

## 6.06 Gelatinous Zooplankton and Their Trophic Roles

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### Abstract

The ecological role of gelatinous zooplankton is as diverse as the taxa that composed this watery group. The most abundant gelatinous zooplankton in coastal waters are a few species of ctenophores and cnidarians that feed primarily on crustacean zooplankton or, in some cases, other gelatinous zooplankton. A few species of pelagic tunicates, including salps, doliolids, and larvaceans/appendicularians, which feed on very small particulates, can also be present in large numbers. All of these taxa are characterized by conspicuous annual and inter-annual variability. In productive coastal waters, gelatinous zooplankton exhibit high rates of growth and reproduction resulting in seasonally high abundances (blooms) when conditions are favorable. Direct consumption of prey by these large populations has been documented in several studies to significantly decrease prey abundance. Additionally, gelatinous zooplankton are themselves prey for a variety of other taxa, including both invertebrates and vertebrates. The role of gelatinous zooplankton as competitors, however, is poorly quantified, as are their symbiotic associations. Here we review the current understanding of the trophic role of gelatinous zooplankton in coastal marine ecosystem.

### 6.06.1 Introduction

Gelatinous zooplankton have been capturing the hearts and minds of scientists and artists for centuries. Their fluid nature has been the inspiration for art, jewelry, furniture, and even music, and displays of gelatinous plankton are among the most popular in public aquaria. However, despite increasing public awareness and interest in these organisms, scientists have only recently begun to understand the full importance of gelatinous zooplankton in marine ecosystems.

Gelatinous zooplankton are planktonic heterotrophs, which have a jelly-like composition, and a very high water content ([Table 1](#)). The ratio of dry weight (DW) to wet weight (WW) for medusae, ctenophores, salps, and doliolids is typically <5%, and in low-salinity environments can be even lower, with corresponding increases in carbon (C) as %DW (see [Nemazie et al. \(1993\)](#) for *Chrysaora quinquecirrha*). It should be noted that dried saltwater (salinity = 35) has a DW:WW of 3.5%, so most gelatinous zooplankton have a DW close to an equivalent volume of seawater. The C:DW in gelatinous zooplankton is quite variable depending on the amount of organically rich tissue such as muscle, gonads, and tentacles ([Larson, 1986a](#)). It is typically less than 20% and in lobate ctenophores and some medusae may be less than 2%, producing C:WW less than 0.1%. Larval lobates, with feeding tentacles, typically are enriched organically

compared to the adult forms ([Kremer et al., 1986](#); [Reeve et al., 1989](#); [Finenko et al., 2006](#)). Cydippid and beroid ctenophores, and medusae have C:WW in the range of 0.1–0.8%. For comparison, crustacean zooplankton typically have C:WW about 8% and C:DW about 40% ([Omori, 1969](#); [Gorsky et al., 1988](#)). Although appendicularians are considered among the gelatinous zooplankton because of the house feeding structure they secrete, the animal itself has a C:DW comparable to crustaceans, markedly higher than the composition of other pelagic tunicates (salps and doliolids), medusae, and ctenophores. The elemental ratio of carbon to nitrogen by weight is typically about 4 in gelatinous zooplankton, reflecting the high protein content of the organic matter and presence of only minimal amounts of storage lipids.

The most common gelatinous zooplankton in coastal marine ecosystems are a relatively few species of ctenophores, cnidarians, appendicularians, salps, and doliolids ([Table 2](#), [Figure 1](#)), which are found seasonally in large abundance in coastal waters. Typically, these animals demonstrate both large seasonal and interannual variability, presumably in response to environmental conditions and food availability. It should be noted that most species in these groups, with the exception of the scyphozoa, are not coastal but more typical of the open ocean.

Ctenophores are gelatinous invertebrates belonging to the phylum Ctenophora. Members of this phylum are characterized by the possession of eight external ctenes rows during some stage

**Table 1** Weight relationships for coastal gelatinous zooplankton

<i>Species</i>	<i>Location</i>	<i>Salinity</i>	<i>DW:WW (%)</i>	<i>C:DW (%)</i>	<i>C:WW (%)</i>	<i>C:N by weight</i>	<i>References</i>
Phylum Ctenophora							
Order Cydippida							
<i>Pleurobrachia bachei</i>	Friday Harbor, WA, USA Saanich Inlet, BC, CN	31 28–30	3.6 3.28	4.96 3.28	0.18	4.11 3.77	Kremer (unpublished) Reeve et al. (1978)
Order Lobata							
<i>Bolinopsis infundibulum</i>	Friday Harbor, WA, USA Gulf of Maine, USA	31 33	3.5 3.9	1.92 2.18	0.07 0.09	3.56 4.8	Kremer (unpublished) Bailey et al. (1994)
<i>Bolinopsis vitrea</i>	10–40 mm >40 mm	Bahamas	~35	~4 ~4	1–0.5 0.5	0.04–0.02 0.02	3.46 3.46
<i>Mnemiopsis leidyi</i>		Narragansett Bay, RI, USA Chesapeake Bay, MD, USA	31 6–16	3.4 0.9	1.7 5.1	0.06 0.05	4.00 3.98
<i>Mnemiopsis mccradyi</i>		Biscayne Bay, FL, USA	30–35	4.4	1.3	0.06	3.92
Order Beroida							
<i>Beroe cucumis</i>		Friday Harbor, WA, USA	31	3.9	10.2	0.40	3.93
<i>Beroe ovata</i>		Bahamas	~35		3.72		3.90
Phylum Cnidaria							
Class Hydrozoa							
<i>Aequorea victoria</i>	<65 mm >65 mm	Saanich Inlet, BC, CN Friday Harbor, WA, USA	28–30 31	3.5 3.4 3.5	1.57 2.54	0.05 0.09	Larson (1986a) Kremer (unpublished) Kremer (unpublished)
<i>Aglantha digitale</i>	4.5 mm 13 mm	Saanich Inlet, BC, CN Saanich Inlet, BC, CN Bedford Basin, NS, CN Saanich Inlet, BC, CN Bedford Basin, NS, CN	28–30 ~27–31	4.7	16 10.1	0.75 2.26	Larson (1986a) Matsakis and Conover (1991) Matsakis and Conover (1991)

(Continued)

**Table 1** (Continued)

<i>Species</i>		<i>Location</i>	<i>Salinity</i>	<i>DW:WW (%)</i>	<i>C:DW (%)</i>	<i>C:WW (%)</i>	<i>C:N by weight</i>	<i>References</i>
<i>Craspedacusta sowerbii</i> <sup>a</sup>	10 mm >10 mm	Aachen, Germany	0 0	1.4 0.8	29.8 29.8	0.42 0.24	3.79 3.79	Jankowski (2000)
<i>Clytia (=Phialidium) gregarium</i>		Saanich Inlet, BC, CN	28–30	3.9	9.4	0.37	3.76	Larson (1986a)
<i>Clytia (=Phialidium) lomae</i>		Saanich Inlet, BC, CN	2–30	3.7	6.8	0.25	4.00	Larson (1986a)
<i>Rathkea octopunctata</i>	juveniles adults	Bedford Basin, CN Bedford Basin, CN	~27–31 ~27–31		38.4 25.1		1.60 1.60	Matsakis and Conover (1991) Matsakis and Conover (1991)
<i>Sarsia princeps</i>		Saanich Inlet, BC, CN Bedford Basin, CN	28–30 ~27–31	3.8	6.7 6.7	0.25	3.72 3.00	Larson (1986a) Matsakis and Conover (1991)
Class Scyphozoa								
<i>Aurelia aurita</i>		Saanich Inlet, BC, CN Japan	28–30 >30	3.8 3.6	4.3 3.7	0.16 0.13	3.31 3.7	Larson (1986a) Uye and Shimauchi (2005)
	20 mm 150 mm	Bedford Basin, NS, CN Bedford Basin, NS, CN	~27–31 ~27–31		3.3 2.4		3.8 1.3	Matsakis and Conover (1991) Matsakis and Conover (1991)
<i>Chrysaora fuscescens</i>		Saanich Inlet, BC, CN Newport, OR, USA	28–30 31–33		7 3.3		5.38 3.50	Larson (1986a) Shenker (1985)
<i>Chrysaora quinquecirrha</i>		Chesapeake Bay, USA	6–12	1.0	11.1	0.11	3.96	Nemazie et al. (1993)
<i>Cyanea capillata</i>		Saanich Inlet, BC, CN	28–30	4.2	12.8	0.54	3.46	Larson (1986a)
<i>Periphylla periphylla</i>		Lurefjorden, Norway	33	3.2	19.6	0.64	6.76	Youngbluth and Båmstedt (2001)
Phylum Chordata								
Class Appendicularia								
<i>Oikopleura dioica</i>		NW Mediterranean	~38		50.4		3.60	Gorsky et al. (1988)
Class Thaliacea								
<i>Thalia democratica</i>		Sydney, Australia	~35	8	18	1.4	3.81	Heron et al. (1988)

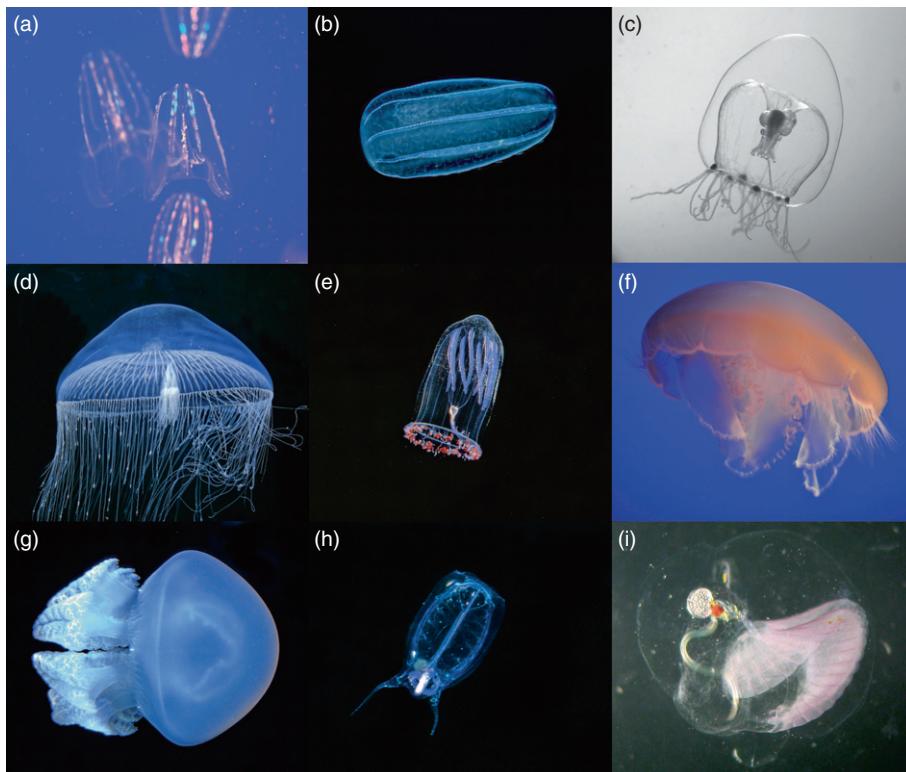
<sup>a</sup>Freshwater jellyfish.

DW, dry weight; WW, wet weight; C, carbon; N, nitrogen.

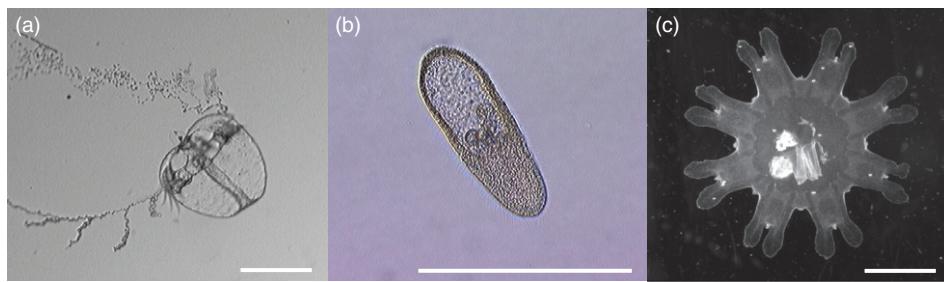
**Table 2** List of gelatinous taxa common in coastal marine ecosystems, including examples of dominant species

<i>Phylum</i>	<i>Classification</i>	<i>Dominant species</i>
Ctenophora, Ctenophores	Order Cydippida Order Lobata	<i>Pleurobrachia</i> spp. <i>Bolinopsis</i> spp. <i>Mnemiopsis</i> spp. <i>Beroe</i> spp.
Cnidaria, Cnidarians	Order Beroida Class Hydrozoa Subclass Anthomedusae Subclass Leptomedusae Subclass Trachymedusae Subclass Limnomedusae Class Scyphozoa Order Coronatae Order Semaeostomae	<i>Rathkea octopunctata</i> <i>Sarsia tubulosa</i> <i>Aequorea</i> spp. <i>Obelia</i> spp. <i>Aglantha digitale</i> <i>Craspedacusta sowerbyi</i> <sup>a</sup>
Chordata, Chordates	Subphylum Urochordata Class Appendicularia Class Thaliacea Order Salpida Order Dolioleida	<i>Periphylla periphylla</i> <i>Aurelia</i> spp. <i>Chrysaora</i> spp. <i>Cyanea capillata</i> <i>Catostylus mosaicus</i> <i>Nemopilema nomurai</i>
		<i>Oikopleura</i> spp.
		<i>Thalia democratica</i> <i>Dolioletta gegenbauri</i> <i>Doliolum</i> spp.

