproduce asexually in some species (reviewed in Boero et al. 2002), including *A. macrodactyla* (in Stretch & King 1980), which would further increase medusa population size.

Seasonal patterns of abundance

The ecology of *A. victoria* medusae has been extensively studied in the Salish Sea, where they occurred throughout the year at the Friday Harbor Laboratories (FHL), Washington, USA (Mills 1981). Recruitment of young *A. victoria* medusae occurred in early spring (Table 1), when biomass of medusae peaked in June and ranked third among 33 species of pelagic cnidarian and ctenophore species (Larson 1986b). *A. victoria* medusae also occurred throughout the year in East Sound, Washington (Fig. 2A). New medusae were produced between March and June, with mean densities rapidly increasing to 52 medusae m^{-3} in July 2004 (Fig. 2A). *A. victoria* medusa numbers were low in 2002 to 2003, when they averaged only 11% of the 10 common pelagic cnidarian and ctenophore species, but high in 2005 to 2006, when they averaged 76% of the total. They maintained high numbers (3 to 5 m^{-3}) through the winter of 2005. *Aurelia labiata* scyphomedusae also overwinter in some years in East Sound. It is not known if individual medusae survive more than 1 yr.

Aequorea spp. medusae also occur in high abundance in other locations (Table 1). In the Mexican Caribbean Sea, *A. aequorea* (*forskalea*) constituted 83% of all medusae over the year and occurred in all months, peaking in autumn (Segura-Puertas & Damas-Romero 1997). Most *Aequorea* sp. medusae in the California Current, USA, were caught in spring; however, *Chrysaora fuscescens* medusae were 10 times more abundant than *Aequorea* sp., with high numbers in summer and autumn (Suchman et al. 2012). *A. vitrina* was present from mid-August to mid-October after high-salinity water entered Skive Fjord, Denmark, from the North Sea (Møller & Riisgård 2007b). *Aequorea* spp. are considered springtime species in the Yellow Sea, China (Zhang et al. 2012), and in the Catalan Sea, Spain. Thus, *Aequorea* species are reported mostly from cool waters.

Individual and population growth rates

Growth rates of pelagic cnidarian and ctenophore species are infrequently known, at least in part because of methodological difficulties (but see supplementary materials in Hirst & Forster 2013, Pitt et al. 2013). Problems arise in the laboratory because many species are large and difficult to collect, maintain in good condition, and feed a natural diet (e.g. Purcell et al. 2013). *Aequorea victoria* medusae

Table 1. Abundance (numbers or biomass) of *Aequorea* spp. medusae. In Method, net size is mouth area. BCC: British Columbia, Canada; SS: Salish Sea

| Species	Location	Duration	Method	Abundance	Reference
A. victoria	Saanich Inlet, BCC, SS	15 mo 1980–1981	25 m vertical tow, 0.2 m² net	≤0.8 m⁻³	Larson (1986b)
A. victoria	Kulleet Bay SS, north BCC coast	Spring 1983–1987	Horizontal tow, 0.8 m² net	0.006–5.1 m⁻³	Purcell & Arai (2001 and references therein)
A. victoria	East Sound, WA, USA, SS	60 mo 2002–2006	Horizontal tow, 0.8 m² net	≤52 m⁻³	J. E. Purcell (unpubl.)
Aequorea spp.	Caribbean Sea, Mexico	Apr–Sep 2000–2007	Horizontal tow 0.13 m² net	1.8 m⁻³	Segura-Puertas & Damas-Romero (1997)
A. forskalea	N Benguela Current, Africa	Summer	Fishing trawls	≤2 m⁻³	Buecher et al. (2001)
Aequorea sp.	N California Current, USA	Jun, Aug 2000, 2002	30 m wide trawl	1.9–11.7 1000 m⁻³	Suchman & Brodeur (2005)
A. aequorea (*forskalea*)	N California Current, USA	Apr–Sep 2000–2007	30 m wide trawl	~400 km⁻²	Suchman et al. (2012)
A. forskalea	Skive Fjord, Denmark	2003–2005	0.3 m², 1.8 m² nets	0.2–2.0 m⁻³	Møller & Riisgård (2007c)
Aequorea sp.	S Argentine Sea	Jun 2000	10 m² trawl	2100 m⁻³	Alvarez-Colombo et al. (2003)
A. forskalea	SW Bering Sea, Russia	2004	Horizontal trawls	≤8.6 m⁻³	Zavolokin (2010)
A. forskalea	W Bering Sea, Russia	Summer 1991–2011	Horizontal trawls	52.7 kg km⁻² (mean)	Decker et al. (2014)
A. forskalea	E Bering Sea, USA	Aug–Oct 2004–2007	Surface trawls	≤80 kg km⁻²	Cieciel et al. (2009)
A. forskalea	W Bering Sea, Russia	2009–2012	Trawls	≤177 kg km⁻²	Radchenko (2013)
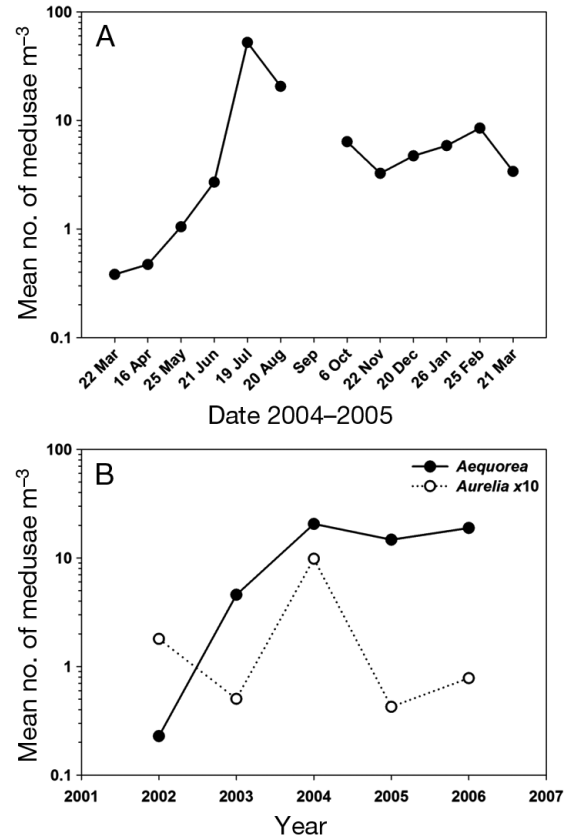
Fig. 2. Mean densities of medusae in East Sound, Washington, USA. (A) Annual pattern of *Aequorea victoria* in 2004 to 2005 shows rapid increase in spring and overwintering. Data are missing from September 2004. (B) Densities of *A. victoria* and *Aurelia labiata* medusae by year of sampling; note different scales for the 2 species. (J. E. Purcell unpubl. data)

(0.6 mm diameter) were kept in ambient water from the Salish Sea (10 to 13°C, 28 to 30 salinity) and fed *Artemia* sp. nauplii supplemented with other jellyfish and ctenophore species for 60 d (Arai 1980). Specific growth rates decreased from 14 to 2% d⁻¹ as medusa size increased. Growth efficiency of *Aequorea victoria* grown for 28 d on known masses of ctenophores was $K = 19.3\%$ of the ash-free dry weight (Arai 1980).

One of the remarkable abilities of pelagic cnidarian and ctenophore species is to shrink (degrow) when food is scarce and regrow when food is restored. Although degrowth has been studied for few species other than *Aequorea victoria* (in Arai 1986), *Aurelia labiata* (as *Aurelia aurita* in Hamner & Jensen 1974), and *Pelagia noctiluca* (in Lilley et al. 2014), it is generally assumed to be true for pelagic cnidarian and ctenophore species.

Estimating growth *in situ* is problematic for animals that lack an internal or external skeleton to measure, that shrink when food is scarce, that are transported in the water, and that are difficult to tag and to follow. Changes in medusa diameter or wet mass *in situ* have been measured over time and growth calculated mostly for scyphozoan populations (e.g. Dong et al. 2009). For newly recruited *Aequorea victoria* medusae in the Salish Sea, the changes in mass over time (coefficient of population biomass increase) averaged 0.14 d^{-1} during spring, which was very similar to that of 10 other pelagic cnidarian and ctenophore species (mean 0.11 d^{-1}) (Larson 1986b).

In Denmark, *Aequorea vitrina* medusae and *Aurelia aurita* ephyrae were grown for 4 d and fed *Artemia* sp. nauplii (Møller & Riisgård 2007a). Maximum specific growth rates (~0.13 d^{-1}) at 2 mg dry weight decreased with size in both species to stabilize at ~0.05 d^{-1}. The maximum specific growth (0.05 d^{-1}) of *Aequorea vitrina* in Skive Fjord corresponded to maximum constant growth in the laboratory, indicating that the growth potential was realized *in situ* (Møller & Riisgård 2007a,b). Growth of *Aequorea vitrina in situ* in autumn was the same as growth of *Aurelia aurita* and *Sarsia tubulosa* (means 0.05 d^{-1}) in spring. Thus, specific growth rates measured in the laboratory and *in situ* and for the 3 species were very similar.

Palomares & Pauly (2009) demonstrated use of the von Bertalanffy growth equation with published size frequency distributions to calculate growth *in situ* for 34 pelagic cnidarian and ctenophore species. For example, diameters of *Aequorea forskalea* medusae yielded the growth coefficient of $K = 0.87$ yr^{-1} in the Benguela Current (Benguela); however, Buecher et al. (2001) reported that only the central disc (56% of the total diameter) remained after collection. It was unclear if Palomares & Pauly (2009) corrected the diameters, which could have affected their results.

Mortality

Although medusae in temperate latitudes generally have seasonal population cycles, few studies address what ends the life of the medusae (reviewed in Pitt et al. 2014). Most damage at FHL in the Salish Sea was due to immature hyperiid amphipods (*Parathemisto pacifica*), which infested the stomachs and canal systems of *A. victoria* medusae, causing pits and tunnels in the swimming bell in 52 to 78% of the medusae by autumn (Mills 1993). The medusae regenerated damaged tissue with food in the labora-

tory but seemed unable to recover when gut fullness decreased in the autumn. Apparent infestation of *A. forskalea* medusae by hyperiids (*Hyperia medusarum*) in the Benguela was very low (3 of 2488 medusae), possibly because adults abandon their host medusa when disturbed and because only the firm central disk of the medusae remained after collection in the fishing trawl (Buecher et al. 2001). Infestations by hyperiid amphipods also are common among scyphomedusae (e.g. Fleming et al. 2014) and other pelagic cnidarian and ctenophore taxa (e.g. Gasca et al. 2015), and their effects may be greater than realized.

The main predators of *A. victoria* medusae at FHL in the 1950s to 1960s probably were humans, who harvested 100 000 to 200 000 medusae for their bioluminescent protein (aequorin) annually for 20 yr (Mills 1983), which eventually led to a small local population at FHL (Mills 2001). Fortunately, green fluorescent protein (GFP) is synthesized now that *A. victoria* is famous for its calcium-activated photoprotein and GFP, which are used in living cells and have revolutionized the fields of cellular and molecular biology and medicine (e.g. Graham et al. 2014).

Although *Aequorea* sp. was among the by-catch in Vietnamese jellyfish fisheries, it was not processed for food (Nishikawa et al. 2008). *Aequorea* spp. have low percentages of carbon and nitrogen relative to edible rhizostome medusae (Kogovšek et al. 2014) and lack their desirable firm texture; therefore, these medusae may be unsuitable as human food.

