

# Chapter 4

## Bloom and Bust: Why Do Blooms of Jellyfish Collapse?

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

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

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## 4.1 Introduction

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

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

Senescing jellyfish typically exhibit increased rates of physical damage, loads of parasites and rates of infection (Mills 1993). The pattern of mortality varies little among taxa and usually involves degeneration of the tentacles, oral structures and gonads, reduced swimming ability and, finally, necrosis of the epithelial tissues of the bell (Brewer 1989; Kikinger 1992). The fate of moribund jellyfish is poorly known, but their specific density exceeds that of seawater and also living jellyfish (Yamamoto et al. 2008) suggesting that they are likely to sink rapidly. The observation of largely

intact moribund jellyfish on the seafloor, so-called jelly-falls (Lebrato et al. 2012), supports this argument. Rapid sinking of medusae may accelerate regional rates of carbon export from surface waters in open ocean regions (Yamamoto et al. 2008; Lebrato and Jones 2009) and increase transfer efficiency of the biological pump to the deep sea (Billett et al. 2006). For example, Billett et al. (2006) observed in the Arabian Sea the massive ‘jelly-flux’ of *Crambionella orsini* carcasses at 3,000 m following a surface bloom, which contained an order of magnitude more carbon than the total annual carbon flux as measured by sediment traps. Given the dearth of long-term time series of jellyfish communities and their biogeochemical influences in the open ocean (Condon et al. 2012), it is unclear on what spatial and temporal scales jelly-falls occur and how they are linked to ‘boom and bust’ dynamics of jellyfish blooms, although recent information suggests that jelly-falls are prevalent in coastal areas and oligotrophic gyres (Yamamoto et al. 2008; Lebrato et al. 2012) and have occurred over geological timescales (Hagadorn et al. 2002; Condon et al. 2012). Similarly, information on how jelly-falls relate to carbon export processes are sparse (but see Lebrato et al. 2013) but jellyfish size, density and shape, physical advection and microbial decomposition (Riemann et al. 2006; Tinta et al. 2012; Lebrato et al. 2013) are likely the primary driving factors influencing sinking of jellyfish blooms (Lebrato et al. 2011).

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

## 4.2 Literature Analysis

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

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

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

Taxon	Species	Location	Spr	Sum	Aut	Win	Potential source of mortality	Reference
H	<i>Aequorea victoria</i>	Puget Sound, USA	.....	.....	.....	.....	Grazing by parasites	Mills 1993
H	<i>Aglaurea hemistoma</i>	Northern Adriatic Sea	.....	.....	.....	.....		Batisic et al. 2007
H	<i>Aglantha digitale</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Bougainvillea</i> spp.	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Clytia gregarium</i>	Puget Sound, USA	.....	.....	.....	.....	Predation by fish & grazing by parasites	Mills 1993
H	<i>Clytia hemisphaerica</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Clytia hemisphaerica</i>	Mondego Estuary, Portugal	.....	.....	.....	.....		Primo et al. 2012
H	<i>Clytia hemisphaerica</i> <sup>b</sup>	Jiazhou Bay, China	.....	.....	.....	.....		Sun et al. 2012
H	<i>Corymorpha nutans</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Coryne eximia</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Diphyria gemmifera</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Euphyssa aurata</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Gonionemus vertens</i>	Puget Sound, USA	.....	.....	.....	.....		Mills 1993
H	<i>Homococconeus playangonon</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....	Senescence, infections, intertidal stranding	Hosia and Båmstedt 2007
H	<i>Hydractinia carnea</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Hydractinia carnea</i>	Mondego Estuary, Portugal	.....	.....	.....	.....		Primo et al. 2012
H	<i>Hydractinia mitina</i>	Mondego Estuary, Portugal	.....	.....	.....	.....		Primo et al. 2012
H	<i>Leuckartiana octoma</i>	Mondego Estuary, Portugal	.....	.....	.....	.....		Primo et al. 2012
H	<i>Liriope tetraphylla</i>	Northern Adriatic Sea	.....	.....	.....	.....		Batisic et al. 2007
H	<i>Liztia blondia</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007
H	<i>Liztia blondia</i>	Mondego Estuary, Portugal	.....	.....	.....	.....		Primo et al. 2012
H	<i>Malgazzia carolinæ</i> <sup>c</sup>	Jiazhou Bay, China	.....	.....	.....	.....		Sun et al. 2012
H	<i>Margelopsis hartlaubii</i>	Korsfjord, Norway <sup>a</sup>	.....	.....	.....	.....		Hosia and Båmstedt 2007



Table 4.1 (continued)