<sup>a</sup>Freshwater species.



**Figure 1** Coastal gelatinous zooplankton. (a) Ctenophora, Lobata, *Bolinopsis infundibulum* (photograph by Craig Wong), (b) Ctenophora, Beroida, *Beroe cucumis*, (photograph by David Wrobel), (c) Hydrozoa, Anthomedusae, *Rathkea octopunctata* (photograph by Lindsay Sullivan), (d) Hydrozoa, Leptomedusae, *Aequorea* sp. (photograph by David Wrobel), (e) Hydromedusae, Trachymedusae, *Aglantha digitale*. (photograph by David Wrobel), (f) Scyphozoa, Semaeostomae, *Aurelia aurita* (photograph by Craig Wong), (g) Scyphozoa, Rhizostomae, *Catostylus mosaicus* (photograph by David Wrobel), (h) Thaliacea, solitary *Thalia democratica* (photograph by David Wrobel), and (i) Appendicularia, *Oikopleura dioica* (photograph by Fabien Lombard). The food concentrating filter and gut have been colored with china ink particles.



**Figure 2** Early life history stages of major gelatinous zooplankton groups. (a) Cydippid larva (*Mnemiopsis leidyi*). Scale bar is 0.5 mm. (b) Planula larva (*Rathkeia octopunctata*). Scale bar is 0.5 mm. (c) Ephyra (*Aurelia aurita*). Scale bar is 1 mm. All photographs by Lindsay Sullivan.

of their life history (Hyman, 1940). Each ctene consists of a transverse plate of fused cilia. The synchronized beating of the ctene rows provides the primary mode of locomotion. Most ctenophores are simultaneous hermaphrodites capable of self-fertilization. Ctenophores possess colloblasts, specialized cells containing secretory granules that produce a sticky material used in prey capture.

The dominant ctenophores in coastal marine environments are comprised of three different orders: Cydippida, Lobata, and Beroida. Members of the order Cydippida are roughly spherical in shape and possess two retractable tentacles that are used to capture and ingest prey. Members of the order Lobata have a distinct larval stage, called a cydippid larva, which resembles adults of the order Cydippida (Figure 2(a)). The tentacles of the larva become reduced in the adult stage and are replaced as the primary feeding mechanism by two large feeding lobes (Harbison and Madin, 1982). Tentacles are absent from the order Beroida. Instead, their bodies are flattened and their stomodeums (=stomachs) enlarged. Additionally, a band of macrocilia lines the mouth, and is used to force prey tissue into the pharynx (Tamm and Tamm, 1993). Although members of the Cydippida and Lobata feed mainly on crustacean zooplankton (Reeve and Walter, 1978), Beroida use their large mouths to feed on other gelatinous zooplankton, primarily ctenophores (Greve, 1970).

The phylum Cnidaria is a diverse assemblage of organisms that includes anemones, corals, and jellies. All members of this phylum possess unique stinging or adhesive structures called 'cnidae', which are used in prey capture and settlement. Gelatinous zooplankton are confined to three classes within the phylum: Cubozoa, Hydrozoa, and Scyphozoa (Marques and Collins, 2004). All three exhibit alternation of generations between a sexual medusoid stage and an asexual polypoid stage, with distinct variations between the classes. Sexual reproduction results in a distinct larval stage, called a 'planula larva', which is ciliated and motile, and often settles to become the benthic polyp stage (Figure 2(b)).

The class Cubozoa is a small group of cnidarians, notorious for their sting, which is highly toxic and, in some cases, fatal to humans. In the class Cubozoa, each polyp is solitary and develops directly into a single medusa. The bell of the medusa is nearly square in cross-section, hence the class and common names (box jellyfish). Fertilization occurs internally following courtship and spermatophore transfer between medusae (Werner, 1973; Hartwick, 1991; Lewis and Long, 2005). This group was historically placed within the Scyphozoa (Hyman, 1940). Box jellies are found in coastal regions; however, because of their low abundance, limited distribution, and threat to human health, little published information is

available on their trophic role. As a result, our discussion focuses on members of the Hydrozoa and Scyphozoa only.

In the class Hydrozoa, the polyp stage predominates. The polyps are usually colonial and the medusae are often retained on the polyps or absent. Groups with free-living medusa stages include the following subclasses: Anthomedusae, Leptomedusae, Limnomedusae, Langiomedusae, Narcomedusae, Trachymedusae, and Siphonophorae (Bouillon and Boero, 2000). The organization of this group is currently under debate. Some characterizations list these groups as orders rather than subclasses within the Hydrozoa (Marques and Collins, 2004). Anthomedusae and Leptomedusae are seasonally abundant in many coastal systems. Anthomedusae are tall and bell-shaped and have athecate (naked) polyps. Leptomedusae are short and flat and have thecate (encased in an exoskeleton) polyps. The Langiomedusae is the smallest group of hydromedusae containing only four species that have not been well-studied. The Limnomedusae is another small group that contains several freshwater species (Dumont, 1994; Jankowski, 2001). Some freshwater Limnomedusae can reach extremely high abundances and have been estimated to significantly impact prey populations. As a result, they will be considered for comparison (Angradi, 1998; Spadiner and Maier, 1999; Jankowski et al., 2005). Narcomedusae, trachymedusae, and siphonophores are typically oceanic including many deep-sea forms, so are not discussed.

Often considered true jellies, the class Scyphozoa has a conspicuous medusoid stage. The benthic polypoid individuals (scyphistomae) are small and inconspicuous. Scyphistomae produce medusae by asexual reproduction called strobilation, which entails repeated transverse fission of the scyphistoma resulting in the release of small, flattened larval medusae called 'ephyrae' (Figure 2(c)). The class Scyphozoa contains three orders with planktonic medusae: Coronatae, Semaeostomae, and Rhizostomae. In the Coronatae, medusae possess a constriction around the middle of the bell called the 'coronal groove'. Many members of this order are bathypelagic, although some species are seasonally abundant in fjords (Sørnes et al., 2007) and tropical waters (Suarez-Morales et al., 1999). The coronal groove is absent in the Semaeostomae and Rhizostomae. The order Semaeostomae possesses marginal tentacles, lappets, and rhopalia (small sensory structures) on the bell margin and the manubrium is elongate and divided into four oral arms. In the order Rhizostomae, marginal tentacles are absent and the oral arms of the manubrium are branched and fused.

Pelagic tunicates (phylum Chordata, subphylum Urochordata) include salps and doliolids (class Thaliacea) and appendicularians or larvaceans (class Appendicularia). Like all chordates, they possess a notochord, hollow dorsal

nerve cord, gill slits, and a postanal tail. In the Thaliacea, these characteristics occur only in larvae. Appendicularian adults, on the other hand, retain the larval characteristics (Bone, 1998).

The class Thaliacea contains two orders: Salpida (salps) and Doliolida (doliolids). Although more commonly found in open water, both groups can reach extremely high densities in coastal waters, though not typically estuarine regions. Unlike their benthic counterparts, the sea squirts, pelagic tunicates possess an incurrent and excurrent siphon at opposite ends of their body. Muscular contractions of the body wall pump water through the siphons to create water movement used for propulsion. Salps feed using the same mechanism; water is pumped through their hollow bodies by muscles that partially encircle the body and food particles are captured on an internal mucous net. Unlike salps, doliolids create feeding currents using cilia and use the muscle bands that circle their entire bodies only for locomotion.

Salps and doliolids also differ in their reproductive strategies (Madin and Madin, 1991). Like the Cnidaria, they both exhibit alternation between sexual and asexual generations; however, all stages are planktonic. In most salps, a solitary form asexually produces a chain of sexual individuals. Individuals in these chains are sequential hermaphrodites, first female then male. Fertilized embryos develop within the chains and are released as 'solitaries' that then produce the aggregate chains asexually. Reproduction in doliolids is more complex (Deibel, 1998). Sexual hermaphroditic individuals (gonozoids) release cross-fertilized eggs that develop via a short larvae stage into solitary asexual individuals (oozoids). Each oozoid develops a thread-like structure, called a 'cadophore', which sprouts two types of buds: first trophozooids and then phorozooids. The trophozooids nourish the colony as the internal organs of the oozoid degenerate and it begins to act only as a carrier or 'nurse'. The phorozooids produce buds that develop into the next generation of gonozoids.

Appendicularians, or larvaceans, are a peculiar group of gelatinous zooplankton as it is not the actual animal that has a watery composition but rather its feeding structure. Coastal appendicularians are generally small (<5 mm), solitary planktonic filter feeders. Appendicularians secrete a mucous house, which is attached near the mouth and encompasses the entire body. They feed by pumping water through the house with their tails. Food particles are concentrated within the house and transported to the mouth for consumption. Several houses may be built per day. Unlike the Cnidaria and Thaliacea, Appendicularia reproduce only sexually (Fenaux, 1977).

This chapter focuses on the most abundant and presumably most ecologically important members of these groups in coastal environments. As we are limited by what is available in the literature, the content is biased both taxonomically and geographically and we recognize that many species and locales have been overlooked. Problems associated with sampling methodology, sample volume, and preservation have severely limited the amount of reliable quantitative information available for many groups. Often species and even trophic guilds have been combined in estimates of abundance. Additionally, these estimates are commonly reported by the presence/absence information or biovolume and without counts or information on size distribution. Furthermore, the fragile nature and large size of some species have presented difficulties in live collection and experimental manipulation, thereby

limiting the range of species studied to date. This results in biases toward the most abundant organisms of a convenient size that are relatively easy to investigate. Additionally, the importance of financial support for scientific research and the research interests of individual investigators should not be underestimated, all of which adds to a bias in the selection of the species and locales that are studied. Finally, there are still a relatively small number of investigators interested in the quantitative ecology of gelatinous zooplankton, and their individual research decisions greatly influences what has been studied in the past and research directions for the future.

### **6.06.2 Growth**

Despite their taxonomic diversity and major differences in life cycles, food sources, and basic biology, coastal gelatinous zooplankton share an opportunistic life history. In general, their life cycles and growth rates are adapted so they are able to rapidly exploit changes in environmental conditions such as increased temperature or food availability. As a result, populations of gelatinous zooplankton typically demonstrate large annual and interannual variability, as well as the ability to create biomass accumulations, called 'blooms', relatively quickly in direct response to favorable environmental conditions. Both field measurements and experimental studies have demonstrated that somatic growth (Table 3) and rates of reproduction for gelatinous zooplankton are influenced by a variety of factors, most notably temperature, consumer size, prey concentration, and prey type. Due to the relatively small number of experimental studies for the various taxonomic groups, some of these factors have been demonstrated more clearly in some gelatinous forms than in others.

For ctenophores, several studies have shown a clear relationship between increased availability of mesozooplankton prey and growth rate (Reeve et al., 1989; Kasuya et al., 2002; Grove and Breitburg, 2005). Furthermore, at the same food concentration, smaller sizes grow faster than larger ctenophores (Hirota, 1974; Reeve and Walter, 1976; Reeve et al., 1989; Finenko et al., 2003; Grove and Breitburg, 2005). Experimental studies have measured specific growth rates in excess of  $0.7\text{ d}^{-1}$ , more than a doubling in biomass per day, for small ctenophores at warm temperatures in high food concentrations (Table 3). Although less well-studied, somatic growth rate in ctenophores has also been shown to be affected by the type of food as well as its availability (Stanlaw et al., 1981; Sullivan and Gifford, 2007).