Spatial and vertical distributions

Species of Aequoreidae are found globally, except in polar waters (Purcell et al. 2015a, Nogueira et al. 2016). Distributions of the various species generally are unknown because of uncertainties in identification. Regional distributions of pelagic Hydrozoa show 7 *Aequorea* and 2 *Zygocanna* species in waters around southern Africa (supplementary data in Gibbons et al. 2010) and 4 *Aequorea* spp. and *Rhacostoma atlanticum* in waters around southern South America (Rodriguez et al. 2017); however, data are lacking for much of the world's oceans (e.g. Nogueira et al. 2016).

Distributions of the *Aequorea* spp. medusae have been studied mostly where large scyphomedusae (*Chrysaora* spp.) have bloomed and created concerns for fisheries (the northern Benguela, the Bering Sea, and the northern California Current). Species of *Aequorea* also have bloomed in those areas and have

been included in the large-scale sampling with fishing trawls (Brierley et al. 2001, Zavolokin et al. 2008, Suchman et al. 2012). In those regions, *Aequorea* spp. medusae are mainly further offshore than *Chrysaora* spp., which tend to be in shallower upwelling waters (Fig. 3). In each region, *Aequorea* spp. medusae are more widely distributed than the *Chrysaora* spp. medusae and, therefore, more numerous overall (Brierley et al. 2001, Zavolokin et al. 2008, Suchman et al. 2012). *Aequorea* spp. medusae also occurred along the entire coastline sampled in the northern California Current, throughout nearshore waters of the Salish Sea, British Columbia, Canada, and of Prince William Sound (PWS), Alaska, USA (Purcell 1989, 1990, 2003, Suchman et al. 2012, Greene et al. 2015).

The vertical distributions of *A. forskalea* medusae were estimated with several methods: acoustics (Brierley et al. 2001) and a submersible (Sparks et al. 2005) in the Benguela, trawls (Zavolokin 2010) and a remotely operated vehicle (ROV) (Brodeur et al. 2002) in the Bering Sea. Fishing trawls are usually semi-quantitative (catch per time or distance) and not depth specific. Therefore, the visual counts of medusae from the submersible and ROV provided the most accurate estimates of the weighted mean depths (24 m) in the Bering Sea and 23, 43, and 42 m

at 3 stations in the Benguela (Fig. 3). Acoustic sampling showed that *Aequorea* sp. medusae formed dense layers near bottom (~100 m) during the day, ascended at dusk and distributed throughout the water column, and then descended after dawn in the southern Argentine Sea (Alvarez-Colombo et al. 2003). Those authors and Brierley et al. (2001) found similar acoustic target strengths for *Aequorea* spp. medusae (−64.15 and −66.3 dB, respectively). The distributions of pelagic cnidarians and ctenophores are not uniform throughout the water column or static, which are important factors when considering their ecosystem effects.

AEQUOREA SPP. RELATIONSHIPS WITH ENVIRONMENTAL CONDITIONS AND BLOOM FORMATION

Eutrophication

Eutrophication, the addition of nutrients to waterways, is one of the major global pollution problems (Rabalais et al. 2014). Generally, eutrophication creates poor conditions for visually feeding fish because of small prey and turbidity but not for non-visual jellyfish (reviewed in Purcell 2012). The coastal environments where jellyfish have increased generally are eutrophic with high prey densities. In general, jellyfish eat more when more food is available, and feeding does not saturate at natural prey densities (e.g. Purcell 1997, Stibor & Tokle 2003). Therefore, more prey could be available for jellyfish in eutrophic waters.

In addition to altered feeding conditions, eutrophication often leads to low oxygen concentrations (hypoxia) in bottom waters. Increasing atmospheric carbon dioxide levels also are causing acidification of marine waters. Jellyfish are more tolerant of hypoxic and low pH conditions than are fish (reviewed in Purcell 2012, see also Tills et al. 2016 and references therein). *Aequorea victoria* medusae were the most tolerant of hypoxia of 12 species of jellyfish and ctenophores tested in the Salish Sea (Rutherford & Thuesen 2005). Thus, hypoxic and acidic environments may favour tolerant jellyfish, such as *A. victoria*, over fish.
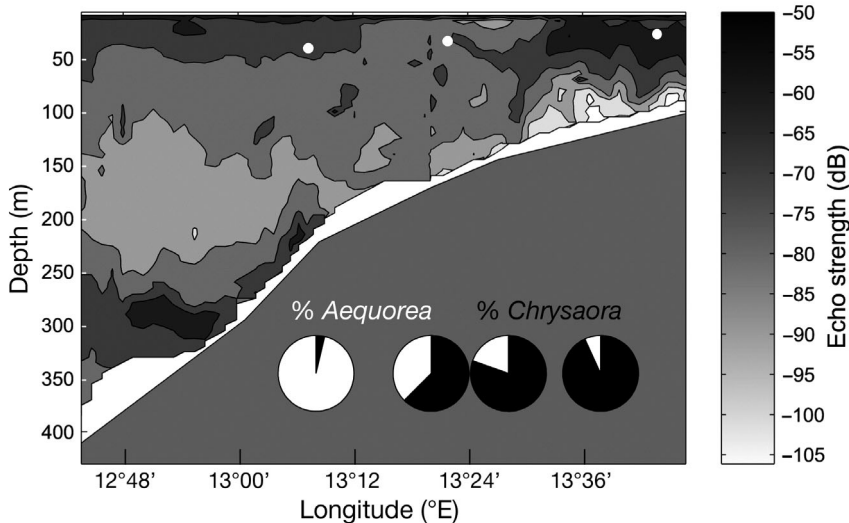

Fig. 3. Offshore/inshore echogram (38 kHz) along 22° S latitude showing the prominent scattering layer inshore (top right) caused by *Chrysaora fulgida* medusae and the diffuse scattering layer offshore caused by *Aequorea forskalea* medusae. The pie charts at the bottom show the relative proportions (by wet mass) of *C. fulgida* (black) and *A. forskalea* (white) in trawl catches in the waters above the pies, where jellyfish catch rates were greater than 100 kg min⁻¹. White dots are the weighted mean depths of *A. forskalea* calculated from daytime submersible transects (n = 26 and 46) in November 1997 and April 1999, respectively, in Sparks et al. (2005). Echogram modified from Brierley et al. (2001) and reprinted with permission from ©Springer

Temperature

Accumulating evidence indicates that temperature is a key influence on interannual variation in pelagic cnidarian and ctenophore species population sizes (e.g. reviews Purcell 2005, 2012, Purcell et al. 2012, also Condon et al. 2013, Sun et al. 2015). In the eastern Bering Sea, *A. forskalea* constituted 5.0 to 8.5% of the jellyfish collected in fishing trawl samples, second to *Chrysaora melanaster* (82.5 to 91.0%) in 1995 to 1999 (Brodeur et al. 2002) (Table 1). *A. forskalea* and *C. melanaster* abundances were significantly associated with higher temperatures, occurring in 60% of the trawls in warm years but in only 39% in cool years (Cieciel et al. 2009). The jellyfish biomass in the western Bering Sea increased from the 1990s to the mid-2000s mainly from the abundance of *A. forskalea*, which had its largest biomass during the warmest year (reviewed in Decker et al. 2014). The greatest biomass of *A. forskalea* there in 2012 was over 500 kg km^{-2} (Radchenko 2013).

Aequorea spp. medusa abundances were also greater in warm years in other locations in the northeastern Pacific. *A. victoria* (log$_{10}$ medusae m^{-3}) in the Salish Sea were positively correlated with temperature (Pearson product moment correlation coefficient, CC = 0.771 [p = 0.02] in Kulleet Bay, British Columbia, Canada, and CC = 0.980 [p < 0.01] in East Sound) (Fig. 4). The CCs were not significant for salinity. In the California Current, general additive models indicated that catches in 2000 to 2007 of *Aequorea* sp. were positively correlated with temperature and salinity (Suchman et al. 2012). Thus, in the cool waters where they occur, *Aequorea* spp. numbers increase with temperature.

AEQUOREA SPP. IMPORTANCE IN THE ECOSYSTEM

Swimming and feeding

Cnidarians catch their planktonic prey with feeding tentacles bearing millions of intracellular stinging capsules called cnidocytes (nematocysts) that affect which types of prey are captured (Purcell & Mills 1988, Corrales-Ugalde et al. 2017). Movement of the prey relative to their tentacles, created by swimming of the prey and the predator species, also affects prey capture (Purcell 1997). Costello, Colin, and colleagues studied the water flow generated by swimming of hydromedusae, including *Aequorea victoria*, scyphomedusae, cubomedusae, and cteno-
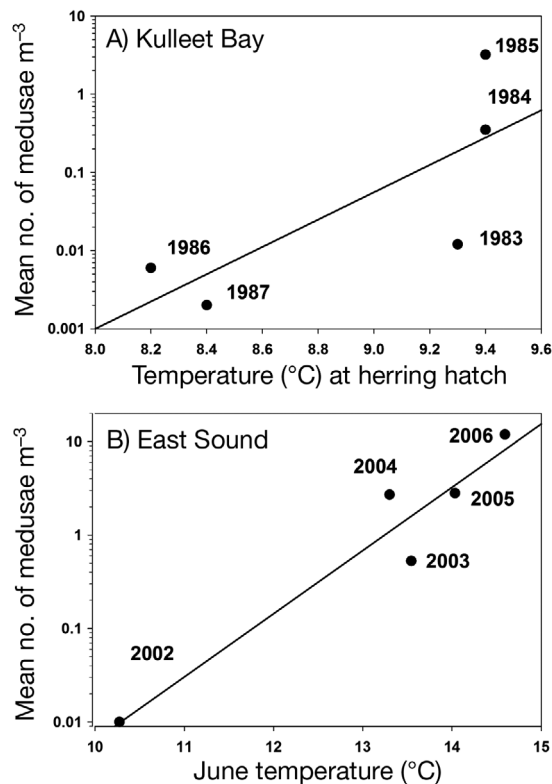

Fig. 4. Densities of *Aequorea victoria* medusae showing significantly positive correlation with temperature in the Salish Sea in (A) Kulleet Bay, British Columbia, Canada, at the time herring larvae hatched in 1983 to 1986 (data from Purcell & Arai 2001), and (B) East Sound, Washington, USA, in June for the years 2002 to 2006 (J. E. Purcell unpubl. data)

phores (e.g. references in Colin & Costello 2002, Dabiri et al. 2010, Costello et al. 2012, Colin et al. 2013). Prolate (bell-shaped) jellyfish are ambush predators that do not swim during feeding. Oblate (umbrella-shaped) jellyfish are cruising predators that maximize their feeding rates by moving high volumes of water through the tentacles and by the time spent swimming (e.g. Colin & Costello 2002). For example, *in situ* videos by SCUBA divers showed that *A. victoria* medusae (oblate) averaged 79% of the time swimming, clearly indicating a cruising mode of foraging (Colin et al. 2003). In contrast, *A. vitrina* medusae observed *in situ* at the surface in still water swam little and appeared to be ambush, not cruising, predators (Riisgård 2007).

Diet

Gut content data should be collected *in situ* for meaningful data on the types of prey eaten and feed-

ing rates of pelagic cnidarian and ctenophore species (reviewed in Purcell 1997, 2009). Gut contents from net-collected jellyfish are often not accurate due to gut evacuation or feeding on prey in the net (Purcell 1997, 2009). *Aequorea* spp. medusae open their large mouths and egest the consumed foods upon disturbance. Therefore, dietary data have been collected extensively only for *Aequorea* spp. in the Salish Sea and PWS, where they were dipped from the surface and preserved immediately (Purcell & Arai 2001, Costello & Colin 2002, Purcell 2003). Presumably, gut evacuation prevented feeding analysis for *Aequorea* spp. collected in trawls in the California Current (Suchman et al. 2008, 2012) and in the Bering Sea, where gut fullness was evaluated at only 0.01% (Radchenko 2013).