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

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

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

<sup>b</sup>Reported as *Phialidium hemisphaerica*

<sup>c</sup>Reported as *Phialactium caroliniae*

<sup>d</sup>Invasive species

<sup>e</sup>Reported as *Podocoryne minima*

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

<sup>g</sup>Mostly represented by ephyrae

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

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

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

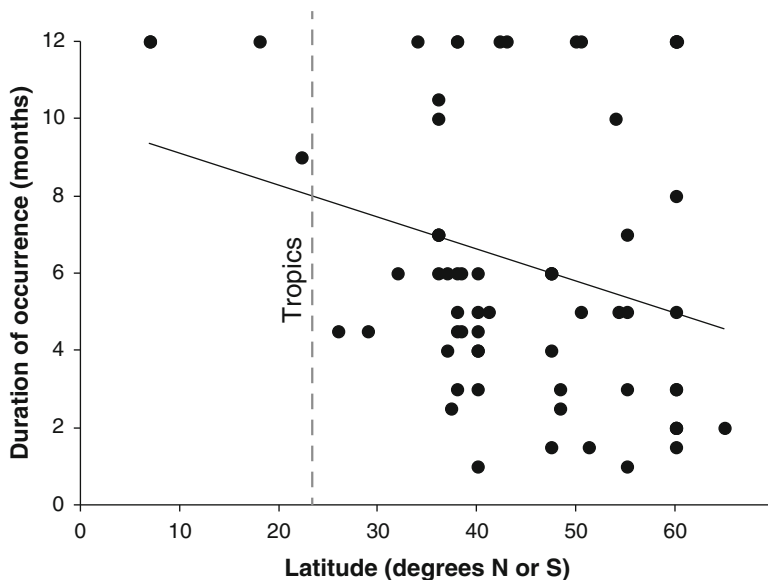


Fig. 4.1 Relationship between duration of occurrence of medusae and latitude

### 4.3 Common Causes of Mortality of Medusae

#### 4.3.1 Food Limitation

Medusae can be voracious predators of zooplankton. The very high water content of medusae enables them to attain body sizes that are much larger than other planktivores of equivalent carbon content (Acuña et al. 2011). This trait enables medusae to support large feeding structures that can efficiently clear large volumes of water and theoretically enables medusae to survive in lower concentrations of prey than other competing planktivores, such as fish (Acuña et al. 2011). Changes in growth (Olesen et al. 1994) and biomass (Möller 1980; Miglietta et al. 2008) of medusae populations often correlate with zooplankton production after correcting for temporal lags. When prey are plentiful, medusae can grow rapidly (e.g. wet weight-specific growth of  $0.88 \text{ d}^{-1}$  for *Cotylorhiza tuberculata*; Kikinger 1992), and the biomass of the population has the potential to accumulate until rates of predation by medusae exceed secondary production of zooplankton and the biomass of medusae cannot be sustained (Purcell and Decker 2005). When prey become limited, however, growth of medusae may be inhibited, and individuals may attain smaller sizes than when food is unlimited (e.g. Schneider and Behrends 1994; Lucas et al. 1997). Indeed, food limitation is regularly cited as a major cause of population declines (Table 4.1). However, sometimes medusae have continued to grow (Møller and Riisgård 2007) and accumulate biomass (Olesen et al. 1994) despite the biomass of



zooplankton appearing to be too low to support the population. This may be because rates of secondary production are very high despite the low standing biomass or that medusae efficiently exploit patches of zooplankton or may be able to supplement their diet by feeding on picoplankton (e.g. cyanobacteria) and microplankton (e.g. ciliates). Alternatively, the biomass of zooplankton in these studies may have been underestimated because neither study sampled the demersal zooplankton that emerges from the benthos into the water column at night. Emergent zooplankton are an important dietary source for jellyfish because tactile predators such as jellyfish can feed continuously during the day and night (Pitt et al. 2008), which may also allow them to outcompete visual predators for food resources in waters that are dark or contain high humic content (Aksnes et al. 2004). Indeed, in Kertinge Nor, Denmark, densities of epibenthic copepods in the water column can be 20 times greater at night than during the day (Olesen et al. 1994) and could, therefore, provide a significant food source.