The dominant species of coastal ctenophores are holoplanktonic and simultaneous hermaphrodites. Capable of self-fertilization, these ctenophores release eggs into the water which typically hatch into larvae within 1–2 days (Baker and Reeve, 1974; Reeve and Walter, 1978). Reproduction in coastal ctenophores is affected by food availability, temperature, and ctenophore size. Larger ctenophores in abundant food are capable of producing hundreds (*Pleurobrachia*: Hirota (1972); *Beroe*: Arashkevich et al. (2001) and Finenko et al. (2003)) to thousands (*Mnemiopsis*: Baker and Reeve (1974), Kremer (1976b), Reeve et al. (1989), and Costello et al. (2006)) of eggs per day on a sustained basis. Appreciable egg production in *Mnemiopsis* seems to be constrained both by temperature ( $>10\text{ }^{\circ}\text{C}$ ; Costello et al. (2006)) and ctenophore size ( $>35\text{ mm}$ ; Baker and Reeve (1974)) and is also affected by

**Table 3** Growth rates of gelatinous zooplankton from coastal marine systems

<i>Species</i>	<i>Location</i>	<i>Method</i>	<i>Temperature</i> (°C)	<i>Predator size</i> (mm)	<i>Prey</i>	<i>Prey concentration</i>	<i>Specific growth</i> (d <sup>-1</sup> )	<i>Reference</i>
Phylum Ctenophora								
Order Cydippida								
<i>Pleurobrachia bachei</i>	La Jolla Bight, CA, USA	LI	15	<2.5 (D)	Copepods (A)	20 µg C l <sup>-1</sup> (~10 l <sup>-1</sup> )	0.12–0.17	Hirota (1974)
			15	2.5–6.5 (D)	Copepods (A)	20 µg C l <sup>-1</sup> (~10 l <sup>-1</sup> )	0.21–0.47	
			15	>6.5 (D)	Copepods (A)	20 µg C l <sup>-1</sup> (~10 l <sup>-1</sup> )	0.04–0.17	
		FO	14–21		<i>In situ</i> assemblage		0.02	
	CEPEX (Saanich Inlet, BC, CN)	ISI	13	<5 (OA)	<i>In situ</i> assemblage		0.47	
				>5 (OA)	<i>In situ</i> assemblage		0.09	Reeve and Walter (1976)
<i>Pleurobrachia pileus</i>	Gullmar Fjord, Sweden	LI	15	10 (D)	Copepods	40 l <sup>-1</sup>	0.07	Martinez (2008)
Order Lobata								
<i>Bolinopsis mikado</i>	Tateyama, Japan	LI	21	15–18 (TL)	Copepods (A)	10 l <sup>-1</sup>	0.32	Kasuya et al. (2002)
			21	15–18 (TL)	Copepods (A)	50 l <sup>-1</sup>	0.46	
			17	15–18 (TL)	Copepods (A)	100 l <sup>-1</sup>	~0.30	
			27	15–18 (TL)	Copepods (A)	100 l <sup>-1</sup>	0.71	
larae	Tateyama, Japan	LI	21	7–9 (TL)	Copepods (A)	2 l <sup>-1</sup>	~ -0.18	Kasuya et al. (2002)
			21	7–9 (TL)	Copepods (A)	10 l <sup>-1</sup>	0.44	
			21	7–9 (TL)	Copepods (A)	100 l <sup>-1</sup>	0.61	
<i>Mnemiopsis leidyi</i>	Chesapeake Bay, USA	LI	24.7–26.3	0.2–2.0 ml (BV)	Primarily copepods	2–4 l <sup>-1</sup>	0.02–0.25	Grove and Breitburg (2005)
			24.7–26.3	0.2–2.0 ml (BV)	Primarily copepods	4–6 l <sup>-1</sup>	0.17–0.26	
			24.7–26.3	0.2–2.0 ml (BV)	Primarily copepods	9–11 l <sup>-1</sup>	0.29–0.35	
			24.7–26.3	0.2–2.0 ml (BV)	Primarily copepods	15 l <sup>-1</sup>	0.44	
			24.7–26.3	8–18 ml (BV)	Primarily copepods	2–4 l <sup>-1</sup>	-0.04 to 0.08	
			24.7–26.3	8–18 ml (BV)	Primarily copepods	4–6 l <sup>-1</sup>	0.02–0.06	
			24.7–26.3	8–18 ml (BV)	Primarily copepods	9–11 l <sup>-1</sup>	0.08	
larae	Narragansett Bay, RI, USA	LI	18	0.40 (OA)	Natural microzooplankton	15 µg C l <sup>-1</sup>	0.16	Sullivan and Gifford (2007)
			21	0.44 (OA)	Natural microzooplankton	17 µg C l <sup>-1</sup>	0.03	
			19	0.38 (OA)	Natural microzooplankton	48 µg C l <sup>-1</sup>	<0.01	
			19	0.50 (OA)	Natural microzooplankton	62 µg C l <sup>-1</sup>	0.05	
			19	0.44 (OA)	Natural microzooplankton	357 µg C l <sup>-1</sup>	0.08	
<i>Mnemiopsis mccradyi</i>	Biscayne Bay, FL, USA	LI	26	5 (OA)	Copepods	1 l <sup>-1</sup>	~ -0.40	Reeve et al. (1978)
			26	5 (OA)	Copepods	3 l <sup>-1</sup>	~0.20	
			26	5 (OA)	Copepods	300 l <sup>-1</sup>	0.80	
	Biscayne Bay, FL, USA	LI	26	5–84 (L)	Copepods (Co, A)	5–200 l <sup>-1</sup>	0.05–0.87	Reeve et al. (1989)
			26	6 (L)	Copepods (Co, A)	100 l <sup>-1</sup>	0.83	
			26	10 (L)	Copepods (Co, A)	100 l <sup>-1</sup>	0.57	

(Continued)

**Table 3** (Continued)

<i>Species</i>	<i>Location</i>	<i>Method</i>	<i>Temperature</i> (°C)	<i>Predator size</i> (mm)	<i>Prey</i>	<i>Prey concentration</i>	<i>Specific growth</i> ( $d^{-1}$ )	<i>Reference</i>
Order Beroida <i>Beroe ovata</i>	Biscayne Bay, FL, USA	LI	26	17 (L)	Copepods (Co, A)	100 l <sup>-1</sup>	0.32	
			26	6 (L)	Copepods (Co, A)	20 l <sup>-1</sup>	0.43	
			26	10 (L)	Copepods (Co, A)	20 l <sup>-1</sup>	0.22	
			26	17 (L)	Copepods (Co, A)	20 l <sup>-1</sup>	0.05	
			26	11 (L)	Copepods (Co, A)	10 l <sup>-1</sup>	0.09	
			21	0.3–0.4 (D)	Copepods (N)	500 l <sup>-1</sup> N	0.35	Stanlaw et al. (1981)
			21	0.3–0.4 (D)	Copepods (N, Co)	500 l <sup>-1</sup> N, 300 l <sup>-1</sup> Co	0.72	
			21	0.3–0.4 (D)	Copepods (N, Co, A)	500 l <sup>-1</sup> N, 300 l <sup>-1</sup> Co, 25 l <sup>-1</sup> A	0.79	
Phylum Cnidaria Class Hydrozoa <i>Sarsia tubulosa</i>	Savastopol Bay, Black Sea	LI	18	20–50 (TL)	<i>Mnemiopsis leidyi</i>	1.8 g WW l <sup>-1</sup>	0.08–0.2	Finenko et al. (2003)
			18	45–65 (TL)	<i>Mnemiopsis leidyi</i>	1.8 g WW l <sup>-1</sup>	–0.05 to 0.05	
			26	30–35 (TL)	<i>Mnemiopsis leidyi</i>	1 l <sup>-1</sup>	0.07–0.11	Kideys et al. (2004)
Aequorea vitrina	Norwegian fjords	LI	12	3–6 (H)	Copepods (Co, A)	ad libitum (>250 l <sup>-1</sup> )	0.13–0.33	Daan (1986)
			12	8–10 (H)	Copepods (Co, A)	ad libitum (>250 l <sup>-1</sup> )	0.04–0.08	
			7–15		<i>In situ</i> assemblage		–0.10	
			15	2.3 (D)	Copepod (N)	30 l <sup>-1</sup>	~ –0.04	Møller and Riisgård (2007a)
			15	2.3 (D)	Copepod (N)	80–500 l <sup>-1</sup>	0.32	
		FO	15	4.2 (D)	Copepod (N)	30 l <sup>-1</sup>	~ –0.10	
			15	4.2 (D)	Copepod (N)	80–500 l <sup>-1</sup>	0.10	
			–1 to 6		<i>In situ</i> assemblage		–0.07–0.16	Møller and Riisgård (2007b)
			15	50 (D)	<i>Artemia</i> sp. (1-d old)	>90 l <sup>-1</sup>	0.05	
			14–22		<i>In situ</i> assemblage		–0.02–0.05	
Class Scyphozoa <i>Aurelia aurita</i>	Kertenge Nor, Denmark	LI	15	4 (D)	<i>Brachionus plicatilis</i>	130 l <sup>-1</sup>	0.14	Olesen et al. (1994)
			15	4 (D)	<i>Brachionus plicatilis</i>	700 l <sup>-1</sup>	0.18	
			15	4 (D)	<i>Brachionus plicatilis</i>	6000 l <sup>-1</sup>	0.25	
			15	4 (D)	<i>Brachionus plicatilis</i>	13,000 l <sup>-1</sup>	0.20	
			15	10 (D)	<i>Brachionus plicatilis</i>	60 l <sup>-1</sup>	–0.06	
		FO	2–22		<i>In situ</i> assemblage		<0.10	

(Continued)

**Table 3** (Continued)

Species	Location	Method	Temperature (°C)	Predator size (mm)	Prey	Prey concentration	Specific growth ( $d^{-1}$ )	Reference	
C. quinquecirrha ephyrae	Bergen, Norway Inland Sea of Japan Norwegian fjords	FO	8–16		<i>In situ</i> assemblage		-0.03–0.20	Ishii and Båmstedt (1998)	
		FO	9–30		<i>In situ</i> assemblage		0.05–0.08	Uye and Shimauchi (2005)	
		LI	15	45 (D)	<i>Artemia</i> sp. (1 d old)	>90 l <sup>-1</sup>	0.08	Møller and Riisgård (2007a)	
			15	45 (D)	<i>Acartia tonsa</i> (A)	50 l <sup>-1</sup>	0.08		
			8	40 (D)	<i>Artemia</i> sp. (1 d old)	>90 l <sup>-1</sup>	~0.03		
		FO	19	40 (D)	<i>Artemia</i> sp. (1 d old)	>90 l <sup>-1</sup>	~0.22		
			23	40 (D)	<i>Artemia</i> sp. (1 d old)	>90 l <sup>-1</sup>	~0.10		
	Norwegian fjords NR		5–22		<i>In situ</i> assemblage		-0.09 to 0.17	Møller and Riisgård (2007b)	
			6	~1 (CD)	<i>Artemia</i> sp. (N)	222 l <sup>-1</sup>	0.19	Båmstedt et al. (1999)	
C. capillata ephyrae		LI	9.5	~1 (CD)	<i>Artemia</i> sp. (N)	222 l <sup>-1</sup>	0.16		
			12	~1 (CD)	<i>Artemia</i> sp. (N)	222 l <sup>-1</sup>	0.25		
			15	~1 (CD)	<i>Artemia</i> sp. (N)	222 l <sup>-1</sup>	0.21		
			18	~1 (CD)	<i>Artemia</i> sp. (N)	222 l <sup>-1</sup>	0.31		
			15	3.5–7 (D)	<i>Artemia</i> sp. (1 d old)	55 l <sup>-1</sup>	0.22	Møller and Riisgård (2007a)	
Norwegian fjords	LI	15	3.5–7 (D)	<i>Balanus</i> sp. (nauplii/cypris)	40 l <sup>-1</sup>	0.23			
		15	3.5–7 (D)	<i>Brachionus</i> sp.	500 l <sup>-1</sup>	0.23			
		15	3.5–7 (D)	<i>Rathkeea octopunctata</i>	5 l <sup>-1</sup>	~0.22			
		15	3.5–7 (D)	<i>Acartia tonsa</i> (A)	25 l <sup>-1</sup>	-0.02			
		15	3.5–7 (D)	<i>Acartia tonsa</i> (A)	100 l <sup>-1</sup>	0.13			
N. nomurai	Kamo Inlet, Japan	FO	15	3.5–7 (D)	<i>Acartia tonsa</i> (A)	190 l <sup>-1</sup>	0.06		
			4	5 (D)	<i>Brachionus</i> sp.	500 l <sup>-1</sup>	~0.05		
			19	5 (D)	<i>Brachionus</i> sp.	500 l <sup>-1</sup>	~0.45		
			26	5 (D)	<i>Brachionus</i> sp.	500 l <sup>-1</sup>	~ -0.04		
			-1 to 6		<i>In situ</i> assemblage		0.00–0.12	Møller and Riisgård (2007b)	
		LI	14	3 (D)	<i>Brachionus plicatilis</i>	375 l <sup>-1</sup>	0.32	Olesen et al. (1996)	
			14	3 (D)	<i>Mnemiopsis leidyi</i>	23 l <sup>-1</sup>	0.66		
			FO	14	<i>In situ</i> assemblage		0.60		
			7–21		<i>In situ</i> assemblage		0.02–0.13	Brewer (1989)	
			10	~2 (D)	<i>Bolinopsis infundibulum</i>	ad libitum	0.17	Båmstedt et al. (1997)	

(Continued)