The wide variety of jellyfish displays a diversity of diets (reviewed in Purcell 1997). Large jellyfish, i.e. scyphomedusae (see Tilves et al. 2016, Zeman et al. 2016) and *Aequorea* spp., tend to eat more different prey types than do small hydromedusae (Purcell & Mills 1988). In the Salish Sea and in PWS, *Aequorea* spp. consumed a wide variety of prey: tintinnids, all stages of copepods, cladocerans, barnacle nauplii, decapod larvae, mollusc veligers, polychaete larvae, invertebrate and fish eggs, fish larvae, appendicularians, hydromedusae, siphonophores, and ctenophores (Purcell 1989, 1991a, 2003, references in Purcell & Arai 2001). Comparison of the main prey types of *Aequorea* spp. showed great similarity between regions; copepods plus appendicularians totalled 78% of the diet in Kulleet Bay and 80% in PWS (Purcell 1989, 2003). The numbers of copepods plus appendicularians eaten in Kulleet Bay (214 medusa^{-1} d^{-1}) were about 40% of those in PWS (537 medusa^{-1} d^{-1}), which could be attributed both to the lower densities of those prey (969 vs. 2134 m^{-3}) and the smaller medusae (60 vs. 73 mm diameter) in Kulleet Bay.

Prey selection

Jellyfish are often described as generalist predators, but most species studied show some selection among prey (consumption of prey types in disproportion to their availability in the plankton) (reviewed in Purcell 1997). Although *A. victoria* medusae have very broad diets, they select positively for soft-bodied prey (fish larvae, appendicularians, and pelagic cnidarians and ctenophores) and negatively for copepods (Purcell 1989, 1991a, Purcell & Sturdevant 2001, Costello & Colin 2002). The soft-bodied prey taxa are especially vulnerable to capture by tentaculate pred-

ators, because of their large sizes, weak swimming and escape abilities, and lack of protective exoskeleton (reviewed in Purcell 1997). Some predators, such as *A. victoria* medusae, are predisposed to catch soft prey because they lack the adhesive nematocysts found in pelagic hydrozoans that eat primarily crustaceans (Purcell & Mills 1988). The remarkable escape speeds of copepods (references in Bradley et al. 2013) undoubtedly contribute to the apparent negative selection for them by pelagic cnidarians and ctenophores (e.g. Purcell & Sturdevant 2001, Costello & Colin 2002, Zeman et al. 2016).

Feeding rates

To determine the feeding rates of pelagic cnidarians and ctenophores on zooplankton, the number of prey captured divided by the digestion time gives the predation rate, which can be multiplied by the predator density and divided by the prey density to give the proportion of each prey population consumed. Predation rates of *A. forskalea* in PWS on copepods estimated from gut contents, digestion rates, and prey densities were ≤1% of the prey standing stock d^{-1} (Purcell 2003), which suggests that predation on copepods by *A. forskalea* was negligible there. Clearance rates (the volume of water cleared of prey) differed by prey type by 2 orders of magnitude in PWS among copepods, cladocerans, and appendicularians (Purcell 2003). Clearance rates for medusae of a given species of similar size can be used to estimate their predation effects on a given prey type from *in situ* data on predator sizes and prey densities. Thus, to estimate the feeding of *A. victoria* on copepods in Kulleet Bay (5 April 1983), we can use the average clearance rate on copepods (0.0003 m^{-3} medusa^{-1} d^{-1}) in PWS for *A. forskalea* medusae multiplied by the densities of prey (661.4 copepods m^{-3}) and medusae (0.02 medusae m^{-3}) in Kulleet Bay, which equals 0.4% of the copepods daily, also a low predation effect.

Feeding rates of jellyfish measured in laboratory containers are usually lower than those estimated from gut contents (Purcell 1997, 2009). The average clearance rate of *A. vitrina* medusae (mean 3.3 mg dry weight) fed copepods in 5 l containers was 0.3 l d^{-1} medusa^{-1} (Møller & Riisgård 2007a). For *A. forskalea* medusae the same size in PWS (Purcell 2003), clearance *in situ* was 7-fold that of *A. vitrina* in laboratory containers. When the clearance rate for *A. vitrina* was applied to medusa and copepod densities *in situ*, Møller & Riisgård (2007c) concluded that

those medusae had no effect on the zooplankton population.

Katija et al. (2011) photographically tracked the fluid flow *A. victoria* medusae generated while swimming (11.4 l h^{-1} medusa^{-1}) together with videotaped prey capture efficiencies at room temperature in the laboratory. The potential clearance rate of a 50 mm diameter medusa on copepods was ~3.5 l h^{-1} (Katija et al. 2011). The *in situ* clearance rate of copepods by a 50 mm *A. forskalea* medusa in PWS (Purcell 2003) was about twice the rate estimated by flow for *A. victoria*.

Proxies of feeding rates

Respiration rates (RRs) can be used to estimate minimum ingestion by pelagic cnidarians and ctenophores *in situ*, as detailed in Ishii & Tanaka (2006), and by the polyps (Ikeda et al. 2017). Although this method underestimates ingestion *in situ*, because it does not include growth or reproduction, it requires much less effort and can be applied to similar species anywhere given predator body mass (Purcell 2009, Purcell et al. 2010). To estimate their minimum ingestion, I use RRs for 50 mm diameter *A. victoria* and *A. vitrina*, which were very similar (25 and 27 µl O$_2$ h^{-1} medusa^{-1}, respectively), as calculated from Larson (1986c, 1987) and Møller & Riisgård (2007c). Larson (1987) calculated a 5% C d^{-1} turnover using the carbon content of 2% dry weight (Larson 1986c), equivalent to ~6 mg C d^{-1} medusa^{-1}. Therefore, 6 mg C would be the minimum daily carbon ingestion for 50 mm *Aequorea* spp. medusae. Such estimates of ingestion are important to determine the importance of jellyfish in ecosystems.

Although normalization of metabolic measurements by dry weight is standard practice (Hirst & Forster 2013), several authors caution against its use for gelatinous species because dry weight differs with salinity (e.g. Nemazie et al. 1993, Purcell 2009). Additional problems were revealed by comparisons of oven-dried, freeze-dried, dialysed (desalted), and non-dialysed medusae, including *A. forskalea* in Kogovšek et al. (2014), who found 15-fold greater percent carbon in dialysed than in non-dialysed medusae.

Predation on fish

Human interest in jellyfish is, in part, because of their potential effects on fish populations (Purcell & Arai 2001). Although most recent scientific and media reports declare that jellyfish are important predators and competitors of fish, data on those topics are rare. *A. victoria* medusae provide some of the best examples available.

The focus of studies on *A. victoria* medusae in British Columbia, Canada, was predation on herring larvae (references in Purcell & Arai 2001). At the times herring larvae hatched in 5 yr in Kulleet Bay, the percentages of larvae consumed (0.7 to 72.8% d^{-1}) increased with medusa densities that differed by 3 orders of magnitude (Purcell & Arai 2001). Thus, *A. victoria* medusae are consistently predators in herring spawning grounds with devastating reduction of larvae in some years.

In addition to herring, *A. victoria* medusae consumed larvae from 7 other families of fish (Purcell 1989). Predation by *A. victoria* medusae was ≤17% d^{-1} of those larvae, assuming similar digestion times (2 to 3 h at 8 to 10°C) as for herring larvae. Eggs from 6 families of fish were common in the gut contents of *A. victoria* medusae; however, the lack of data on digestion times of eggs prevented estimation of predation rates or effects in Kulleet Bay (Purcell 1989).

Feeding by pelagic cnidarians and ctenophores typically does not saturate at prey densities occurring *in situ*; they ingest more prey as prey densities increase (reviewed in Purcell 1997). Feeding saturation often is shown in laboratory containers, where prey is given at unnaturally high densities (e.g. Stibor & Tokle 2003); however, saturation rarely has been tested *in situ*. One striking example showed no saturation for *A. victoria* medusae, whose ingestion increased linearly over 4 orders of magnitude when the number of herring larvae available differed over 4 orders of magnitude (Purcell & Arai 2001).

Competition with fish

Effects of pelagic cnidarians and ctenophores on fish include potential competition for zooplankton food. All fish larvae eat zooplankton, and small schooling pelagic fish (forage fish), such as anchovies, herrings, and sardines, eat zooplankton throughout life. The few studies of dietary overlaps between jellyfish and fish include one on *A. forskalea* in PWS. The diet overlaps among 4 forage fish species and 4 large pelagic cnidarians and ctenophores ranged from 5.3 to 78.1%, depending on the numbers of crustaceans versus soft-bodied prey in the diets; overlaps of the fish species with *A. forskalea* were moderate (35.5 to 59.0%), reflecting their broad diet (Purcell & Sturdevant 2001). In the California Cur-

rent, spatial and dietary overlaps of scyphomedusae with 9 pelagic fish species were incorporated into an overlap index (Brodeur et al. 2008); presumably, lack of dietary data for *Aequorea* sp. prevented their inclusion in the analysis. Similarly, 2 of the 3 ecosystems (Bering Sea, California Current) modeled by Robinson et al. (2014) contain *Aequorea* spp., but their trophic effects were not included. Stable isotopes showed considerable overlaps among fish and jellyfish, including *Aequorea* sp., which generally were enriched in ^{13}C and depleted in ^{15}N relative to fish in Puget Sound (Naman et al. 2016).

Competition requires that resources are limiting, which is difficult to demonstrate. Competition for food usually has been inferred from inverse relationships among zooplankton, fish, and pelagic cnidarians and ctenophores (e.g. Daskalov et al. 2007) and has been tested directly only once, to my knowledge. Predation by *A. victoria* and 6 other gelatinous species was estimated to be only 0.2% d^{-1} of the standing stocks of the microzooplankton prey of post-yolksac herring by Purcell & Grover (1990), who concluded that although the diets overlapped, competition for food did not occur in Kulleet Bay at that time because prey densities were too high (41 l^{-1}) to be affected.

Aequorea spp. as hosts of fish parasites

The transmission of parasites to fish is potentially an extremely important, but inadequately known, consequence of fish eating gelatinous species (reviewed in Arai 1988, Purcell & Arai 2001, Diaz Briz et al. 2012). Trematode, cestode, and nematode larvae are widely distributed among pelagic cnidarians and ctenophores, with digenetic trematodes the most studied. Their first larval stages develop in gastropods, followed by metacercaria larvae that develop in pelagic cnidarians and ctenophores or other intermediate hosts. The trematodes become sexually mature in the definitive host fish, such as mackerel, which eats gelatinous species. In the southwestern Atlantic Ocean, 21.7% of the examined *Aequorea* spp. medusae were parasitized by 2 species (Diaz Briz et al. 2012). The high parasite prevalence in *Aequorea* spp. suggests that they and other large medusae are especially important as hosts (Nogueira et al. 2015). Molecular genetics to identify the parasites in medusae would further knowledge of medusae as hosts of fish parasites and could indicate feeding interactions among medusa and fish species.

Intraguild predation on gelatinous zooplanktivores

A possible benefit of some jellyfish to fish is creating a trophic cascade that results in more zooplankton food. Some gelatinous taxa, especially large medusae, consume other jellyfish (reviewed in Purcell 1991b, 1997). When the predator and prey species are both zooplanktivores, the intraguild predation may benefit the predator species by reducing potential competition for food (Polis et al. 1989). Medusae in the family Aequoreidae are large with large mouths and gastric areas (Fig. 1) and well adapted to consume other pelagic cnidarian and ctenophore species. The gut contents of *A. victoria* contained ≥11 pelagic cnidarians and ctenophores in spring, constituting 10.5% of the prey items (Purcell 1991a). The densities of *A. victoria* and other gelatinous prey species were significantly negatively correlated, suggesting that *A. victoria* might control their populations (Purcell 1991a). Densities of zooplankton and other gelatinous prey species also were significantly negatively correlated, suggesting that *A. victoria* could indirectly increase zooplankton densities (Purcell 1991a) and create a trophic cascade.