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

### 4.3.2 Predation

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

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



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

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

### 4.3.3 Parasitism

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

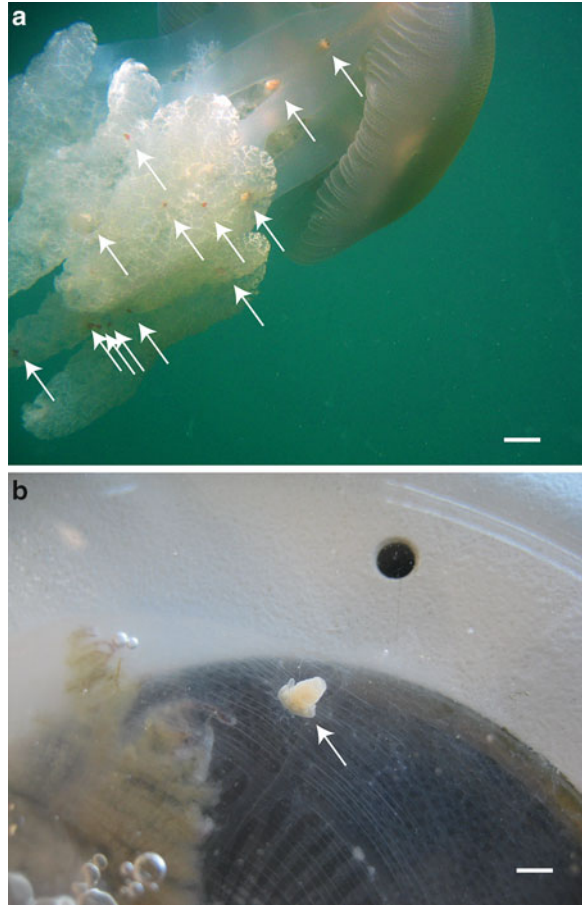
fish: Heins et al. 2010), and there is strong circumstantial evidence to suggest that hyperiid amphipods may contribute to declines in medusa populations (Mills 1993), and ctenophore populations have also been adversely affected by platyhelminth worms (Yip 1984) and parasitic anemones (Reitzel et al.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

#### 4.3.3.1 Hyperiid Amphipods

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

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

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



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

#### 4.3.3.2 Digenean Trematodes

Digenean trematodes, which are parasitic flatworms (flukes), infect at least 62 species of medusae (Browne unpubl.). Although there are approximately 18,000 species

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

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

#### 4.3.3.3 Parasitic Anemones

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

#### 4.3.3.4 Importance of Medusae Parasites and Relevance to Blooms

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

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

#### 4.3.4 Disease

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

### 4.3.5 *Death Post-Spawning*

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

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

### 4.3.6 *Metabolic Intolerances to Physical Conditions*

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

#### 4.3.6.1 *Temperature*

Although populations of medusae often disappear when water temperatures decrease during autumn, only in Chesapeake Bay is there robust evidence that death of medusae is caused by cooling water temperatures. In laboratory experiments, the pulsation rate of *Chrysaora quinquecirrha* slows with declining water temperature, and at 10 °C medusae cease to pulse and die (Gatz et al. 1973). These results are consistent

with observations in the field and laboratory, whereby medusae sink deeper into the water column when the temperature decreases to 15 °C and then disappear entirely from the water column at 10 °C (Sexton et al. 2010), suggesting that the cold water may have been the dominant cause of death. Warm temperatures can also invoke mortality. For example, following an ENSO event in 1997–1998 which elevated temperatures 1–2 °C above their long-term seasonal average, the normally perennial population of the zooxanthellate rhizostome *Mastigias papua* disappeared from Ongeim'l Tketau lake in Palau (Dawson et al. 2001; Martin et al. 2006). Concurrent laboratory experiments showed that mortality of medusae increased greatly at temperatures similar to those measured in the lake; therefore, warm water was considered the major cause of mass mortality (Dawson et al. 2001).

#### 4.3.6.2 Salinity

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

#### 4.3.6.3 UV Radiation

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





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

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

### 4.3.7 *Stranding*

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

## 4.4 Factors That Promote Survival of Jellyfish

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

### 4.4.1 Ability to Shrink When Starved

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

*Aurelia aurita* and *Cladonema californicum* can both regrow following more than 6 weeks of starvation (Hamner and Jenssen 1974; Costello 1998). In both species the pattern of growth following starvation is normal, and individuals can reinstate normal feeding and reproductive processes. However, whilst in the laboratory medusae exhibit an extraordinary ability to degrow and regrow, we could find no examples of cohorts of medusae recovering after shrinking in the field. In the field,

degrowth is usually determined from a decrease in the average size of medusae (Möller 1980); however, decreases in average size can also be explained by selective mortality or advection of the larger size classes in the population (Brewer 1989; Olesen et al. 1994) and, therefore, need to be interpreted cautiously. Degrowth (where it has been claimed) is usually observed during autumn (e.g. Möller 1980; Ishii and Båmstedt 1998; Møller and Riisgård 2007) which coincides with cooling water temperatures and reduced rates of zooplankton production, conditions that typically persist for several months. Whilst medusae can sustain at least three months starvation in the laboratory (Hamner and Jensen 1974), the two studies of regrowth by medusae have been undertaken at relatively warm and constant temperatures (16–18 °C, Hamner and Jensen 1974; 18 °C, Costello 1998 – both studies done in California). Indeed, interactive effects between regrowth and temperature are yet to be tested but may demonstrate that regrowth is not viable when water temperatures approach the thermal minimum for a species.

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

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

## 4.5 Conclusions

Rarely have the causes of mortality of medusae been reliably identified. Extreme variability in persistence of populations of the same species among locations and between years indicates that medusae may only rarely attain their maximum

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

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