**Table 3** (Continued)

<i>Species</i>	<i>Location</i>	<i>Method</i>	<i>Temperature</i> (°C)	<i>Predator size</i> (mm)	<i>Prey</i>	<i>Prey concentration</i>	<i>Specific growth</i> (d <sup>-1</sup> )	<i>Reference</i>
Phylum Chordata								
Class Appendicularia								
<i>Oikopleura dioica</i>	Fukuyama Harbor, Japan	FO	9–28		<i>In situ</i> assemblage		0.26–3.0	Uye and Ichino (1995)
	North Sea	LI	13	~0.1 µg AFDW	Algal culture	21–85 µg C l <sup>-1</sup>	0.57–1.0	Paffenhöfer (1976)
	Mediterranean Sea	LI	14	0.1 (LT)	Algal monoculture	1.5 × 10 <sup>5</sup> cells ml <sup>-1</sup>	1.3	Fenaux (1977)
			22	0.1 (LT)	Algal monoculture	1.5 × 10 <sup>5</sup> cells ml <sup>-1</sup>	1.9	
	Kingston Harbour, Jamaica	ISI	28–29	0.1–0.6 (L)	<i>In situ</i> assemblage	2.0–2.5 mg Chl a m <sup>-3</sup>	1.38–3.18	Hopcroft and Roff (1995)
	Mediterranean Sea	LI	23	~0.2 (LT)	Algal monoculture	2.6–13 × 10 <sup>6</sup> µm <sup>3</sup> ind. <sup>-1</sup> d <sup>-1</sup> <sup>a</sup>	0.08–1.2	Gorsky and Palazzoli (1989)
	CEPEX, Saanich Inlet, Canada	ISI	14	0.2 (LTR)	<i>In situ</i> assemblage		0.3–1.57	King (1982)
	Seto Inland Sea, Japan	ISI	25	0.03 µg C ind. <sup>-1</sup>	<i>In situ</i> assemblage		1.7	Nakamura et al. (1997)
Class Thaliacea								
<i>Thalia democratica</i> (aggregates)	Georgia Bight, USA	LI	20	7–15 µg C ind. <sup>-1</sup>	Cultured phytoplankton	0.2–0.9 mm <sup>3</sup> l <sup>-1</sup>	0.15–0.36	Deibel (1982a)
				15–17 µg C ind. <sup>-1</sup>	Cultured phytoplankton	0.2–0.9 mm <sup>3</sup> l <sup>-1</sup>	0.04–0.05	
<i>Dolioletta gegenbauri</i> gonozoids	Georgia Bight, USA	LI	20	3–23 µg C ind. <sup>-1</sup>	Cultured phytoplankton	0.2–0.9 mm <sup>3</sup> l <sup>-1</sup>	0.08–0.25	
	Mid-shelf waters, GA, USA	LI	20	5 µg C ind. <sup>-1</sup>	Cultured phytoplankton	20–390 µg C l <sup>-1</sup>	0.5–0.6	Gibson and Paffenhöfer (2000)
				15 µg C ind. <sup>-1</sup>	Cultured phytoplankton	20–390 µg C l <sup>-1</sup>	0.34–0.7	
				35 µg C ind. <sup>-1</sup>	Cultured phytoplankton	20–390 µg C l <sup>-1</sup>	0.2–0.38	
			16.5	5 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.3	
				15 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.26	
				35 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.08	
			26.5	5 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.6	
				15 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.68	
				35 µg C ind. <sup>-1</sup>	Cultured phytoplankton	60 µg C l <sup>-1</sup>	0.46	

<sup>a</sup>Ration NR, not reported; FO, field observation; LI, laboratory incubation; ISI, *in situ* incubations; TL, total length; L, length; LT, tail length; LTR, trunk length; OA, oral–aboral length, without lobes; D, diameter; CD, central disc diameter; H, height; BV, biovolume; N, nauplii; Co, copepodites; A, adults; ind., individual; WW, wet weight; AFDW, ash-free dry weight; C, carbon

low dissolved oxygen concentrations (Grove and Breitburg, 2005). Generation times for *Mnemiopsis* in temperate and subtropical coastal waters have been estimated to be 2–3 weeks under favorable conditions (Kremer, 1976b; Reeve et al., 1989), enabling multiple generations per year.

Coastal species of medusae have generally been measured to have somatic growth rates of  $<0.3\text{ d}^{-1}$  in both field and laboratory conditions (Table 3) and overall the effect on growth of environmental conditions and size are less clear than for ctenophores. In one study (Båmstedt et al., 1999), temperature in the range of 6–18 °C was measured to have a relatively modest effect on the growth of *Aurelia aurita* ephyrae, while a second study (Møller and Riisgård, 2007a) of both ephyrae and adults of the same species showed a clear increase in growth with temperature up to 19 °C, and depressed growth at higher temperatures (Table 3). At comparable food densities, smaller *Sarsia tubulosa* had higher specific growth rates than larger ones (Daan, 1986; Møller and Riisgård, 2007a), and *S. tubulosa* of comparable size grew faster in higher food concentrations (Møller and Riisgård, 2007a). Results with *A. aurita* are not as clear, however. There have been an insufficient number of laboratory experiments with postephyrae scyphomedusae to show a clear decline in specific growth with size at comparable food densities (Table 3). Additionally, large ranges in the concentration of prey (rotifers) had only a modest effect on the growth of ephyrae (Olesen et al., 1996; Frandsen and Riisgård, 1997), and comparable growth rates were reported for a variety of prey types (Møller and Riisgård, 2007a). For two other species of scyphomedusae, the availability of prey ctenophores resulted in much higher growth rates of ephyrae than prey composed of either rotifers (Olesen et al., 1996) or crustaceans (Båmstedt et al., 1997).

Although a favorable nutritional environment can lead to larger, faster growing medusae and higher biomass, the actual number of medusae in coastal populations is primarily determined by asexual reproduction of benthic polyps and there is usually only one generation of medusae per year. Even for the best studied of the scyphozoans, *A. aurita*, there are still more questions than answers about how environmental variables control the initiation of strobilation and the subsequent release of ephyrae, but both temperature and food availability are implicated in the timing and magnitude of their development and release (reviewed in Lucas (2001)). The timing of the peak production of *C. quinquecirrha* ephyrae has also been shown experimentally to be influenced by temperature (Purcell et al., 1999). The abundance of benthic polyps is determined both by asexual budding of existing polyps and by the recruitment of new polyps from planula larvae produced by sexual reproduction of the medusae. Although recruitment success is not well-understood or quantified, some medusae are extremely fecund, with egg production  $>50\,000$  per individual (e.g., Mingxia et al., 1985; Lucas and Lawes, 1998). As with ctenophores, sexual reproduction can be constrained by temperature (*Cyanea* sp. at  $>15\text{ }^{\circ}\text{C}$ : Brewer (1989); *A. aurita* at  $>10\text{ }^{\circ}\text{C}$ : Lucas and Lawes (1998)). Some hydromedusae can also reproduce asexually by budding. For *Rathkea octopunctata*, in particular, asexual budding can result in rapid increases in abundance and large total biomass (Blanner, 1982; Toyokawa and Terazaki, 1994; Jacobsen and Norrbom, 2009). The initiation of this budding is closely linked to changes in temperature

(*R. octopunctata* at  $>6\text{--}7\text{ }^{\circ}\text{C}$ : Werner (1957); *Craspedacusta sowerbyi* at  $>15\text{ }^{\circ}\text{C}$ : Acker and Muscat (1976)).

High somatic growth rates have also been measured for coastal pelagic tunicates (Table 3). Decreased specific growth with size was quantified experimentally for the aggregate stage of the salp *Thalia democratica* (Deibel, 1982a), and the gonozoid stage of the doliolid *Dolioletta gegenbauri* (Gibson and Paffenhöfer, 2000). Increased temperature and increased food availability resulted in higher doliolid growth rates (Gibson and Paffenhöfer, 2000). For the appendicularian *Oikopleura dioica*, several studies have measured specific growth rates in both laboratory and field conditions over a wide range of temperatures (13–29 °C). Even at the lower temperatures (13–14 °C), if food was sufficient, the specific growth rate exceeded  $1.0\text{ d}^{-1}$ , an increase in biomass of over 270% (Paffenhöfer, 1976; Fenaux, 1977; King, 1982). At the warmest temperatures, growth rates of about  $3.0\text{ d}^{-1}$  were observed (Hopcroft and Roff, 1995; Uye and Ichino, 1995). More recent experimental studies (Troedsson et al., 2002; Lombard et al., 2009) have shown that the specific growth rate of the body of *O. dioica* is primarily set by temperature, while gonadal growth and egg production is a function of food availability. Appendicularians spawn when the gonad:total volume ratio is about 0.7, producing up to several hundred eggs under favorable food conditions, then they die. Generation time was measured to be 7 d at 15 °C and 5.5 d at 20 °C (Troedsson et al., 2002). The short generation time and reproductive potential have been observed to respond rapidly to favorable conditions both in a large mesocosm and in the field, creating large blooms (King 1982; Uye and Ichino, 1995; Nakamura et al., 1997).

### 6.06.3 Abundance

We have compiled data (Table 4) to report typical values for seasonal maxima in ctenophores, medusae, and pelagic tunicates in a variety of coastal habitats. These results represent only studies with multiple sampling stations and dates, not just a single high abundance that might have been due to physical or behavioral concentration. Although these aggregations or swarms are common, the mechanisms that control them and their ecological impacts are not well-understood (e.g., Arai, 1992; Purcell et al., 2000; Graham et al., 2003).

Generally very high abundances ( $>100\text{ m}^{-3}$ ) are found only for small species including appendicularians, doliolids, and hydromedusae (e.g., *Obelia* and *Rathkea*), or for early life history stages such as ephyrae (e.g., *Aurelia*) and larval ctenophores (e.g., *Mnemiopsis*) (Table 4). The magnitude and timing of peak abundance for small fast-growing hydromedusae and ephyrae correspond to asexual reproduction of benthic polyp stages, which is initiated by environmental cues (e.g. Loeb, 1972; Ma and Purcell, 2005; Liu et al., 2009). For species that lack benthic life history stages, including ctenophores, small refuge populations that endure periods of suboptimal environmental conditions act as seed populations as environmental conditions improve (Costello et al., 2006). Rapid reproduction under optimal environmental conditions then results in high larval abundances ( $>1000\text{ m}^{-3}$ ).

Peak abundances of  $1\text{--}20\text{ m}^{-3}$  are more typical of larger predatory species and later life history stages (Table 4). With a few exceptions, such as subtropical warm-water environments,

**Table 4** Peak abundance of gelatinous zooplankton in coastal marine systems

Species	Location	No. seasons sampled	Peak season	Max. abundance ( $m^{-3}$ )	Reference
Phylum Ctenophora					
Class Cydippida					
<i>Pleurobrachia bachei</i>	La Jolla Bight, CA, USA San Francisco Bay, CA, USA	2 3	S W	40 2	Hirota (1974) Gewant and Bollens (2005)
<i>Pleurobrachia pileus</i>	North Sea, Scotland German Bight, North Sea Wadden Sea, Netherlands Benguela Current, South Africa	32 3 2 1	S, F Sp Sp S	7 20 18 5	Fraser (1970) Greve (1971) van der Veer et al. (1983) Gibbons and Buecher (2001)
<i>Pleurobrachia rhodopis</i>	Bay of Villerfache-sur-Mer, Mediterranean	3	S	5	Buecher (1997)
Class Lobata					
<i>Bolinopsis infundibulum</i>	North Sea Resolute Passage, CN Kushiro, Hokkaido, Japan	3 1 3	Sp S S	10 0.002 0.8	Greve (1971) Siferd and Conover (1992) Toyokawa et al. (2003)
<i>Bolinopsis vitrea</i>	Bimini, Bahamas Kingston, Jamaica	1 1	Sp, S S	0.7 4	Swanberg (1974) Persad et al. (2003)
<i>Mnemiopsis leidyi</i>	Patuxent River, MD, USA Pamlico River, NC, USA Narragansett Bay, RI, USA Barnegat Bay, NJ, USA Narragansett Bay, RI, USA Sevastopol Bay, Black Sea Black Sea Narragansett Bay, RI, USA Narragansett Bay, RI, USA Chesapeake Bay, USA Chesapeake Bay, USA	1 2 3 1 5 1 2 2 2 4 4	S Sp, F S S S S S, F S S Sp, S Sp, S	100 70 50 68 666 562 304 430 1,400 ~450 ~500	Ziegenfuss and Cronin (1958) Miller (1970) Kremer and Nixon (1976) Mountford (1980) Deason (1982) Finenko and Romanova (2000) Shiganova et al. (2001a) Costello et al. (2006) Costello et al. (2006) Condon and Steinberg (2008) Condon and Steinberg (2008)
larae					
Class Beroida					
<i>Beroe cucumis</i>	North Sea Resolute Passage, CN	3 1	S S	0.5 1.0	Greve (1971) Siferd and Conover (1992)
<i>Beroe ovata</i>	Bimini, Bahamas Sevastopol Bay, Black Sea Kingston, Jamaica Northeastern Black Sea, Russia	1 1 1 4	Sp, S S, F Sp Sp, S	1.1 0.1 0.7 3.6	Swanberg (1974) Finenko et al. (2001) Persad et al. (2003) Shiganova et al. (2004)
<i>Beroe</i> sp.	Benguela Current, South Africa Chesapeake Bay, USA	1 4	S Sp, S	12 ~4.0	Gibbons and Buecher (2001) Condon and Steinberg (2008)
Phylum Cnidaria					
Class Hydrozoa					
<i>Rathkeia octopunctata</i>	Limfjorden, Denmark Bedford Basin, Nova Scotia, CN Tokyo Bay, Japan Eel Pond, MA, USA Hardangerfjord, Norway Limfjorden, Denmark Nordbotn, Norway	1 1 1 1 1 1 1	Sp Sp W W, Sp Sp Sp S	976 95 588 ~90 15 44 511	Blanner (1982) Matsakis and Conover (1991) Toyokawa and Terazaki (1994) Costello and Mathieu (1995) Pagès et al. (1996) Hansson et al. (2005) Jacobsen and Norrbom (2009)
<i>Sarsia tubulosa</i>	Wadden Sea, Netherlands Wadden Sea, Netherlands Kuleet Bay, BC, CN Eel Pond, MA, USA Limfjorden, Denmark Limfjorden, Denmark	2 1 1 1 1 3	Sp Sp S W, Sp Sp W, Sp	6 1.2 1.3 ~50 12 2.5	van der Veer et al. (1983) Daan (1986) Purcell and Grover (1990) Costello and Mathieu (1995) Hansson et al. (2005) Møller and Riisgård (2007a)
<i>Aequorea aeqourea</i>	Prince William Sound, AK, USA	3	S	0.02	Purcell (2003)
<i>Aequorea victoria</i>	Kuleet Bay, BC, CN	3	Sp, S	5.1	Purcell (1991a)
<i>Aequorea vitrina</i>	Kuleet Bay, BC, CN Limfjorden, Denmark	1 3	S F	17 2	Purcell and Grover (1990) Møller and Riisgård (2007a)