Predation by *Aequorea victoria* on ephyrae and small *Aurelia labiata* medusae (Arai & Jacobs 1980) may explain why *Aurelia labiata* populations were low in 2005 and 2006 in East Sound when temperatures were highest (Fig. 4B), even though more *Aurelia labiata* ephyrae are produced in warm years (Purcell 2007, Purcell et al. 2009). No scyphomedusae that could consume large *Aurelia labiata* were present in East Sound (pers. obs.). Predation among pelagic cnidarians and ctenophores is common, and large jellyfish may be more important in controlling populations of other gelatinous zooplankton and balancing pelagic food webs than realized.

Lessons learned from *Aequorea* spp.

Studies reviewed here on *Aequorea* spp. provide some important insights into their ecology. Nevertheless, those studies are relatively few considering that the genus and family are globally distributed. Of key importance are their high abundances in commercial fishing areas and their predation and competition with fish. The topics reviewed (population dynamics and bloom formation, trophic ecology) are important for all zooplanktivorous gelatinous species. An overview of other gelatinous species is provided below using examples of current research.

NEW APPROACHES TO CONTINUING CHALLENGES IN JELLYFISH RESEARCH

Identification

Recent molecular genetics have opened new horizons in evolutionary biology, population genetics, and species identification. Several species of *Aurelia* and *Cyanea* have been distinguished instead of one or a few (Dawson 2005, Dawson et al. 2005, Scorrano et al. 2016). Molecular genetics can be used to describe new species, identify larvae, and reveal relationships among the pelagic cnidarians and ctenophores (Podar et al. 2001, Bentlage et al. 2010, Kayal et al. 2015) as well as to link the attached stages with the corresponding free-living medusae among the scyphomedusae, cubomedusae, and hydromedusae (e.g. Stampar et al. 2015). Continuing advances in molecular genetics will facilitate identification of gelatinous species.

Contributions of sexual reproduction to blooms

Much remains to be learned about all aspects of sexual reproduction by pelagic cnidarians and ctenophores. Medusae of at least some species concentrate before spawning (Hamner et al. 1994, Kingsford & Mooney 2014); gamete ripening (Uye 2014) and release may be stimulated by light (Purcell 1995). At least some cubomedusae and *Periphylla periphylla* mate (Tiemann et al. 2009, Kingsford & Mooney 2014). Histological and behavioural evidence suggests that spawning in pelagic cnidarian and ctenophore species occurs repeatedly over an extended period and depends, at least in part, on environmental conditions and the food available (Jaspers et al. 2011a, 2015, Lilley et al. 2014, Lucas & Dawson 2014, Milisenda et al. 2017). Species without attached stages may be preferable to develop new techniques to more fully understand the population dynamics of blooming jellyfish.

The subsequent survival of eggs and planulae also is poorly known. A few studies report that predation by *Aurelia* spp. scyphistomae on planulae of conspecifics and other species could affect settlement (Gröndahl 1988, Kuplik et al. 2015). Other predators also could reduce survival and settlement of planulae (Mercier et al. 2013, Kuplik et al. 2015, Miyajima-Taga et al. 2016). Factors that determine settlement and metamorphosis of planulae need more study (see Riascos et al. 2013, Gambill et al. 2016). Methods to discourage settlement would be useful to reduce blooms (Guenther et al. 2009), especially given the increases in aquaculture and other marine construction.

Asexual reproduction and blooms

Most of the scyphomedusan polyps found in nature are *Aurelia* spp. from harbours (Toyokawa et al. 2011, references in Duarte et al. 2013, Janßen et al. 2013, Makabe et al. 2014, Marques et al. 2015). Molecular genetics used to search for scyphistomae revealed only those of *Aurelia aurita* in their samples from the North Sea (van Walraven et al. 2016). To predict the probabilities and magnitudes of jellyfish blooms, data on the sizes of the attached populations *in situ* are necessary.

Seasonal changes in various environmental factors, including light, temperature, salinity, and food, may stimulate attached stages to produce jellyfish. Interannual variations in these conditions affect the timing and numbers of medusae produced, as for *Aurelia labiata* scyphistomae *in situ* that produced medusae 1 mo earlier in a year when high temperature, sunlight, and salinity coincided than in years when those factors were lower (Purcell et al. 2009). Most scyphozoan species examined produced more medusae in higher temperatures (reviews Purcell 2012, Purcell et al. 2012).

Although salinity and light have been studied less than temperature, the effects on asexual reproduction of scyphozoan and hydrozoan species are significant (summarized in Purcell 2007). In cubozoans, which often occur in or near estuaries, salinity may be especially important for medusa production (reviewed in Kingsford & Mooney 2014). Significant positive effects of light at low levels were shown for *Aurelia* spp. asexual reproduction (Purcell 2007, Liu et al. 2009). Metamorphosis of cubopolyps with zooxanthellae depended on increasing temperature and daylight (Straehler-Pohl & Jarms 2011). Thus, temperature, salinity, and light affect asexual production of many medusozoan taxa, and experiments on environmental factors that may contribute to blooms of more species are needed.

Survival of the young medusae is another little-studied component of bloom formation. Environmental factors, food, and predators all could affect their survival and bloom size (e.g. Wang & Li 2015). Adults and ephyrae of *Aurelia* spp. are tolerant of starvation (Hamner & Jenson 1974, Fu et al. 2014). Scyphistomae of several scyphozoan species eat the planula larvae and ephyrae of their own species (summarized in Pennington 1990). Small *Lychnorhiza lucerna* rhizostome medusae ate the ephyrae and young medusae of other scyphomedusan species but not of their own (Carrizo et al. 2015).

Abundance and biomass of gelatinous species

Net sampling can be used for most cnidarians and is necessary for the desperately needed quantitative data on abundance and biomass of pelagic cnidarians and ctenophores (Lucas et al. 2014b). Small hydromedusae are routinely captured in traditional zooplankton nets; however, large mouth area and mesh size are needed for large, sparse species (Purcell 2009). Special care must be taken with most ctenophore species, which are destroyed by the standard sampling and preservation methods (exceptions include *Pleurobrachia* spp., *Mertensia ovum, Beroe* spp.).

In addition to typical methods like nets and trawls, new methods are being used to sample jellyfish. A new towed camera system shows promise for quantitative photographic sampling of small gelatinous organisms (Luo et al. 2014). Citizen scientist programs collect sightings and photographs for verification of conspicuous jellyfish, including *Aequorea* spp. (e.g. www.medjelly.com, www.jellywatch.org/, www. mcsuk.org/sightings/jellyfish.php, www.ciesm.org/marine/programs/jellywatch.htm).Those records provide semi-quantitative data on dates, distributions, and abundances that can be used to compare among locations and years, as in Canepa et al. (2014, also A. Canepa et al. unpubl.) and Purcell et al. (2015b). Shoreline surveys can be used to develop monitoring programs (Fleming et al. 2013). Aerial methods also enable low-cost sampling over large areas and multiple years, especially for aggregations of *Aurelia* spp. medusae (Purcell et al. 2000, EOPS 2016) but also for large, highly visible medusae of other species (Houghton et al. 2006, Barrado et al. 2014). The large-scale semi-quantitative methods need to be combined with concurrent *in situ* sampling to determine jellyfish densities quantitatively, which has been accomplished rarely (see Graham et al. 2003, Bastian et al. 2011).

Effects of environmental conditions on abundance

Abundances of pelagic cnidarians and ctenophores are known to cycle with long-term environmental conditions, such as temperature and salinity (e.g. reviewed in Purcell 2005). On the other hand, human activities have greatly changed coastal environments in ways that may benefit gelatinous species (e.g. reviewed in Purcell 2012). Pelagic cnidarian and ctenophore species that have been studied can flourish in eutrophic waters with low visibility, low light, small food, and low oxygen that are detrimental to fish. Further insight into the consequences of eutrophication may be gained by experimental manipulations (e.g. McNamara et al. 2014) and long-term studies (van Walraven et al. 2015). That ocean temperatures are rising is clear (Wijffels et al. 2016). For most gelatinous species tested, their numbers are positively correlated with temperature (e.g. reviewed in Purcell 2012); however, some *Chrysaora* spp. medusae apparently benefit from the increased production in cold, high-nutrient upwelling water, where large populations of some of them live (Suchman et al. 2012, Roux et al. 2013, Quiñones et al. 2015).

Non-indigenous species

Blooms of several scyphozoan, hydrozoan, and ctenophore species have been increased by accidental introductions (reviews Bayha & Graham 2014, González-Duarte et al. 2016). The main vectors for these non-indigenous species (NIS) have been in the ballast tanks and on the hulls of ships (González-Duarte et al. 2016). The harbour destinations of the vessels provide excellent habitats for the NIS. Both ship transport and marine construction, including aquaculture and energy installations, continue to increase dramatically (reviewed in Duarte et al. 2013). Thus, the opportunities for population expansion have greatly increased, as demonstrated recently (Janßen et al. 2013, Makabe et al. 2014). The cnidarian fauna attached to marine construction is cryptic, and small medusae in the surrounding water may be unnoticed. Therefore, the extent that jellyfish blooms have been enhanced by human activities probably is greatly underestimated (Carlton 2009), and invasions are likely to increase with the widening of the Suez and Panama canals and more shipping.

Positions in the food web

Recent studies have indicated broader ecological roles for pelagic cnidarians and ctenophores than their traditional trophic level as zooplanktivores in pelagic food webs, as understood from gut content analyses that underestimate consumption of microplankton. *Aurelia aurita* medusae, for example, were recognized decades ago as consumers of microplankton (Southward 1955), and recent analyses using stable isotopes support those results (e.g. D'Ambra et al. 2014, Fleming et al. 2015). The hydromedusa *Aglaura*

hemistoma feeds on protozoa and other zooplankton and has ciliated tentacles (Colin et al. 2005), as does *Aglantha digitale*. I suggest that other trachymedusae in their family (Rhopalonematidae) may also feed on microplankton using ciliary currents. Other species were demonstrated to feed on microplankton, such as *Mnemiopsis leidyi* larvae and adults (reviewed in Costello et al. 2012, Vansteenbrugge et al. 2016). The potential importance of medusozoans and ctenophores in benthic trophic pathways also is becoming increasingly apparent (e.g. Pitt et al. 2008).

Biomarkers (stable isotope and fatty acids) have become popular tools to study feeding in pelagic cnidarians and ctenophores. Those results may differ depending on many factors and can lead to conclusions that do not agree with dietary data, such as for *Beroe* spp. (e.g. Vansteenbrugge et al. 2016). The trophic enrichment factors (TEFs) of jellyfish have been determined experimentally only for *Aurelia* sp. by D'Ambra et al. (2014); however, those TEFs contrasted markedly with the average TEFs usually used and gave unreasonably high trophic positions for *Aurelia aurita* and other species in another environment (Fleming et al. 2015). Stable isotope niches differed by season and by species, as reported by Fleming et al. (2015), who emphasized that all gelatinous species should not be treated as one functional group in fishery and ecosystem models. Standardization and improvements will increase the insights gained from these methods (Phillips et al. 2014). For example, Kogovšek et al. (2014) recommended freeze-drying and dialysis for organic and biochemical analyses rather than the usual methods, which represent jellyfish biomass poorly.