(Continued)

**Table 4** (Continued)

<i>Species</i>	<i>Location</i>	No. seasons sampled	Peak season	Max. abundance ( $m^{-3}$ )	Reference
<i>Obelia</i> sp.	Limfjorden, Denmark	1	Sp	305	Blanner (1982)
	Eel Pond, MA, USA	1	W, Sp	~8	Costello and Mathieu (1995)
	Hardangerfjord, Norway	1	Sp	158	Pagès et al. (1996)
	Benguela Current, South Africa	1	S	0.13	Gibbons and Buecher (2001)
<i>Aglantha digitale</i>	Nordbotn, Norway	1	S	70	Jacobsen and Norrbin (2009)
	Northeast Atlantic Ocean	22	S	40	Williams and Conway (1981)
	Kullen Bay, BC, CN	1	S	0.06	Purcell and Grover (1990)
	Bedford Basin, Nova Scotia, CN	1	Sp	11	Matsakis and Conover (1991)
<i>Craspedacusta sowerbyi</i>	Hardangerfjord, Norway	1	Sp	57	Pagès et al. (1996)
	Korsfjord, Norway	1	Sp	2.9	Hosia and Båmstedt (2007)
	Ulm, Germany	1	S, F	1	Spadinger and Maier (1999)
	Lake Kainui, New Zealand	2	S	236	Boothroyd et al. (2002)
Class Scyphozoa					
<i>Periphylla periphylla</i>	Lurefjorden, Norway	1	F	0.01	Fosså (1992)
	Lurefjorden, Norway	4	F	0.10	Jarms et al. (1999)
	Lurefjorden, Norway	2	F, W	2.5	Youngbluth and Båmstedt (2001)
<i>Aurelia aurita</i>	Lurefjorden, Norway	2	F, W	0.50	Båmstedt et al. (2003)
	Lurefjorden, Norway	1	Sp	0.90	Sørnes et al. (2008)
	Limfjorden, Denmark	1	Sp	61	Blanner (1982)
	Wadden Sea, Netherlands	2	Sp	0.50	van der Veer et al. (1983)
	Bedford Basin, Nova Scotia, CN	1	Sp	0.90	Matsakis and Conover (1991)
<i>ephyræ</i>	Sea of Marmara	1	S	0.03	Kideys and Niermann (1994)
	Kertenge Nor, Denmark	2	S, F	300	Olesen et al. (1994)
	Kertenge Nor, Denmark	2	S, F	220	Olesen et al. (1994)
	Kiel Bight, Baltic Sea	5	S	0.24	Behrends and Schneider (1995)
	Eel Pond, MA, USA	1	Sp, S	~80	Costello and Mathieu (1995)
<i>Aurelia labiata</i>	Limfjorden, Denmark	3	W, Sp	5	Møller and Riisgård (2007a)
	Tapong Bay, Taiwan	4	Sp	15	Lo and Chen (2008)
	Tapong Bay, Taiwan	4	Sp	328	Lo and Chen (2008)
	Prince William Sound, AK, USA	3	S	0.002	Purcell (2003)
	Chesapeake Bay, USA	4	Sp, S	~0.1	Condon and Steinberg (2008)
<i>Chrysaora fuscescens</i>	Northern California Current	1	S, F	0.02	Suchman et al. (2008)
<i>Chrysaora quinquecirrha</i>	Chesapeake Bay, USA	1	S	10	Purcell et al. (1991)
<i>Cyanea capillata</i>	Chesapeake Bay, USA	2	S	19	Purcell (1992)
	Chesapeake Bay, USA	4	Sp, S	~0.1	Condon and Steinberg (2008)
	Prince William Sound, AK, USA	3	S	0.003	Purcell (2003)
	Niantic River, CT, USA	6	Sp, S	4	Brewer (1989)
<i>Catostylus mosaicus</i>	Chesapeake Bay, USA	4	Sp	~0.2	Condon and Steinberg (2008)
	New South Wales, Australia	3	W	~2.5	Pitt and Kingsford (2000)
	East Asian Marginal Seas	4	S	0.003	Uye (2008)
Phylum Chordata					
Class Appendicularia					
<i>Oikopleura dioica</i>	Saanich Inlet, B.C. CN	1	S	25 600	Seki (1973)
	Sylt. Is, SE North Sea	2	S	14 000	Paffenhofer (1976)
	Fukuyama Harbor, Japan	1	S	53 200	Uye and Ichino (1995)
	Skagerrak, Denmark	1	S	1200	Maar et al. (2004)
	Tokyo Bay, Japan	1	F, W, Sp	21 000	Sato et al. (2008)
	Seto Inland Sea, Japan	1	S	100 000	Nakamura (1998)
<i>Oikopleura</i> spp.	Toyama Bay, Japan	1	S	330	Tomita et al. (2003)
	Kaneohe Bay, HI, USA	1	W, Sp	2600	Scheinberg et al. (2005)
	Kaneohe Bay, HI, USA	1	W, Sp	900	Scheinberg et al. (2005)
<i>Oikopleura fusiformis</i>	Toyama Bay, Japan	1	W	201	Tomita et al. (2003)
<i>Fritillaria borealis</i>					

(Continued)

**Table 4** (Continued)

<i>Species</i>	<i>Location</i>	No. seasons sampled	Peak season	Max. abundance ( $m^{-3}$ )	Reference
Class Thaliacea					
<i>Thalia democratica</i>	Port Hacking, Sydney, Australia	1	S	44	Heron and Benham (1984)
	South-eastern continental shelf, USA	1	S	>1000	Paffenhofer and Lee (1987)
	South-eastern continental shelf, USA	1	W	100	Paffenhofer et al. (1995)
<i>Dolioletta gegenbauri</i>	Mediterranean Sea	6	Sp, S	23	Licandro et al. (2006)
	California Current	1	S, F	>50	Blackburn (1979)
	South-eastern continental shelf, USA	1	W	2500	Paffenhofer et al. (1995)
<i>Dolioletta denticulatum</i>	Seto Inland Sea, Japan	1	S	48 000	Nakamura (1998)
	Seto Inland Sea, Japan	1	S	7298	Koga (1986)

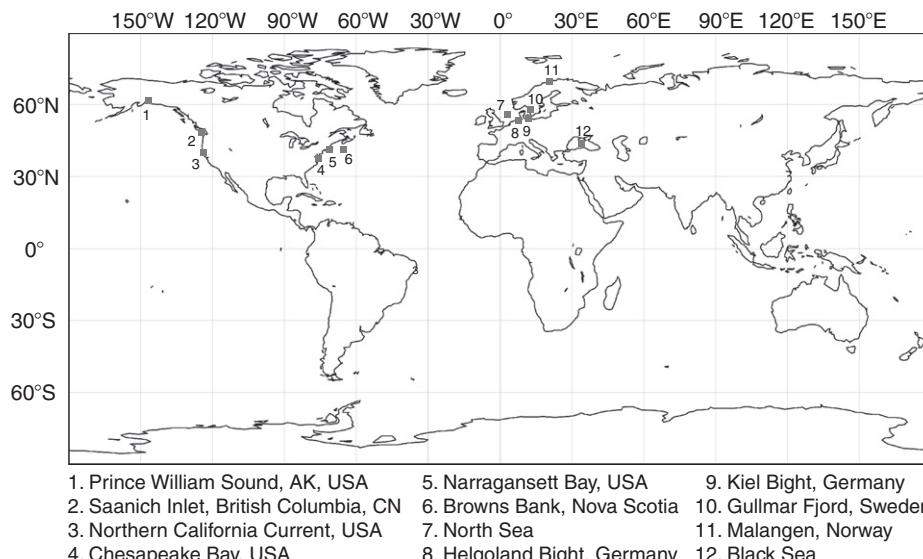
Sp, Spring; S, Summer; F, Fall; W, Winter.

predatory gelatinous zooplankton demonstrate strong seasonal peaks in spring–summer, typically following peaks in the abundance of their mesozooplankton prey. In Saanich Inlet, British Columbia, Canada, an increase of three orders of magnitude in gelatinous zooplankton stock, composed primarily of the ctenophore *Pleurobrachia*, and the hydromedusae *Clytia* (= *Phialidium*) and *Aequorea*, was observed in less than 3 months (Larson, 1986b) (Figure 3). The abundance of the ctenophore *Mnemiopsis leidyi* routinely varies five or six orders of magnitude between winter and spring–summer in its native habitat, including Narragansett Bay and Chesapeake Bay, USA (Kremer and Nixon, 1976; Condon and Steinberg, 2008) (Figure 3). This pattern has also been observed in its non-native habitat of the Black Sea (Mutlu, 1999) (Figure 3). Additionally, data from studies over multiple seasons and/or years often report inter-annual variability as much as an order of magnitude in both abundance and biomass. For the ctenophores *Pleurobrachia*, *Bolinopsis*, and *Mnemiopsis*, which feed primarily on crustacean

zooplankton, food availability is likely the proximate cause of that variability. For secondary consumers such as *Beroe* spp. that depend on other ctenophores as prey (Greve and Reiners, 1988), their abundance is generally much lower and the cause of inter-annual variability is less straightforward.

#### 6.06.4 Prey

Gelatinous zooplankton can be divided into two groups based on their primary mode of nutrition: predators and grazers. Ctenophores and cnidarian medusae are predators. Their diets are dominated by crustacean zooplankton, including copepods, cladocerans, amphipods, and decapod larvae (Table 5). Other reported prey items include fish eggs and larvae, chaetognaths, appendicularians, rotifers, protozoa, as well as the larval stages of mollusks, ascidians, annelid worms (polychaetes), and invertebrate eggs. Additionally, some coastal