The apparent increase of pelagic cnidarians and ctenophores and the realization that large biomasses (jelly-falls) settle to the sea floor globally (e.g. Lebrato et al. 2012) have renewed interest in them in carbon recycling. The protein-rich mucous secretions of living jellyfish and decay of dead biomass are readily assimilated by bacteria and can redirect carbon towards bacteria (Condon et al. 2011). Thus, gelatinous species are important to nutrient recycling in the water column (e.g. Condon et al. 2011, McNamara et al. 2013) and on the benthos, where they are scavenged and decompose (e.g. Sweetman et al. 2014, 2016, Chelsky et al. 2016).

Proxies of feeding estimates

Respiration and other metabolic measurements could allow rapid large-scale estimation of food requirements from densities and sizes of pelagic cnidarians and ctenophores. The electron transport system (ETS) activity in eukaryotes shows the capacity of organisms to consume oxygen (Packard et al. 1971). The ETS method has been used extensively on marine zooplankton and provides good estimates of RRs *in situ* (Packard 1985). Data on the ETS activity of 5 small medusa and 1 ctenophore species indicate that this method works on them (King & Packard 1975, Owens & King 1975). Application of the ETS method to jellyfish in nature would help to alleviate the problems associated with laboratory confinement (Purcell et al. 2010) and could enable estimation of the energetic requirements and ecological effects for net-collected specimens and the largest species.

Predation on fish

Studies using gut contents and digestion analyses to estimate jellyfish predation on ichthyoplankton, as shown for *Aequorea victoria*, are rare. Predation on fish eggs and larvae by *Pelagia noctiluca* was high over the Catalan Shelf in the Mediterranean Sea (Tilves et al. 2016). Although all larvae (mean 2.5 h) and anchovy eggs (mean 8.5 h) were digested by *P. noctiluca* ephyrae, only 45% of another egg of the same size (0.8 mm) was digested (mean 17.4 h; Purcell et al. 2014). Similarly, anchovy eggs were quickly digested by *Mnemiopsis leidyi* ctenophores (Purcell et al. 1994), but cod eggs were not digested (Jaspers et al. 2011b). Possible survival of some fish eggs after egestion from pelagic cnidarians and ctenophores is important to determine. Molecular genetics may facilitate fish egg and larva identification in gut contents (Fox et al. 2012).

Predation by fish on gelatinous species

The juveniles of numerous commercially harvested fish associate with jellyfish (reviewed in Arai 1988, Purcell & Arai 2001, Ohtsuka et al. 2009, Graham et al. 2014, Kondo et al. 2014). The associations are mainly between scyphozoan medusae and fish in the families Carangidae, Stromateidae, and Gadidae. These associations probably benefit the fish, providing food and protection from other predators, but the importance is nearly unknown. The reliance of the associated fish on the host for food can be clarified by stable isotopes (D'Ambra et al. 2015).

Predation on jellyfish is not limited to associated fish (reviews Arai 1988, 2005, Purcell & Arai 2001).

Several studies since those reviews document predation (e.g. Milisenda et al. 2014, Miyajima-Taga et al. 2016), with jellyfish being considered as food for some aquaculture fish (Liu et al. 2014, Marques et al. 2016, Miyajima-Taga et al. 2016). Some stable isotope studies on fish predation have yielded results that conflict with known diets (Cardona et al. 2012), while other studies (Cardona et al. 2015) confirm earlier dietary studies. The magnitude of fish predation on gelatinous species *in situ* is unknown. No direct evidence links reduction of those fish populations to positive effects on pelagic cnidarian or ctenophore populations, to my knowledge. Estimates of predation rates of fish on gelatinous species are scarce because digested gelatinous species are difficult to identify and quantify and digestion times are almost completely lacking. The only study showed that gelatinous food was digested ~20 times faster than shrimp by gelativorous chum salmon (Arai et al. 2003). The combination of stable isotope compositions and gut content analysis can offer insights into the diets of predators of jellyfish (Nakamura & Sato 2014).

Jellyfish, fisheries, and aquaculture

Humans may have unintentionally benefitted gelatinous populations by fishing, thus removing their predators and competitors. In most ecosystems, the largest predatory fish were depleted first and the forage fish second, i.e. fishing down marine food webs (e.g. Pauly et al. 2009). Although the reduction of piscivorous fish would favour small zooplanktivorous fish, those forage fishes are heavily fished to produce oil and meal for aquaculture feeds (Tacon & Metian 2009). Where populations of forage fish are reduced by fishing, zooplanktivorous gelatinous species have bloomed, presumably due to reduced competition for food (e.g. Purcell 2012, Robinson et al. 2014). A dramatic example of overfishing is in the Benguela, where jellyfish seem to have replaced heavily fished forage fish (Lynam et al. 2006).

The large populations of pelagic cnidarians increasingly interfere with fisheries. Numerous examples document jellyfish filling the nets of fishers, making it impossible to fish, or reducing the catches (e.g. reviewed in Graham et al. 2014, Lucas et al. 2014a, Mianzan et al. 2014, Robinson et al. 2014). This has a substantial economic cost for shellfish and finfish fisheries (Graham et al. 2014).

Similarly, jellyfish have been costly to aquaculture farms, sometimes causing mass mortality in penned fish (reviewed in Purcell et al. 2013, Lucas et al. 2014a). The damage caused by jellyfish to penned fish ranges from skin and gill lesions to metabolic and neurological impairment (Baxter et al. 2011, Bosch-Belmar et al. 2016a,b, 2017). Such studies have just begun. The contribution of jellyfish stings to the less dramatic background fish mortality is much more difficult to determine.

Aquaculture facilities and other structures in coastal waters can have attached scyphistomae and hydroids and thereby could increase jellyfish populations nearby (reviewed in Duarte et al. 2013, Bosch-Belmar 2016). Partly because of the cryptic nature of most of these small organisms, they have been inadequately documented in general. Because of decreasing wild fish stocks and increasing human demands for seafood, aquaculture is expected to increase dramatically, and consequently, its problems with jellyfish are likely to increase (Purcell 2012).

CONCLUSIONS

Although *Aequorea* spp. provide a case study illustrating the ecological importance of pelagic cnidarians and ctenophores, data exist for few of the known species (201 scyphozoans, >1000 hydromedusae, 176 siphonophores, 37 cubozoans, and 190 ctenophores), with as many as 60% of the species remaining to be discovered (Appeltans et al. 2012). Data are lacking for vast regions of the oceans as well (Condon et al. 2013). The extreme shortage of quantitative data on species of pelagic cnidarians and ctenophores globally is a major impediment to understanding and predicting their abundances, biomasses, and effects on ecosystems and humans. Large-scale and long-term monitoring is necessary to understand the natural fluctuations of those species and environmental effects on their population sizes (Brodeur et al. 2016).

Many basic life history characteristics of pelagic cnidarians and ctenophores are inadequately studied, including rates of sexual reproduction, growth, and mortality that contribute to their population dynamics. The ecology of the attached stages is not well known but must play a key role in bloom formation in species having them (Lucas et al. 2012). Studies on their distributions, abundances, asexual reproduction rates, and environmental factors that lead to blooms are needed. All of these data are needed to understand the importance of pelagic cnidarians and ctenophores and for their inclusion in ecosystem models.

Respiration and other metabolic measurements allow rapid large-scale estimation of food requirements from densities and sizes of pelagic cnidarians and ctenophores. Ingestion calculated from metabolic rates can be used in ecosystem models instead of more laborious feeding rates. New techniques (stable isotopes, fatty acids, and molecular genetics) are producing new insights into jellyfish trophic interactions; however, those methods are not yet quantitative and need to be validated by gut analysis.

The various interactions between jellyfish and fish are inadequately understood but of great potential significance for fisheries and aquaculture. These interactions are mostly negative for the fish (predation and competition for food, parasite transmission, stinging in aquaculture pens), but some are positive (associations, food for fish). Overfishing, especially of forage fish, may have increased populations of pelagic cnidarians and ctenophores. Fishing on forage fish should be reduced and different aquaculture feeds developed. Jellyfish should be included in fishery and ecosystem studies and fishery management plans.

Pelagic cnidarians and ctenophores are likely to continue to have large populations in regions damaged by human activities. Some species are known to be more tolerant than fish of degraded conditions including low visibility, small zooplankton foods, and low oxygen. Improved water quality in coastal areas may reduce medusa and ctenophore populations. Most of the studied pelagic cnidarians and ctenophores reproduce more and have larger populations in higher-than-normal water temperatures, suggesting that those species may proliferate with ocean warming. Populations of jellyfish with attached stages may increase with more marine construction. Introductions of NIS are likely to intensify from more transport through the widened Suez and Panama canals. All of these factors are likely to escalate with increasing human populations and use of the ocean.

Jellyfish are known mostly for the problems they cause humans, such as stinging and direct interference with fishing, aquaculture, and power plant operations. These problems are likely to intensify with larger human and jellyfish populations. New countermeasures can be developed. New uses for jellyfish are being developed, with many potential benefits in medicine and as food for both humans and cultured fish.

LITERATURE CITED

Alvarez-Colombo G, Mianzan H, Madirolas A (2003) Acoustic characterization of gelatinous-plankton aggregations: four case studies from the Argentine continental shelf. ICES J Mar Sci 60:650–657

Appeltans W, Ahyong ST, Anderson G, Angel MV and others (2012) The magnitude of global marine species diversity. Curr Biol 22:2189–2202

Arai MN (1980) Growth rates of *Aequorea* medusae. In: Tardent P, Tardent R (eds) Developmental and cellular biology of coelenterates. Elsevier, Amsterdam, p 163–169

Arai MN (1986) Oxygen consumption of fed and starved *Aequorea victoria* (Murbach and Shearer, 1902) (Hydromedusae). Physiol Zool 59:188–193

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, Jacobs JR (1980) Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. Can J Fish Aquat Sci 37:120–123

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

Barrado C, Fuentes JA, Salamí E, Royo P, Olariaga AD (2014) Jellyfish monitoring on coastlines using remote piloted aircraft. In: Guo H, Wang C, Jing L, Wang L, Chen F (eds) Proc 35th Int Symp Remote Sens Environ (ISRSE 35). IOP Conf Ser: Earth Environ Sci 17:012195

Bastian T, Haberlin D, Purcell JE, Hays GC and others (2011) Large-scale sampling reveals the spatio-temporal distributions of the jellyfish *Aurelia aurita* and *Cyanea capillata* in the Irish Sea. Mar Biol 158:2639–2652

Baxter EJ, Rodger HD, McAllen R, Doyle TK (2011) Gill disorders in marine farmed salmon: investigating the role of hydrozoan jellyfish. Aquacult Environ Interact 1:245–257

Bayha KM, Graham WM (2014) Nonindigenous marine jellyfish: invasiveness, invasibility, and impacts. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 45–77

Bentlage B, Cartwright P, Yanagihara AA, Lewis C, Richards GS, Collins AG (2010) Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. Proc Biol Sci 277:493–501

Boero F, Bouillon J, Piraino S, Schmid V (2002) Asexual reproduction in the Hydrozoa (Cnidaria). In: Hughes RN (ed) Reproductive biology of invertebrates, XI. Progress in asexual reproduction. Oxford & IBH Publishing, New Delhi, p 141–158

Bosch-Belmar M (2016) Jellyfish blooms impacts on Mediterranean aquaculture: a multidisciplinary approach. PhD thesis, University of Salento, Lecce

Bosch-Belmar M, Giomi F, Rinaldi A, Mandich A and others (2016a) Concurrent environmental stressors and jellyfish stings impair caged European sea bass (*Dicentrarchus labrax*) physiological performances. Sci Rep 6:27929

Bosch-Belmar M, M'Rabet C, Dhaouadi R, Chalghaf M and others (2016b) Jellyfish stings trigger gill disorders and

increased mortality in farmed *Sparus aurata* (Linnaeus, 1758) in the Mediterranean Sea. PLOS ONE 11:e0154239