**Figure 3** Map of study locations referenced in the text

**Table 5** Diet composition of gelatinous zooplankton from coastal marine systems

Species	Location	Season	Copepods	Copepod nauplii	Amphipods	Cladocerans	Crustaceans	Barnacle larvae	Euphausiids	Isopods	Ostracods	Myiids	Crab larvae	Insect larvae	Polychaete larvae	Veliger larvae	Chaetognaths	Ascidian larvae	Scyphomedusae	Hydromedusae	Siphonophores	Ctenophores	Appendicularians	Invertebrate eggs	Fish larvae	Fish eggs	Rotifers	Microzooplankton	Microphytoplankton	Nanoplankton	Picoplankton	Method	n	Reference
Phylum Ctenophora																																		
Order Cydippida																																		
<i>Pleurobrachia bachei</i>	La Jolla Bight, CA, USA	Sp, S	x x	x	x x	x	x x	x x	x	x x	x	x	x x	x	x	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	1352	Hirota (1974)					
<i>Pleurobrachia pileus</i>	Scottish waters	Sp, S	x x x	x x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	6162	Fraser (1970)					
	Norwegian Sea, Norway	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	91	Bämstedt (1998)					
	Woods Hole, MA, USA	Sp	x x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	>120	Costello and Coverdale (1998)					
	Black Sea, Turkey	Sp, S	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	27424	Mutlu and Bingel (1999)					
Order Lobata																																		
<i>Bolinopsis infundibulum</i>	Woods Hole, MA, USA	Sp	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	>120	Costello and Coverdale (1998)					
<i>Mnemiopsis leidyi</i>	Northeastern Black Sea, Russia	F	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	290	Tsikhon-Lukanina and Reznichenko (1991)					
	Northeastern Black Sea, Russia	S	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	192	Tsikhon-Lukanina et al. (1992)					
	Black Sea, Turkey	Sp, S	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	9709	Mutlu (1999)					
	Chesapeake Bay, USA	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	131	Purcell and Decker (2005)					
<i>Mnemiopsis mccradyi</i>	Indian River Estuary, FL, USA	F	+	-	+	x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	107	Larson (1987)					
Order Beroida																																		
<i>Beroe ovata</i>	Northeastern Black Sea, Russia	S																												GC	NR	Shiganova et al. (2001b)		
Phylum Cnidaria																																		
Class Hydrozoa																																		
<i>Rathkeia octopunctata</i>	Bedford Basin, Nova Scotia, CN	Sp	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	1436	Matsakis and Conover (1991)					
	Hardangerfjord, Norway	Sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GC	314	Pagès et al. (1996)				
<i>Sarsia tubulosa</i>	Yaquna Bay, OR, USA	Sp, S, F	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	37	McCormick (1969)					
	Wadden Sea, Netherlands	Sp	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	30	Daan (1986)					
	Kuleet Bay, BC, CN	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	56	Purcell and Grover (1990)					
	Friday Harbor, WA, USA	S	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GC	160	Costello and Colin (2002)				
<i>Aequorea aequorea</i>	Prince William Sound, AK, USA	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	63	Purcell (2003)					
<i>Aequorea Victoria</i>	Kuleet Bay, BC, CN	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	322	Purcell and Grover (1990)					
	Kuleet Bay, BC, CN	Sp, S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	424	Purcell (1991a)					
	Friday Harbor, WA, USA	S	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GC	509	Costello and Colin (2002)				
<i>Obelia geniculata</i>	Wellington Harbor, New Zealand	F, W	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	FE	NR	Fulton and Wear (1985)				
<i>Obelia</i> sp.	Kuleet Bay, BC, CN	S																											GC	7	Purcell and Grover (1990)			
<i>Aglantha digitale</i>	Kuleet Bay, BC, CN	S	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	4	Purcell and Grover (1990)					
	Bedford Basin, Nova Scotia, CN	Sp	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	x x	GC	499	Matsakis and Conover (1991)					
	Hardangerfjord, Norway	Sp	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	GC	694	Pagès et al. (1996)					
	Friday Harbor, WA, USA	S	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	GC	75	Costello and Colin (2002)					
<i>Craspedacusta sowerbyi</i>	Ulm, Germany	S, F	+ x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GC	120	Spadinger and Maier (1999)					
	Lake Kainui, New Zealand	S	x -	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	GC	78	Boothroyd et al. (2002)					
Class Scyphozoa																																		
<i>Periphylla periphylla</i>	Lurefjorden, Norway	F	x																										GC	39	Fosså (1992)			
	Lurefjorden, Norway	Sp	x																										GC	70	Sørnes et al. (2008)			
	Lurefjorden, Norway	F, W	x																										GC	325	Youngbluth and Bämstedt (2001)			

(Continued)

**Table 5** (Continued)

Species	Location	Season	Copepods	Copepod nauplii	Amphipods	Cladocerans	Cumaceans	Barnacle larvae	Euphausiids	Isopods	Ostracods	Myiids	Crab larvae	Insect larvae	Polychaete larvae	Veliger larvae	Chaetognaths	Ascidian larvae	Scyphomedusae	Hydromedusae	Siphonophores	Ctenophores	Appendicularians	Invertebrate eggs	Fish larvae	Fish eggs	Rotifers	Microzooplankton	Microphytoplankton	Nanoplankton	Picoplankton	Method	n	Reference
<i>Aurelia aurita</i>	Bedford Basin, Nova Scotia, CN	Sp	x x											x		x	x x		x x					GC	189	Matsakis and Conover (1991)								
	Narragansett Bay, RI, USA	Sp	x -			x										+								GC	529	Sullivan et al. (1994)								
	Kertinge Nor, Denmark	S, F	x											x x										GC	100	Olesen et al. (1994)								
	Raunefjorden, Norway	S	-	x				x		x x	+						x -	x		x x				GC	<261	Martinussen and Båmstedt (1995)								
	Ondo Strait, Japan	S	x x	x	x	x	x										x	x x x					GC	71	Uye and Shimauchi (2005)									
	Tapong Bay, Taiwan	Sp	+ -	x		x	x	x		x	x						x	x		x x x			GC	143	Lo and Chen (2008)									
	Narragansett Bay, RI, USA	Sp	- -		x																		GC	360	Sullivan et al. (1997)									
	Prince William Sound, AK, USA	S	x x	x	x	x				x	x						x	x x					GC	72	Purcell (2003)									
	Chrysaora fuscescens	S	-	+		x		x						x									GC	31	Suchman et al. (2008)									
	Chrysaora quinquecirrha	S	+ -	x	x	x								-						x x			GC	390	Purcell (1992)									
<i>Aurelia labiata</i>	Chesapeake Bay, USA	S	+ +																				GC	80	Purcell et al. (1994)									
	Chesapeake Bay, USA	S	+ +																				GC	31	Purcell et al. (1996)									
	Chesapeake Bay, USA	Sp	x x														x	x x x					GC/FE	31	Olesen et al. (1988)									
	Port Phillip Bay, Australia	F, W	- +	x										x x		+	x		x	x x x			GC	>6	Fancett (1988)									
<i>Cyanea capillata</i>	Raunefjorden, Norway	S	-	x			x		x	x x	x						x	x +					GC	<261	Martinussen and Båmstedt (1995)									
	Prince William Sound, AK, USA	S	x x	x	x	x	x		x	x x	x			x x			x	x +					GC	198	Purcell (2003)									
	Niantic River, CT, USA	Sp, S	x x x	x	x	x	x	x x x	x x	x x	x x	x	x x	x x	x x	x x	x x	x x x					GC	2060	Brewer (1989)									
	Moreton Bay, QLD, Australia	W	x x x	x	x	x	x	x x x	x x	x x	x x	x	x x	x x	x x	x x	x x x					GC	60	Carr and Pitt (2008)										
<i>Nemopilema nomurai</i>	Tsushima Island, Japan	S	x											x					x x					GC	NR	Uye (2008)								
Phylum Chordata																																		
Class Appendicularia																																		
<i>Oikopleura dioica</i>																																		
Skagerrak																																		
Gulf of California																																		
<i>Oikopleura longicauda</i> , <i>O. fusiformis</i>																																		
Kaneohe Bay, HI, USA																																		
<i>Oikopleura vahoeffeni</i>																																		
Baffin Bay																																		
Class Thaliacea																																		
<i>Thalia democratica</i>																																		
Georgia shelf, USA																																		
Cape Cleveland, Australia																																		
<i>Dolioletta gegenbauri</i>																																		
San Miguel Island, CA, USA																																		
<i>Doliolum denticulatum</i>																																		
Mediterranean Sea																																		

Sp, spring; S, summer; F, fall; W, winter; x, present; +, significant positive selection; -, significant negative selection; NR, not reported; n, sample size; GC, gut contents; FE, feeding experiments; FP, fecal pellet contents.

gelatinous predators feed on other jellies, sometimes exclusively (e.g., the ctenophore *Beroe* spp.). Several of these prey items, particularly soft gelatinous prey, may be seriously under represented or even missing from diet studies, because they were not considered/ counted, were unrecognizable or were not present in the prey assemblage at the time the study was conducted.

Although there is a significant amount of overlap in the diets of most gelatinous predators, variations in diet composition and percent contribution commonly occur as a result of prey selection, the differential consumption of prey (Table 5). Detailed investigations of the component processes of predation have demonstrated that this selection is due to a combination of factors including the encounter rates of predators and their prey, the flow fields surrounding the predator, and the vulnerability of prey to capture once it has been encountered (Costello and Colin, 1995). Among gelatinous predators, these factors are influenced by differences in spatial and temporal distribution, morphology, and behavior.

Spatial distribution patterns regulate encounter. For example, cladocerans are restricted to the diets of estuarine (e.g., *M. leidyi*, *A. aurita*, *C. quinquecirrha*, and *Cyanea capillata*) and freshwater (*Crasspedacusta sowerbyi*) jellies. Conversely, ostracods and euphausiids are more frequently observed in the diets of open- and deep-water species (*Periphylla periphylla*). Finer-scale differences in diet composition are also frequently observed among sampling locations. Although *Acartia tonsa* dominates the diet of *M. leidyi* along the east coast of North America, *A. clausi* and *Calanus euxinus* dominate the diet of *M. leidyi* in the Black Sea (Purcell et al., 2001) (Figure 3). Similarly, mysids have been reported in the diets of *Phuerobrachia pileus* (Fraser, 1970) and isopods in the guts of *Cyanea* sp. (Brewer, 1989) in only one of the many locations they have been studied. In addition to areal differences in diet composition, the vertical distribution of gelatinous zooplankton can also influence prey encounter as a result of diel vertical migrations (Arkett, 1984; Spadiner and Maier, 1999; Pitt et al., 2008).

Diet also varies with sampling time and date (Table 5). Neither ctenophores nor medusae appear to exhibit diel differences in feeding rate (Fancett and Jenkins, 1988; Martinussen and Bämstedt, 1995; Kremer, 2005; Uye and Shimauchi, 2005). However, diet composition has been reported to change over the diel cycle in conjunction with vertical migration patterns of their prey. For example, the consumption of nocturnal demersal plankton (e.g., decapods, ostracods, amphipods, and cumaceans) corresponds to the migrations of these organisms into the water column at night (Arkett, 1984; Pitt et al., 2008). Seasonal changes in diet both among and between species are also frequently observed. Specifically, increases in the consumption of soft-bodied prey, particularly invertebrate eggs, frequently occur in association with peaks in prey reproduction (Larson, 1986b; Suchman et al., 2008).

Although spatial and temporal distribution regulates predator-prey encounter, morphology and behavior influence the consumption of prey through impacts not only on encounter, but also on capture efficiency and ingestion as well. For most gelatinous predators, flow motion created by swimming entrains prey, bringing them into contact with feeding surfaces, such as tentacles and oral arms. Although all medusae use flow created during bell pulsation to capture prey, the type of flow used for prey capture and the capture surface morphology differ

significantly among species. Costello and Colin (1995) summarized some of the major differences among scyphomedusae. The umbrella of semaeostome medusae is relatively flattened or oblate. The edge of their umbrella is divided into broad flap-like structures called 'lappets' and 'marginal tentacles' arise from the subumbrellar surface. They also possess a single central mouth surrounded by curtain-like oral arms. During bell contraction (=power stroke), water is entrained from the area adjacent to the bell and then shed from the bell margin as a series of vortices. As the bell relaxes (=recovery stroke), water is drawn inward toward the subumbrellar surface and additional vortices are created. Prey is captured on the tentacles and oral arms as they are dragged through the vortices created in the wake of the medusa. Coronate medusae are more prolate (streamlined) and have stiff noncontractile tentacles inserted between their prominent marginal lappets. Water is expelled from the bell during the power stroke. During the recovery stroke, water flows inward past the bell margin and prey are captured as they are brought into contact with the lappets, oral arms, and subumbrellar surface. Rhizostome medusae lack marginal tentacles and instead of a central mouth like semaeostome medusae, they possess numerous small suctorial mouths along eight highly branched oral arms, which become fused as they approach the subumbrellar surface. Fluid expelled from the bell during the power stroke is pushed downward along the channeled surfaces of the oral arms and during the recovery stroke prey are drawn into contact with the capture surfaces. Similar interactions between morphology, fluid motion, and predation have been reported for hydromedusae and ctenophores (Costello, 1992; Waggett and Costello, 1999; Colin and Costello, 2002; Waggett and Buskey, 2006).

The presence, number, length, spacing, and morphology (branching) of tentacles also play an important role in encounter and prey capture (Mills, 1981; Madin, 1988). The tentacle length and arrangement, combined with swimming behavior, determine the shape and size of the encounter area. Tentacle density, spacing, and properties of the nematocysts/collabolasts determine the capture efficiency. Numerous finely spaced tentacles capture small prey more efficiently, while widely spaced tentacles are used to catch larger prey. The upper limit of prey size may also be determined by tentacle strength (Greene et al., 1986) and/or density. Additionally, some species of hydromedusae (e.g., *Aglaura hemistoma* and *Aglantha digitale*) possess ciliated tentacles (Mackie et al., 1989; Colin et al., 2005). They generate feeding currents highly effective at entraining and capturing protists and other small microplankton.