Bosch-Belmar M, Milisenda G, Girons A, Taurisano V and others (2017) Consequences of stinging plankton blooms on finfish mariculture in the Mediterranean Sea. Front Mar Sci, doi:10.3389/fmars.2017.00240

Bouillon J, Boero F (2000) Synopsis of the families and genera of the hydromedusae of the world, with a list of the worldwide species. Thalassia Salent 24:47–296

Bouillon J, Gravili C, Pagès F, Gili JM, Boero F (2006) An introduction to Hydrozoa. Mem Mus Natl Hist Nat, Vol. 194

Bradley CJ, Strickler JR, Buskey EJ, Lenz PH (2013) Swimming and escape behavior in two species of calanoid copepods from nauplius to adult. J Plankton Res 35: 49–65

Brierley AS, Axelsen BE, Buecher E, Sparks CAJ, Boyer H, Gibbons MJ (2001) Acoustic observations of jellyfish in the Namibian Benguela. Mar Ecol Prog Ser 210:55–66

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

Brodeur RD, Suchman CL, Reese D, Miller T, Daly E (2008) Spatial overlap and trophic interactions between fish and large jellyfish in the northern California Current. Mar Biol 154:649–659

Brodeur RD, Link JS, Smith BE, Ford MD, Kobayashi D, Jones TT (2016) Ecological and economic consequences of ignoring jellyfish: a plea for increased monitoring of ecosystems. Fisheries 41:622–629

Buecher E, Sparks CAJ, Brierley AS, Boyer HE, Gibbons MJ (2001) Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum.* J Plankton Res 23: 1073–1080

Canepa A, Fuentes V, Sabatés A, Piraino S, Boero F, Gili JM (2014) *Pelagia noctiluca* in the Mediterranean Sea. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 237–266

Cardona L, Álvarez de Quevedo I, Borrell A, Aguilar A (2012) Massive consumption of gelatinous plankton by Mediterranean apex predators. PLOS ONE 7:e31329

Cardona L, Martínez-Iñigo L, Mateo R, González-Solís J (2015) The role of sardine as prey for pelagic predators in the western Mediterranean Sea assessed using stable isotopes and fatty acids. Mar Ecol Prog Ser 531:1–14

Carlton JT (2009) Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems. Springer, Berlin, p 13–56

Carrizo SS, Schiariti A, Nagata RM, Morandini AC (2015) Preliminary observations on ephyrae predation by *Lychnorhiza lucerna* medusa (Scyphozoa; Rhizostomeae). Zool Garten NF 85:74–83

Chelsky A, Pitt KA, Ferguson AJP, Bennett WW, Teasdale PR, Welsh DT (2016) Decomposition of jellyfish carrion *in situ*: short-term impacts on infauna, benthic nutrient fluxes and sediment redox conditions. Sci Total Environ 566–567:929–937

Chiaverano L, Mianzan H, Ramírez F (2004) Gonad development and somatic growth patterns of *Olindias sambaquiensis* (Limnomedusae, Olindiidae). Hydrobiologia 530–531:373–381

Cieciel K, Farley EV Jr, Eisner LB (2009) Jellyfish and juve-

nile salmon associations with oceanographic characteristics during warm and cool years in the eastern Bering Sea. N Pac Anadromous Fish Comm Bull 5:209–224

Colin SP, Costello JH (2002) Morphology, swimming performance and propulsive mode of six co-occurring hydromedusae. J Exp Biol 205:427–437

Colin SP, Costello JH, Klos E (2003) *In situ* swimming and feeding behavior of eight co-occurring hydromedusae. Mar Ecol Prog Ser 253:305–309

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

Colin SP, Costello JH, Katija K, Seymour J, Kiefer K (2013) Propulsion in cubomedusae: mechanisms and utility. PLOS ONE 8:e56393

Collins AG, Schuchert P, Marques AC, Jankowski T, Medina M, Schierwater B (2006) Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. Syst Biol 55:97–115

Condon RH, Steinberg DK, del Giorgio PA, Bouvier TC and others (2011) Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc Natl Acad Sci USA 108:10225–10230

Condon RH, Duarte CM, Pitt KA, Robinson KL and others (2013) Recurrent jellyfish blooms are a consequence of global oscillations. Proc Natl Acad Sci USA 110: 1000–1005

Corrales-Ugalde M, Colin SP, Sutherland KR (2017) Nematocyst distribution corresponds to prey capture location in hydromedusae with different predation modes. Mar Ecol Prog Ser 568:101–110

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

Costello JH, Bayha KM, Mianzan HW, Shiganova TA, Purcell JE (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. Hydrobiologia 690:21–46

Dabiri JO, Colin SP, Katija K, Costello JH (2010) A wakebased correlate of swimming performance and foraging behavior in seven co-occurring jellyfish species. J Exp Biol 213:1217–1225

D'Ambra I, Carmichael RH, Graham WM (2014) Determination of δ^{13}C and δ^{15}N and trophic fractionation in jellyfish: implications for food web ecology. Mar Biol 161:473–480

D'Ambra I, Graham WM, Carmichael RH, Hernandez FJ Jr (2015) Fish rely on scyphozoan hosts as a primary food source: evidence from stable isotope analysis. Mar Biol 162:247–252

Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc Natl Acad Sci USA 104:10518–10523

Dawson MN (2005) *Cyanea capillata* is not a cosmopolitan jellyfish: morphological and molecular evidence for *C. annaskala* and *C. rosea* (Scyphozoa: Semaeostomeae: Cyaneidae) in south-eastern Australia. Invertebr Syst 19: 361–370

Dawson MN, Gupta S, England MH (2005) Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. Proc Natl Acad Sci USA 102:11968–11973

Decker MB, Cieciel K, Zavolokin A, Lauth R, Brodeur RD, Coyle KO (2014) Population fluctuations of jellyfish in the

Bering Sea and their ecological role in this productive shelf ecosystem. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 153–183

Diaz Briz LM, Martorelli SR, Genzano GN, Mianzan HW (2012) Parasitism (Trematoda, Digenea) in medusae from the southwestern Atlantic Ocean: medusa hosts, parasite prevalences, and ecological implications. Hydrobiologia 690:215–226

Dong J, Jiang LX, Tan KF, Liu HY, Purcell JE, Li PJ, Ye CC (2009) Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review. Hydrobiologia 616:113–118

Duarte CM, Pitt KA, Lucas CH, Purcell JE and others (2013) Is global ocean sprawl a cause for jellyfish blooms? Front Ecol Environ 11:91–97

EOPS (Eyes Over Puget Sound) (2016) Water surface conditions. www.ecy.wa.gov/programs/eap/mar_wat/surface.html (accessed 10 Sep 2016)

Fleming NEC, Harrod C, Houghton JDR (2013) Identifying potentially harmful jellyfish blooms using shoreline surveys. Aquacult Environ Interact 4:263–272

Fleming NEC, Harrod C, Griffin DC, Newton J, Houghton JDR (2014) Scyphozoan jellyfish provide short-term reproductive habitat for hyperiid amphipods in a temperate near-shore environment. Mar Ecol Prog Ser 510:229–240

Fleming NEC, Harrod C, Newton J, Houghton JDR (2015) Not all jellyfish are equal: isotopic evidence for inter- and intraspecific variation in jellyfish trophic ecology. PeerJ 3:e1110

Fox CL, Taylor MI, van der Kooij J, Taylor N and others (2012) Identification of marine fish egg predators using molecular probes. Mar Ecol Prog Ser 462:205–218

Fu Z, Shibata M, Makabe R, Ikeda H, Uye SI (2014) Body size reduction under starvation, and the point of no return, in ephyrae of the moon jellyfish *Aurelia aurita.* Mar Ecol Prog Ser 510:255–263

Gambill M, McNaughton SL, Kreus M, Peck MA (2016) Temperature-dependent settlement of planula larvae of two scyphozoan jellyfish from the North Sea. Estuar Coast Shelf Sci, doi:10.1016/j.ecss.2016.08.042

Gasca R, Hoover R, Haddock SHD (2015) New symbiotic associations of hyperiid amphipods (Peracarida) with gelatinous zooplankton in deep waters off California. J Mar Biol Assoc UK 95:503–511

Genzano GN, Kubota S (2003) Synchronous mass release of mature medusae from the hydroid *Halocordyle disticha* (Hydrozoa, Halocordylidae) and experimental induction of different timing by light changes. Publ Seto Mar Biol Lab 39:221–228

Genzano G, Mianzan H, Diaz-Briz L, Rodriguez C (2008) On the occurrence of *Obelia* medusa blooms and empirical evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. Lat Am J Aquat Res 36:301–307

Gershwin L (2006) *Aldersladia magnificus*: a new genus and species of hydromedusae Cnidaria: Hydrozoa: Leptomedusae: Aequoreidae) from tropical and subtropical Australia. Beagle 22:9–13

Gibbons MJ, Buecher E, Thibault-Bothe D, Helm R (2010) Patterns in marine hydrozoan richness and biogeography around southern Africa: implications of life cycle strategy. J Biogeogr 37:606–616

González-Duarte MM, Megina C, López-González PJ, Galil B (2016) Cnidarian alien species in expansion. In: Gof-

fredo S, Dubinsky Z (eds) The Cnidaria, past, present and future. Springer, Cham, p 139–160

Graham WM, Martin DL, Felder DL, Asper VL, Perry HM (2003) Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. Biol Invasions 5:53–69

Graham WM, Gelcich S, Robinson KL, Duarte CM and others (2014) Linking human wellbeing and jellyfish: ecosystem services, impacts and social responses. Front Ecol Environ 12:515–523

Greene C, Kuehne L, Rice C, Fresh K, Penttila D (2015) Forty years of change in forage fish and jellyfish abundance across greater Puget Sound, Washington (USA): anthropogenic and climate associations. Mar Ecol Prog Ser 525:153–170

Gröndahl F (1988) Interactions between polyps of *Aurelia aurita* and planktonic larvae of scyphozoans: an experimental study. Mar Ecol Prog Ser 45:87–93

Guenther J, Carl C, Sunde LM (2009) The effects of colour and copper on the settlement of the hydroid *Ectopleura larynx* on aquaculture nets in Norway. Aquaculture 292:252–255

Hamner WM, Jensen RM (1974) Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. Am Zool 14:833–849

Hamner WM, Hamner RR, Strand SW (1994) Sun-compass migration by *Aurelia aurita* (Scyphozoa): population retention and reproduction in Saanich Inlet, British Columbia. Mar Biol 119:347–356

Hirst AG, Forster J (2013) When growth models are not universal: evidence from marine invertebrates. Proc R Soc B 280:20131546

Houghton JDR, Doyle TK, Davenport J, Hays GC (2006) Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. Mar Ecol Prog Ser 314:159–170

Ikeda H, Mizota C, Uye SI (2017) Bioenergetic characterization in *Aurelia aurita* (Cnidaria: Scyphozoa) polyps and application to natural polyp populations. Mar Ecol Prog Ser 568:87–100

Ishii H, Tanaka F (2006) Respiration rates and metabolic demands of *Aurelia aurita* in Tokyo Bay with special reference to large medusae. Plankton Benthos Res 1:64–67

Janßen H, Augustin CB, Hinrichsen HH, Kube S (2013) Impact of secondary hard substrate on the distribution and abundance of *Aurelia aurita* in the western Baltic Sea. Mar Pollut Bull 75:224–234

Jarms G, Båmstedt U, Tiemann H, Martinussen MB, Fosså JH (1999) The holopelagic life cycle of the deep-sea medusa *Periphylla periphylla* (Scyphozoa, Coronatae). Sarsia 84:55–65

Jaspers C, Møller LF, Kiørboe T (2011a) Salinity gradient of the Baltic Sea limits the reproduction and population expansion of the newly invaded comb jelly *Mnemiopsis leidyi.* PLOS ONE 6:e24065

Jaspers C, Titelman J, Hansson LJ, Haraldsson M, Ditlefsen CR (2011b) The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. Limnol Oceanogr 56:431–439

Jaspers C, Møller LF, Kiørboe T (2015) Reproduction rates under variable food conditions and starvation in *Mnemiopsis leidyi*: significance for the invasion success of a ctenophore. J Plankton Res 37:1011–1018

Katija K, Beaulieu WT, Regula C, Colin SP, Costello JH, Dabiri JO (2011) Quantification of flows generated by the

hydromedusa *Aequorea victoria*: a Lagrangian coherent structure analysis. Mar Ecol Prog Ser 435:111–123

Kayal E, Bentlage B, Cartwright P, Yanagihara AA and others (2015) Phylogenetic analysis of higher-level relationships within Hydroidolina (Cnidaria: Hydrozoa) using mitochondrial genome data and insight into their mitochondrial transcription. PeerJ 3:e1403

King FD, Packard TT (1975) Respiration and the activity of the respiratory electron transport system in marine zooplankton. Limnol Oceanogr 20:849–854

Kingsford MJ, Mooney CJ (2014) The ecology of box jellyfishes (Cubozoa). In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 267–302

Kogovšek T, Tinta T, Klun K, Malej A (2014) Jellyfish biochemical composition: importance of standardised sample processing. Mar Ecol Prog Ser 510:275–288

Kondo Y, Ohtsuka S, Nishikawa J, Metillo E and others (2014) Associations of fish juveniles with rhizostome jellyfishes in the Philippines, with taxonomic remarks on a commercially harvested species in Carigara Bay, Leyte Island. Plankton Benthos Res 9:51–56

Kuplik Z, Kerem D, Angel DL (2015) Regulation of *Cyanea capillata* populations by predation on their planulae. J Plankton Res 37:1068–1073

Larson RJ (1986a) Ova production by hydromedusae from the NE Pacific. J Plankton Res 8:995–1002

Larson RJ (1986b) Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. Mar Ecol Prog Ser 33:89–98

Larson RJ (1986c) Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. J Exp Mar Biol Ecol 99:107–120

Larson RJ (1987) Respiration and carbon turnover rates of medusae from the NE Pacific. Comp Biochem Physiol A 87:93–100

Lebrato M, Pitt KA, Sweetman AK, Jones DOB and others (2012) Jelly-falls historic and recent observations: a review to drive future research directions. Hydrobiologia 690:227–245

Lilley MKS, Elineau A, Ferraris M, Thiéry A and others (2014) Individual shrinking to enhance population survival: quantifying the reproductive and metabolic expenditures of a starving jellyfish, *Pelagia noctiluca*. J Plankton Res 36:1585–1597

Liu WC, Lo WT, Purcell JE, Chang HH (2009) Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. Hydrobiologia 616:247–258

Liu C, Zhuang Z, Chen S, Shi Z, Yan J, Liu C (2014) Medusa consumption and prey selection of silver pomfret *Pampus argenteus* juveniles. Chin J Oceanol Limnol 32:71–80

Lucas CH, Dawson MN (2014) What are jellyfishes and thaliaceans and why do they bloom? In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 9–44

Lucas CH, Graham WM, Widmer C (2012) Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv Mar Biol 63:133–196

Lucas CH, Gelcich S, Uye SI (2014a) Living with jellyfish: management and adaptation strategies. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 129–150

Lucas CH, Jones DOB, Hollyhead CJ, Condon RH and others (2014b) Gelatinous zooplankton biomass in the global oceans: geographic variation and environmental drivers. Glob Ecol Biogeogr 23:701–714

Luo JY, Grassian B, Tang D, Irisson JO and others (2014) Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. Mar Ecol Prog Ser 510:129–149

Lynam CP, Gibbons MJ, Axelsen BE, Sparks CAJ and others (2006) Jellyfish overtake fish in a heavily fished ecosystem. Curr Biol 16:R492–R493

Makabe R, Furukawa R, Takao M, Uye S (2014) Marine artificial structures as amplifiers of *Aurelia aurita* s.l. blooms: a case study of a newly installed floating pier. J Oceanogr 70:447–455

Maronna MM, Miranda TP, Peña Cantero ÁL, Barbeitos MS, Marques AC (2016) Towards a phylogenetic classification of Leptothecata (Cnidaria, Hydrozoa). Sci Rep 6: 18075

Marques R, Cantou M, Soriano S, Molinero JC, Bonnet D (2015) Mapping distribution and habitats of *Aurelia* sp. polyps in Thau Lagoon, northwestern Mediterranean Sea (France). Mar Biol 162:1441–1449

Marques R, Bouvier C, Darnaude AM, Molinero JC and others (2016) Jellyfish as an alternative source of food for opportunistic fishes. J Exp Mar Biol Ecol 485:1–7

Martell L, Ciavolino E, Gravili C, Piraino S, Boero F (2017) Population dynamics of the non-indigenous hydrozoan *Clytia hummelincki* (Hydrozoa: Campanulariidae) in two contrasting Mediterranean habitats. Mar Biol Res 13:551–559

McNamara ME, Lonsdale DJ, Aller RC (2013) Elemental composition of *Mnemiopsis leidyi* A. Agassiz 1865 and its implications for nutrient recycling in a Long Island estuary. Estuaries Coasts 36:1253–1264

McNamara ME, Lonsdale DJ, Cerrato RM (2014) Role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi*. Mar Ecol Prog Ser 510:151–165

Mercier A, Doncaster EJ, Hamel JF (2013) Contrasting predation rates on planktotrophic and lecithotrophic propagules by marine benthic invertebrates. J Exp Mar Biol Ecol 449:100–110

Mianzan H, Quiñones J, Palma S, Schiariti A and others (2014) *Chrysaora plocamia*: a poorly understood jellyfish from South American waters. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 219–236

Migotto AE, Marques AC, Flynn MN (2001) Seasonal recruitment of hydroids (Cnidaria) on experimental panels in the São Sebastião Channel, southeastern Brazil. Bull Mar Sci 68:287–298

Milisenda G, Rosa S, Fuentes VL, Boero F and others (2014) Jellyfish as prey: frequency of predation and selective foraging of *Boops boops* (Vertebrata, Actinopterygii) on the mauve stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). PLOS ONE 9:e94600:1–10

Milisenda G, Martinez-Quintana A, Fuentes V, Bosch-Belmar M and others (2017) Reproductive and bloom patterns of *Pelagia noctiluca* in the Strait of Messina, Italy. Estuar Coast Shelf Sci, doi:10.1016/j.ecss.2016.01.002

Mills CE (198l) Seasonal occurrence of planktonic medusae and ctenophores in the San Juan Archipelago (NE Pacific). Wasmann J Biol 39:6–29

Mills CE (1983) Vertical migration and diel activity patterns of hydromedusae: studies in a large tank. J Plankton Res 5:619–635

Mills CE (1993) Natural mortality in NE Pacific coastal hydromedusae: grazing predation, wound healing and senescence. Bull Mar Sci 53:194–203

Mills CE (2001) Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55–68

Miyajima-Taga Y, Masuda R, Yamashita Y (2016) Larvae of the threadsail filefish *Stephanolepis cirrhifer* feed on eggs and planulae of the jellyfish *Aurelia* sp. under laboratory conditions. Plankton Benthos Res 11:96–99

Møller LF, Riisgård HU (2007a) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. Mar Ecol Prog Ser 346:167–177

Møller LF, Riisgård HU (2007b) Population dynamics, growth and predation impact of the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*, in Limfjorden (Denmark). Mar Ecol Prog Ser 346:153–165

Møller LF, Riisgård HU (2007c) Respiration in the scyphozoan jellyfish *Aurelia aurita* and two hydromedusae (*Sarsia tubulosa* and *Aequorea vitrina*): effect of size, temperature and growth. Mar Ecol Prog Ser 330:149–154

Nakamura I, Sato K (2014) Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. Mar Biol 161:1263–1273

Naman SM, Greene CM, Rice CA, Chamberlin J and others (2016) Stable isotope-based trophic structure of pelagic fish and jellyfish across natural and anthropogenic landscape gradients in a fjord estuary. Ecol Evol 6:8159–8173

Nemazie DA, Purcell JE, Glibert PM (1993) Ammonium excretion by gelatinous zooplankton and their contribution to the ammonium requirements of microplankton in Chesapeake Bay. Mar Biol 116:451–458

Nishikawa J, Thu NT, Ha TM, Thu PT (2008) Jellyfish fisheries in northern Vietnam. Plankton Benthos Res 3:227–234

Nogueira M Jr, Diaz Briz LM, Haddad MA (2015) Monthly and inter-annual variations of *Opechona* sp. (Digenea: Lepocreadiidae) parasitizing scyphomedusae off southern Brazil. Mar Biol 162:391–400

Nogueira M Jr, Pereira Brandini F, Haddad MA (2016) First record of the hydromedusa *Aequorea macrodactyla* (Leptothecata: Aequoreidae) in Brazilian waters. Mar Biodivers 46:737–742

Ohtsuka S, Koike K, Lindsay D, Nishikawa J and others (2009) Symbionts of marine medusae and ctenophores. Plankton Benthos Res 4:1–13

Owens TG, King FD (1975) The measurement of respiratory electron-transport activity in marine zooplankton. Mar Biol 30:27–36

Packard TT (1985) Measurements of electron transport activity of marine microplankton. In: Williams PJ, Jannasch HW (eds) Advances in aquatic microbiology. Academic Press, New York, NY, p 207–261

Packard TT, Healy ML, Richards FA (1971) Vertical distribution of the activity of the respiratory electron transport system in marine plankton. Limnol Oceanogr 16:60–70

Palomares MLD, Pauly D (2009) The growth of jellyfishes. Hydrobiologia 616:11–21

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

Pennington JT (1990) Predation by hydromedusae on hydrozoan embryos and larvae: planktonic kin selection? Mar Ecol Prog Ser 60:247–252

Phillips DL, Inger R, Bearhop S, Jackson AL and others (2014) Best practices for use of stable isotope mixing models in food web studies. Can J Zool 92:823–835

Pitt KA, Clement AL, Connolly RM, Thibault-Botha D (2008) Predation by jellyfish on large and emergent zooplankton: implications for benthic-pelagic coupling. Estuar Coast Shelf Sci 76:827–833

Pitt KA, Duarte CM, Lucas CH, Sutherland KR and others (2013) Jellyfish body plans provide allometric advantages beyond low carbon content. PLOS ONE 8:e72683

Pitt KA, Chelsky Budarf A, Browne JG, Condon RH (2014) Bloom and bust: Why do blooms of jellyfish collapse? In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 79–104

Podar M, Haddock SHD, Sogin ML, Harbison GR (2001) A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. Mol Phylogenet Evol 21:218–230

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

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

Purcell JE (1990) Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia. Can J Fish Aquat Sci 47:505–515

Purcell JE (1991a) Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. Mar Ecol Prog Ser 72:255–260

Purcell JE (1991b) A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia 216–217:335–342

Purcell JE (1995) Gelatinous zooplankton. In: Dove LE, Nyman RM (eds) Living resources of the Delaware Estuary. The Delaware Estuary Program, Wilmington, p 125–133

Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates and effects on prey populations. Ann Inst Océanogr Paris 73:125–137

Purcell JE (2003) Predation on zooplankton by large jellyfish, *Aurelia labiata, Cyanea capillata,* and *Aequorea aequorea*, in Prince William Sound, Alaska. Mar Ecol Prog Ser 246:137–152