The type, size, and number of nematocysts are also an important factor in determining the type of prey consumed by medusae (Purcell, 1984; Purcell and Mills, 1988). Gelatinous predators that feed primarily on crustacean zooplankton possess a variety of nematocyst types that entangle or adhere to their prey. Those that feed on soft-bodied prey, including fish and gelatinous zooplankton, lack surface-adhering nematocysts and possess only piercing nematocysts that harpoon and poison their prey. The properties of nematocyst discharge (velocities, path, and length) interact with the surface characteristics of prey to determine penetration (Colin and Costello, 2007). Unlike nematocysts, the collabolasts of ctenophores adhere to both crustacean and soft-bodied prey (Madin, 1988).

In addition to morphological differences among species, ontogenetic changes in morphology also influence diet. Due to their small size and delicate nature, newly hatched coastal lobate ctenophores are highly vulnerable to damage by large copepods, which dominate the diet of adult ctenophores. Ctenophore-copepod interactions damage larval tentacles preventing ctenophores from feeding effectively and significantly reducing survival rates (Greve, 1977; Stanlaw et al., 1981; Waggett and Sullivan, 2006). Protistan microplankton offer a safe alternative to larger crustacean prey and are a major component of the diet of larval ctenophores (Stoecker et al., 1987; Sullivan and Gifford, 2004; Rapoza et al., 2005). In particular, protistan microplankton may be essential to the nutrition and survival of ctenophores, such as *Mnemiopsis* spp., during the first few days after hatching when the larvae are most vulnerable (Sullivan and Gifford, 2007). However, these ctenophores soon require nutrition from larger prey to support significant growth (Stanlaw et al., 1981). Thus, the relative abundance of micro- and mesoplankton has the potential to greatly influence the population dynamics of ctenophores through the survivorship and growth of offspring early in the season when the population is rapidly increasing.

Ontogenetic shifts in diet related to changes in morphology have also been observed between adult medusae and their ephyrae. Ephyrae are small (diameter <10 mm), flat, and have few or no tentacles. Typically, ephyrae have a more narrow diet and different prey selection patterns from adults (Olesen et al., 1996; Sullivan et al., 1997). First, mouth diameter restricts the size of prey that can be consumed by ephyrae. Sullivan et al. (1997) estimated an upper limit of prey size as 4 times the relaxed manubrium width for the ephyrae of *A. aurita*. As a result, bigger prey items such as cladocerans and fish larvae are rare in the diets of ephyrae, while smaller and more abundant prey items, including protists and rotifers, often dominate the diet. As flow velocity is a function of bell shape and diameter, ephyrae also produce entrainment flows of lower velocities than adult medusae, resulting in selection for prey with slower escape velocities (Costello and Colin, 1994; Sullivan et al., 1994). Thus, the availability of large, slow-moving gelatinous prey (ctenophores and small hydromedusae) may be particularly important to the development and population success of scyphomedusae (Olesen et al., 1996; Båmstedt et al., 1997; Sullivan et al., 1997).

Behavioral differences result in more broad-scale differences in diet between species. Cydippid ctenophores, most hydromedusae, and some scyphomedusae (*P. periphylla*) are ambush foragers. They feed by extending their tentacles into the water column and remaining stationary. As a result, encounter rates and prey capture are most strongly influenced by prey-swimming velocities (Gerritsen and Strickler, 1977), favoring fast-swimming organisms, such as euphausiids. Beroid and lobate ctenophores, some hydromedusae (e.g., *Aquorea* spp.), and most scyphomedusae are cruising foragers. They feed as they move through the water column. For cruising predators, encounter rates are influenced by the relative velocities of predators and their prey, as well as the predator encounter area and entrainment velocities (Gerritsen and Strickler, 1977). This foraging mode favors slow-moving prey, such as veligers and eggs.

In contrast to ctenophores and medusae, pelagic tunicates are grazers. Salps are true filter feeders, pumping water through a fine mucous net and ingesting the particles that are retained. Doliolids feed by the motion of cilia and appendicularians

move their tails to pump water into their house that contains an external, food-concentrating filter with very small pores. Pelagic tunicates feed on seston and are generally considered to be nonselective feeders except to the extent they are limited by the size spectrum they are physically capable of ingesting. Because pelagic tunicates are able to ingest very small particles, their diet is dominated by nano- and picoplankton (Table 5).

Particle capture by salps and appendicularians is a function of the shape and size of the pores of their feeding net (Madin and Deibel, 1998). Selection in these taxa is then merely a matter of particle size. Particle retention efficiencies vary significantly with animal size and among species. Experimental investigations have demonstrated high retention efficiencies by smaller sizes of the appendicularian *O. dioica* for particles of only 0.5 µm in diameter (Fernandez et al., 2004). Larger sizes of this and other species of coastal appendicularians retain slightly larger particles (>2 µm) with near 100% efficiency. For appendicularians, however, the rate of particle removal is not equivalent to ingestion as larger particles can be retained by the filter on the outside of the house but are not ingested by the animal itself. When considering the potential impact of appendicularians on the standing stock of seston, it is the clearance or feeding rate (*F*) that is of importance. Clearance rate is the volume of water cleared of prey per unit time, regardless of actual ingestion. The critical subset of this volume available for growth and reproduction is the energy contained in the volume cleared minus the energy contained in discarded houses (often several a day) minus undigested material.

The feeding process is much simpler for salps where particles retained on the mucous feeding net are ingested along with the net itself as the aboral end is compressed and taken into the gut and a new net is secreted at the oral end. Unfortunately, the size-retention efficiency has not been measured for the dominant coastal salp, *T. democratica*, but studies of oceanic salps show high retention (60%) of particles >2 µm and reaching nearly 100% for particles 4 µm and larger (Harbison and McAlister, 1979; Kremer and Madin, 1992). Increased retention efficiency of larger particles, 2.5 µm compared to 1 µm, has also been observed for doliolids (Tebeau and Madin, 1994).

## 6.06.5 Grazing and Predation Rates

Usually, one of two approaches is used to quantify rates of grazing/predation by gelatinous zooplankton. In one approach, predators and prey are confined in containers, and the depletion of the prey is measured over time. In this approach, the prey types and concentration can be controlled and the results are normally expressed as clearance or feeding rates (*F*) that are broadly applicable beyond a single geographic area. The main weakness of this approach is the potential artifacts associated with confining animals in a limited space. There is a large amount of variability in the results using this approach, even for the same-sized predators at similar temperatures (Table 6). Results for larger ctenophores and medusae using this method have typically underestimated clearance rates because container volumes were too small and the behavior of the predators was disrupted by contact with the container walls (Monteleone and Duguay, 1988; Gibbons and Painting, 1992; Purcell and Cowan, 1995; Buecher and Gasser, 1998). Likewise, measurements of *F* for salps based

**Table 6** Clearance rates of gelatinous zooplankton from coastal marine systems

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance (l <sup>-1</sup> )	Container size (l)	Clearance rate (l ind. <sup>-1</sup> d <sup>-1</sup> )	Specific clearance rate	Ingestion rate ('ration')	Reference
Phylum Ctenophora									
Order Cydippida									
<i>Pleurobrachia bachei</i>	12	8 (D)	<i>Acartia clausii</i>	5–27	4	5.6			Greene et al. (1986)
		8 (D)	<i>Pseudocalanus</i> sp.	4–32	4	8.4			
		8 (D)	<i>Calanus pacificus</i> (NI, NII)	13	4	1			
		8 (D)	<i>Calanus pacificus</i> (NV–NVI)	13	4	4.2			
		8 (D)	<i>Calanus pacificus</i> (Co)	7	4	2.9			
		8 (D)	<i>Calanus pacificus</i> (Co)	7	4	6.2			
		8 (D)	<i>Calanus pacificus</i> (A)	7	4	2			
	12	10 (OA)	<i>Acartia longiremis</i> (A)	20–60	1	5			Chandy and Greene (1995)
		10 (OA)	<i>Pseudocalanus newmani</i> (A)	20–60	1	11.5			
		10 (OA)	<i>Pseudocalanus newmani</i> (A)	80	1	6			
<i>Pleurobrachia pileus</i>	15	7–10 (OA)	<i>Paracalanus parvus</i>	8	6	1.8	14.8 prey ind. <sup>-1</sup> d <sup>-1</sup>		Pavez et al. (2006)
	13–15	8–12 (OA)	<i>Centropoages brachiatus</i>	1–7	20	11 (9–16)	10–70 prey ind. <sup>-1</sup> d <sup>-1</sup>		Gibbons and Painting (1992)
		10–15 (OA)	<i>Centropoages brachiatus</i>	0.5–12	5–20	5–15			
		10–15 (OA)	<i>Centropoages brachiatus</i>	0.5–12	40–80	38–55			
		7–9 (OA)	<i>Centropoages brachiatus</i>	0.5–12	5–20	5.3–12			
		12–16 (OA)	<i>Centropoages brachiatus</i>	0.5–12	40–80	40–62			
		19–22 (OA)	<i>Centropoages brachiatus</i>	0.5–12	80–100	100–147			
	12	10 (OA)	Copepods	10	2	~0–0.5	~10 prey ind. <sup>-1</sup> d <sup>-1</sup>		Bämstedt (1998)
		10 (OA)	Copepods	800	2	~0.2	~200 prey ind. <sup>-1</sup> d <sup>-1</sup>		
<i>Pleurobrachia rhodopis</i>	15	<2 (D)	<i>Acartia clausi</i>	10–125	5	2.41			Buecher and Gasser (1998)
		2.0–3.9 (D)	<i>Acartia clausi</i>	10–125	5	4.01			
		<2 (D)	<i>Acartia clausi</i>	75–225	1	0.49			
		2.0–3.9 (D)	<i>Acartia clausi</i>	75–225	1	1.90			
		>4.0 (D)	<i>Acartia clausi</i>	75–225	1	2.71			
Order Lobata									
<i>Bolinopsis mikado</i>	16	42–54 (TL)	<i>Acartia</i> spp. (A)	61	2	1.06 l g WW <sup>-1</sup> d <sup>-1</sup>			Kasuya et al. (1994)
		42–54 (TL)	<i>Acartia</i> spp. (A)	61	10	1.22 l g WW <sup>-1</sup> d <sup>-1</sup>			
		42–54 (TL)	<i>Acartia</i> spp. (A)	349	1	0.17 l g WW <sup>-1</sup> d <sup>-1</sup>			
		42–54 (TL)	<i>Acartia</i> spp. (A)	349	2	0.19 l g WW <sup>-1</sup> d <sup>-1</sup>			
<i>Bolinopsis vitrea</i>	24–26	6–8 (TL)	Copepods	2	20	~10	1–2 l mg DW <sup>-1</sup> d <sup>-1</sup>	5–15 prey ind. <sup>-1</sup> d <sup>-1</sup>	Kremer et al. (1986)
		6–8 (TL)	Copepods	20	20	1–2	0.1–0.8 l mg DW <sup>-1</sup> d <sup>-1</sup>	20–40 prey ind. <sup>-1</sup> d <sup>-1</sup>	
		33–40 (TL)	Copepods	2	20–50	50–80	0.1–0.2 l mg DW <sup>-1</sup> d <sup>-1</sup>	40–90 prey ind. <sup>-1</sup> d <sup>-1</sup>	
		33–40 (TL)	Copepods	20	20–50	20–30	0.05–0.07 l mg DW <sup>-1</sup> d <sup>-1</sup>	250–400 prey ind. <sup>-1</sup> d <sup>-1</sup>	
		40–60 (TL)	Copepods	20	50	20–60	0.05–0.07 l mg DW <sup>-1</sup> d <sup>-1</sup>	250–800 prey ind. <sup>-1</sup> d <sup>-1</sup>	

(Continued)