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. J Mar Biol Assoc UK 85:461–476

Purcell JE (2007) Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata.* Mar Ecol Prog Ser 348:183–196

Purcell JE (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616:23–50

Purcell JE (2012) Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fishes: 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, Mills CE (1988) The correlation between nema-
tocyst types and diets in pelagic Hydrozoa. In: Hessinger
DA, Lenhoff HM (eds) The biology of nematocysts. Aca-
demic Press, New York, NY, p 463–486

Purcell JE, Sturdevant MV (2001) Prey selection and dietary
overlap among zooplanktivorous jellyfish and juvenile
fishes in Prince William Sound, Alaska. Mar Ecol Prog
Ser 210:67–83

Purcell JE, Nemazie DA, Dorsey SE, Houde ED, Gamble JC
(1994) Predation mortality of bay anchovy *Anchoa mit-
chilli* eggs and larvae due to scyphomedusae and cteno-
phores in Chesapeake Bay. Mar Ecol Prog Ser 114:47–58

Purcell JE, Brown ED, Stokesbury KDE, Haldorson LH,
Shirley TC (2000) Aggregations of the jellyfish *Aurelia
labiata*: abundance, distribution, association with age-0
walleye pollock, and behaviors promoting aggregation
in Prince William Sound, Alaska, USA. Mar Ecol Prog Ser
195:145–158

Purcell JE, Hoover RA, Schwarck NT (2009) Interannual
variation of strobilation by the scyphozoan *Aurelia labi-
ata* in relation to polyp density, temperature, salinity, and
light conditions *in situ*. Mar Ecol Prog Ser 375:139–149

Purcell JE, Fuentes VL, Atienza D, Tilves U and others
(2010) Use of respiration rates of scyphozoan jellyfish to
estimate their effects on the food web. Hydrobiologia
645:135–152

Purcell JE, Fuentes V, Atienza D, Olariaga A and others
(2012) Temperature effects on asexual reproduction rates
of scyphozoan polyps from the NW Mediterranean Sea.
Hydrobiologia 690:169–180

Purcell JE, Baxter EJ, Fuentes VL (2013) Jellyfish as prod-
ucts and problems of aquaculture. In: Allan G, Burnell G
(eds) Advances in aquaculture hatchery technology.
Woodhead Publishing, Cambridge, p 404–430

Purcell JE, Tilves U, Fuentes VL, Milisenda G, Olariaga A,
Sabatés A (2014) Digestion times and predation poten-
tials of *Pelagia noctiluca* eating fish larvae and copepods
in the NW Mediterranean Sea. Mar Ecol Prog Ser 510:
201–213

Purcell JE, Marambio M, Zampardi S, Martell L and others
(2015a) The global importance of the hydromedusae in
the family *Aequoreidae*: a review. 8th Hydrozoan Soc
Workshop, Ischia, 20–27 June 2015. www.researchgate.
net/publication/279913056_The_global_importance_of_
the_hydromedusae_in_the_Family_Aequoreidae_a_review

Purcell JE, Milisenda G, Rizzo A, Carrion SA and others
(2015b) Digestion and predation rates of zooplankton by
the pleustonic hydrozoan *Velella velella* and widespread
blooms in 2013 and 2014. J Plankton Res 37:1056–1067

Quiñones J, Mianzan H, Purca S, Robinson KL, Adams GD,
Marcelo Acha E (2015) Climate-driven population size
fluctuations of jellyfish (*Chrysaora plocamia*) off Peru.
Mar Biol 162:2339–2350

Rabalais NN, Cai WJ, Carstensen J, Conley DJ and others
(2014) Eutrophication-driven deoxygenation in the
coastal ocean. Oceanography (Wash DC) 27:172–183

Radchenko KV (2013) New data on the distribution and
feeding habits of jellyfish in the Northwest Pacific. Russ J
Mar Biol 39:509–520

Riascos JM, Paredes L, González K, Cáceres I, Pacheco AS
(2013) The larval and benthic stages of the scyphozoan
medusa *Chrysaora plocamia* under El Niño–La Niña
thermal regimes. J Exp Mar Biol Ecol 446:95–101

Riisgård HU (2007) Feeding behaviour of the hydromedusa
Aequorea vitrina. Sci Mar 71:395–404

Robinson KL, Ruzicka JJ, Decker MB, Brodeur RD and oth-
ers (2014) Jellyfish, forage fish, and the world's major
fisheries. Oceanography 27:104–115

Rodriguez CS, Marques AC, Mianzan HW, Tronolone V,
Migotto AE, Genzano GN (2017) Environment and life
cycles influence distribution patterns of hydromedusae
in austral South America. Mar Biol Res 13:659–670

Roux JP, van der Lingen CD, Gibbons MJ, Moroff NE, Shan-
non LJ, Smith ADM, Cury PM (2013) Jellyfication of mar-
ine ecosystems as a likely consequence of overfishing
small pelagic fishes: lessons from the Benguela. Bull Mar
Sci 89:249–284

Rutherford LD Jr, Thuesen EV (2005) Metabolic perform-
ance and survival of medusae in estuarine hypoxia. Mar
Ecol Prog Ser 294:189–200

Scorrano S, Aglieri G, Boero F, Dawson MN, Piraino S (2016)
Unmasking *Aurelia* species in the Mediterranean Sea:
an integrative morphometric and molecular approach.
Zool J Linn Soc, https://doi.org/10.1111/zoj.12494

Segura-Puertas L, Damas-Romero M (1997) Variación esta-
cional de la comunidad de medusas (Cnidaria) en la
Laguna Bojórquez, Cancún, México. Hidrobiologica 7:
59–64

Southward AJ (1955) Observations on the ciliary currents of
the jelly-fish *Aurelia aurita* L. J Mar Biol Assoc UK 34:
201–216

Sparks C, Brierley AS, Buecher E, Boyer D, Axelsen B, Gib-
bons MJ (2005) Submersible observations on the daytime
vertical distribution of *Aequorea ?forskalea* off the west
coast of southern Africa. J Mar Biol Assoc UK 85:519–522

Stampar SN, Morandini AC, Branco LC, Da Silveira FL,
Migotto AE (2015) Drifting in the oceans: *Isarachnanthus
nocturnus* (Cnidaria, Ceriantharia), an anthozoan with
an extended planktonic stage. Mar Biol 162:2161–2169

Stibor H, Tokle N (2003) Feeding and asexual reproduction
of the jellyfish *Sarsia gemmifera* in response to resource
enrichment. Oecologia 135:202–208

Straehler-Pohl I, Jarms G (2011) Morphology and life cycle
of *Carybdea morandinii*, sp. nov. (Cnidaria), a cubozoan
with zooxanthellae and peculiar polyp anatomy. Zootaxa
2755:36–56

Stretch JJ, King JM (1980) Direct fission: an undescribed
reproductive method in hydromedusae. Bull Mar Sci 30:
522–526

Suchman CL, Brodeur RD (2005) Abundance and distribu-
tion of large medusae in surface waters of an upwelling
zone off coastal Oregon, USA. Deep-Sea Res 2 52:51–72

Suchman CL, Daly EA, Keister JE, Peterson WT, Brodeur RD
(2008) Feeding patterns and predation potential of
scyphomedusae in a highly productive upwelling region.
Mar Ecol Prog Ser 358:161–172

Suchman CL, Brodeur RD, Daly EA, Emmett RL (2012)
Large medusae in surface waters of the northern Califor-
nia Current: variability in relation to environmental con-
ditions. Hydrobiologia 690:113–125

Sun M, Dong J, Purcell JE, Li Y, Duan Y, Wang A, Wang B
(2015) Testing the influence of previous-year tempera-
ture and food supply on development of *Nemopilema
nomurai* blooms. Hydrobiologia 754:85–96

Sweetman AK, Smith CR, Dale T, Jones DOB (2014) Rapid
scavenging of jellyfish carcasses reveals the importance
of gelatinous material to deep-sea food webs. Proc Biol
Sci 281:20142210

Sweetman AK, Chelsky A, Pitt KA, Andrade H, van Oevelen
D, Renaud PE (2016) Jellyfish decomposition at the

seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs. Limnol Oceanogr 61:1449–1461

Tacon AGJ, Metian M (2009) Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. Ambio 38:294–302

Tiemann H, Sötje I, Johnston BD, Flood PR, Båmstedt U (2009) Documentation of potential courtship-behaviour in *Periphylla periphylla* (Cnidaria: Scyphozoa). J Mar Biol Assoc UK 89:63–66

Tills O, Sun X, Rundle SD, Heimbach T and others (2016) Reduced pH affects pulsing behaviour and body size in ephyrae of the moon jellyfish, *Aurelia aurita.* J Exp Mar Biol Ecol 480:54–61

Tilves U, Purcell JE, Fuentes VL, Torrents A and others (2016) Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. J Plankton Res 38:1243–1254

Toyokawa M, Aoki K, Yamada S, Yasuda A, Murata Y, Kikuchi T (2011) Distribution of ephyrae and polyps of jellyfish *Aurelia aurita* (Linnaeus 1758) *sensu lato* in Mikawa Bay, Japan. J Oceanogr 67:209–218

Uye SI (2014) The giant jellyfish *Nemopilema nomurai* in East Asian marginal seas. In: Pitt KA, Lucas CH (eds) Jellyfish blooms. Springer, Dordrecht, p 185–206

Vansteenbrugge L, Hostens K, Vanhove B, De Backer A, De Clippele L, De Troch M (2016) Trophic ecology of *Mnemiopsis leidyi* in the southern North Sea: a biomarker approach. Mar Biol 163:25

van Walraven L, Langenberg V, Dapper R, Witte JIJ, Zuur AF, van der Veer HW (2015) Long-term patterns in 50 years of scyphomedusae catches in the western Dutch Wadden Sea in relation to climate change and eutrophication. J Plankton Res 37:151–167

van Walraven L, Driessen F, van Bleijswijk J, Bol A and others (2016) Where are the polyps? Molecular identification, distribution and population differentiation of *Aurelia aurita* jellyfish polyps in the southern North Sea area. Mar Biol 163:172

Wang N, Li C (2015) The effect of temperature and food supply on the growth and ontogeny of *Aurelia* sp. 1 ephyrae. Hydrobiologia 754:157–167

Wijffels S, Roemmich D, Monselesan D, Church J, Gilson J (2016) Ocean temperatures chronicle the ongoing warming of Earth. Nat Clim Chang 6:116–118

Wintzer AP, Meek MH, Moyle PB, May B (2011) Ecological insights into the polyp stage of non-native hydrozoans in the San Francisco Estuary. Aquat Ecol 45:151–161

Zavolokin AV (2010) Jellyfish of the far eastern seas of Russia. 2. Vertical distribution and migrations. Izv TINRO 163:67–84 (in Russian with English Abstract)

Zavolokin AV, Glebov II, Kosenok NS (2008) Distribution, quantitative composition, and feeding of jellyfish in the western Bering Sea in summer and fall. Russ J Mar Biol 34:461–467

Zeman SM, Brodeur RD, Daly EA, Sutherland KR (2016) Prey selection patterns of *Chrysaora fuscescens* in the northern California Current. J Plankton Res 38:1433–1443

Zhang F, Sun S, Jin X, Li C (2012) Associations of large jellyfish distributions with temperature and salinity in the Yellow Sea and East China Sea. Hydrobiologia 690:81–96

Zheng LM, Lin YS, Li SJ, Cao WQ, Xu ZZ, Huang JQ (2008) Morphological and molecular evidences of *Aequorea taiwanensis* n. sp. from Taiwan Strait, with mtCOI sequence analysis for genus *Aequorea.* Acta Oceanol Sin 30:139–146