**Table 6** (Continued)

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance (l <sup>-1</sup> )	Container size (l)	Clearance rate (l ind. <sup>-1</sup> d <sup>-1</sup> )	Specific clearance rate	Ingestion rate ('ration')	Reference
<i>Mnemiopsis leidyi</i>	20–25	~15 (OA)	Mesozooplankton	20–100	20–25	~5.4	80 l g DW <sup>-1</sup> d <sup>-1</sup>		Kremer (1979)
		~33 (OA)	Mesozooplankton	20–100	20–25	~13.5	40 l g DW <sup>-1</sup> d <sup>-1</sup>		
	10–15	~15 (OA)	Mesozooplankton	20–100	20–25	~4.0	60 l g DW <sup>-1</sup> d <sup>-1</sup>		
		~33 (OA)	Mesozooplankton	20–100	20–25	~6.7	20 l g DW <sup>-1</sup> d <sup>-1</sup>		
	15–20	36–44 (OA)	Cultured ciliates	1000–3400	1	1.8 (0.3–4.6)	0.24 l cm <sup>-3</sup> d <sup>-1</sup>		Stoecker et al. (1987)
		10–35 (OA)	<i>Strombilidium</i> and <i>Favella</i>	1000–1400	0.5–1.0	0.6–4.8	0.4–1.7 l cm <sup>-3</sup> d <sup>-1</sup>		
		38–54 (OA)	<i>Strombilidium</i> and <i>Favella</i>	1000–1400	0.5–1.0	0.6–6	0.2–0.65 l cm <sup>-3</sup> d <sup>-1</sup>		
		24–50 (OA)	<i>In situ</i> microzooplankton	170–12260	0.5–1.0	1–10	0.8 l cm <sup>-3</sup> d <sup>-1</sup>		
	21–24	20–25 (OA)	Fish eggs	3–5	4–35	2–32			Monteleone and Duguay (1988)
		20–25 (OA)	Fish eggs	3–5	50	20–30			
		20–25 (OA)	Fish eggs	3–5	100–200	30–60			
		45–50 (OA)	Fish eggs	3–5	15	13–42			
		45–50 (OA)	Fish eggs	3–5	50–200	30–168			
		20–25 (OA)	Fish larvae	3	NR	~10–20			
	22–24	2.5–5 (OA)	Copepods	60	2		0.293 l mg DW <sup>-1</sup> d <sup>-1</sup>		Finenko and Romanova (2000)
larvae	2.5–5 (OA)	Copepods	100	2			0.063 l mg DW <sup>-1</sup> d <sup>-1</sup>		
	10–20 (OA)	Copepods	60	5			0.036 l mg DW <sup>-1</sup> d <sup>-1</sup>		
	10–20 (OA)	Copepods	100	5			0.028 l mg DW <sup>-1</sup> d <sup>-1</sup>		
	22	2–6 (TL)	<i>Acartia tonsa</i>	56–1400	1	0.04–0.43 <sup>c</sup>	0.36 l mg DW <sup>-1</sup> d <sup>-1</sup>		Deason (1982)
<i>Mnemiopsis mccradyi</i>	18–25	1–4 (OA)	<i>In situ</i> microzooplankton	59–508 µg C	1	0.96		177 µg C ind. <sup>-1</sup> d <sup>-1</sup>	Sullivan and Gifford (2004)
		5 (OA)	<i>In situ</i> microzooplankton	59–508 µg C	1	0.75		219 µg C ind. <sup>-1</sup> d <sup>-1</sup>	
		6–15 (OA)	<i>In situ</i> microzooplankton	59–313 µg C	1	2.28		356 µg C ind. <sup>-1</sup> d <sup>-1</sup>	
	26	8 (OA)	<i>Acartia tonsa</i>	3–300	3	~1		10–>100% body C d <sup>-1</sup>	Reeve et al. (1978)
Order Beroida		30 (OA)	<i>Acartia tonsa</i>	3–3000	30	~20		10–>100% body C d <sup>-1</sup>	
	25–27	50 (TL)	<i>Acartia</i> sp.	1.1–7.6	<i>in situ</i> (GC)	21.6			Larson (1987)
		50 (TL)	<i>Oithona</i> sp.	7–36	<i>in situ</i> (GC)	2.4			
		50 (TL)	Barnacle nauplii	2–10	<i>in situ</i> (GC)	31.2			
	21	10 (TL)	<i>Acartia tonsa</i> (Co, CA)	100	55	~5	~10 l mg C <sup>-1</sup> d <sup>-1</sup>		Kremer and Reeve (1989)
		50 (TL)	<i>Acartia tonsa</i> (Co, CA)	100	55	~20	~5 l mg C <sup>-1</sup> d <sup>-1</sup>		
	<i>Beroe ovata</i>	18	16 (TL)	<i>Mnemiopsis leidyi</i>	0.8–6	5	2–4 <sup>c</sup>	4.8 l g WW <sup>-1</sup> d <sup>-1</sup>	Finenko et al. (2003)
Phylum Cnidaria Class Hydrozoa		65 (TL)	<i>Mnemiopsis leidyi</i>	0.8–6	5	2–4 <sup>c</sup>	0.05–0.1 l g WW <sup>-1</sup> d <sup>-1</sup>		
	<i>Aequorea vitrina</i>	~14	73 (D)	Copepods	3.2	<i>in situ</i> (GC)	191		Purcell (2003)
		15	~8 (D)	<i>Acartia tonsa</i> (A)	50	5	0.3		Møller and Riisgård (2007b)
	<i>Craspedacusta sowerbyi</i>	22	12 (D)	Nauplii	77	0.5	0.93		Dodson and Cooper (1983)
		12 (D)	Copepods	19	0.5	0.05			
		12 (D)	<i>Daphnia pulex</i>	5.6	0.5	1.95			
	<i>Obelia geniculata</i>	14	~2 (D)	<i>Paracalanus indicus</i> (NI–NVI)	50	1	~0.1		Fulton and Wear (1985)
		~4 (D)	<i>Paracalanus indicus</i> (NI–NVI)	50	1	~0.8			

(Continued)

**Table 6** (Continued)

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance ( $l^{-1}$ )	Container size (l)	Clearance rate ( $l \text{ ind.}^{-1} \text{ d}^{-1}$ )	Specific clearance rate	Ingestion rate ('ration')	Reference
<i>Rathkea octopunctata</i>	4	1.2–2.2 (H)	<i>Acartia tonsa</i> (A)	20–40	0.6	0.06			Hansson et al. (2005)
<i>Sarsia tubulosa</i>	12	3 (H)	<i>Temora longicornis</i>	5–300	~0.1			M=~50 µg C ind. $^{-1}$ d $^{-1}$	Daan (1986)
		12 (H)	<i>Temora longicornis</i>	5–300	~0.6			M=~350 µg C ind. $^{-1}$ d $^{-1}$	
	11	5.1 (H)	<i>Acartia tonsa</i> (A)	115	0.6	0.3		34 prey ind. $^{-1}$ d $^{-1}$	Hansson et al. (2005)
	15	2.3 (H)	<i>Acartia tonsa</i> (NI–NVI)	30	2–4	~0.4		~2 µg C ind. $^{-1}$ d $^{-1}$	Møller and Riisgård (2007b)
		2.3 (H)	<i>Acartia tonsa</i> (NI–NVI)	500	2–4	~0.4		~30 µg C ind. $^{-1}$ d $^{-1}$	
		4.2 (H)	<i>Acartia tonsa</i> (NI–NVI)	30	2–4	~0.6		~4 µg C ind. $^{-1}$ d $^{-1}$	
		4.2 (H)	<i>Acartia tonsa</i> (NI–NVI)	500	2–4	~0.6		~35 µg C ind. $^{-1}$ d $^{-1}$	
Class Scyphozoa									
<i>Periphylla periphylla</i>	6–7	>50 (D)	Copepods	<1	<i>in situ</i> (VO)	760			Sørnes et al. (2008)
<i>Aurelia aurita</i>	9.5	5–30 (D)	Mesozooplankton	2.1	<i>in situ</i> (GC)	360		288 prey ind. $^{-1}$ d $^{-1}$	Martinussen and Bämstedt (1995)
	18–20	100–300 (D)	Copepods	3.5	<i>in situ</i> (GC)		5.04 l g WW $^{-1}$ d $^{-1}$		Uye and Shimauchi (2005)
	8	68 (D)	Fish larvae	0.5–16	27	9.7		M=2640 prey ind. $^{-1}$ d $^{-1}$	Titelman and Hansson (2006)
		39 (D)	Fish larvae	2	27	~120			
		133 (D)	Fish larvae	2	27	~480			
	15	~20 (D)	<i>Acartia tonsa</i>	5–110	70–85	~5			Møller and Riisgård (2007b)
		~60 (D)	<i>Acartia tonsa</i>	5–110	70–85	~40			
	25	<50 (D)	Mesozooplankton	0.65	<i>in situ</i> (GC)	300 <sup>c</sup>		195 prey ind. $^{-1}$ d $^{-1}$	Lo and Chen (2008)
		50–100 (D)	Mesozooplankton	0.65	<i>in situ</i> (GC)	1003 <sup>c</sup>		652 prey ind. $^{-1}$ d $^{-1}$	
		110–150 (D)	Mesozooplankton	0.65	<i>in situ</i> (GC)	1388 <sup>c</sup>		902 prey ind. $^{-1}$ d $^{-1}$	
		>150 (D)	Mesozooplankton	0.65	<i>in situ</i> (GC)	3728 <sup>c</sup>		2423 prey ind. $^{-1}$ d $^{-1}$	
ephyrae	15	5–7 (CD)	<i>Brachionus</i> sp.	40–600	4	0.54			Møller and Riisgård (2007b)
		5–7 (CD)	<i>Acartia tonsa</i> (A)	25–200	4	0.15			
		5–7 (CD)	Barnacle nauplii/cypris	10–50	4	0.45			
		5–7 (CD)	<i>Rathkea octopunctata</i>	2–5	3	0.21			
<i>Aurelia labiata</i>	~14	67 (D)	Copepods	1.4	<i>in situ</i> (GC)	176		506 prey ind. $^{-1}$ d $^{-1}$	Purcell (2003)
<i>Chrysaora quinquecirrha</i>	25–30	50–110 (D)	<i>Mnemiopsis leidyi</i>	0.003 ml	2400		850 l cm $^{-1}$ d $^{-1}$		Miller (1974)
	20–27	40 (D)	Copepods	1–100	<i>in situ</i> (GC)	15.7			Purcell (1992)
	NR	32–55 (D)	Fish larvae	0.01	3000	780 <sup>c</sup>		7.8 prey ind. $^{-1}$ d $^{-1}$	Cowan and Houde (1992)
	21–23	75 (D)	<i>Mnemiopsis leidyi</i>	0.007	1000	702			Purcell and Cowan (1995)

(Continued)

**Table 6** (Continued)

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance ( $\text{l}^{-1}$ )	Container size (l)	Clearance rate ( $\text{l ind.}^{-1} \text{d}^{-1}$ )	Specific clearance rate	Ingestion rate ('ration')	Reference
<i>Cyanea capillata</i>	20–24	81 (D)	<i>Mnemiopsis leidyi</i>	0.006	3200	1657			
		2 (CD)	Protists	>2000	0.5	0.007			Olesen et al. (1996)
		2 (CD)	Nauplii	200	0.5	0.007			
		3 (CD)	<i>Mnemiopsis leidyi</i> larvae	10–40	0.5–1	0.03			
	NR	25 (D)	<i>Paracalanus indicus</i>	1–7	7	~60			Fancett and Jenkins (1988)
		50 (D)	<i>Paracalanus indicus</i>	1–7	25	~120			
		100 (D)	<i>Paracalanus indicus</i>	1–7	25	~480			
		20–65 (D)	Fish eggs	1–10	7	~48–336			
	9.5	2–35 (D)	Mesozooplankton	0.4–19.8	<i>in situ</i> (GC)	1214–2664		276–8933 prey $\text{ind.}^{-1} \text{d}^{-1}$	Martinussen and Båmstedt (1995)
		94 (D)	Copepods	1.4	<i>in situ</i> (GC)	161		1066 prey $\text{ind.}^{-1} \text{d}^{-1}$	Purcell (2003)
		149 (D)	Copepods	1.3	<i>in situ</i> (GC)	950		509 prey $\text{ind.}^{-1} \text{d}^{-1}$	
		149 (D)	Copepods	1.3	<i>in situ</i> (GC)	166		128 prey $\text{ind.}^{-1} \text{d}^{-1}$	
Phylum Chordata									
Class Appendicularia									
<i>Oikopleura dioica</i>	13	0.3–1.1 (LB)	Flagellates and diatoms	0.1–0.4 mm <sup>3</sup>	4	0.005–0.340	6–16 ml µg AFDW <sup>-1</sup> d <sup>-1</sup>		Paffenhofer (1976)
		0.3–1.1 (LB)	Natural bacteria ( <sup>3</sup> H labeled)	natural levels <sup>b</sup>	NR	<0.001–0.2		20–100% body C d <sup>-1</sup>	King et al. (1980)
		0.3 (LB)	Natural bacteria ( <sup>3</sup> H labeled)	natural levels <sup>b</sup>		0.0017	7.2 ml µg C <sup>-1</sup> d <sup>-1</sup>		
		1 (LB)	Natural bacteria ( <sup>3</sup> H labeled)	natural levels <sup>b</sup>		0.069	14 ml µg C <sup>-1</sup> d <sup>-1</sup>		
	23.5	0.6–1.3 (LB)	Bead tracer	115–125 µg C	0.125–0.25	0.072–0.3	7–19 ml µg AFDW <sup>-1</sup> d <sup>-1</sup>		Allardige (1981)
		0.74 (LB)	Cultured phytoplankton	80 µg C (new house)	0.02	0–0.14			Acuña and Kiefer (2000)
				80 µg C (>30 min.)	0.02	0.12		126% body C d <sup>-1</sup>	
				320 µg C (new house)	0.02	0.024–0.17			
				320 µg C (>30 min.)	0.02	0.05–0.07		238% body C d <sup>-1</sup>	
				481 µg C (new house)	0.02	0.07–0.14			
	10	0.5–0.9 (LB)	<i>Isochrysis galbana</i> (4 µm)	481 µg C (>30 min.)	0.02	0.024–0.07		250% body C d <sup>-1</sup>	
				1602 µg C (new house)	0.02	0.07			
				1602 µg C (>30 min.)	0.02	0.012		102% body C d <sup>-1</sup>	
							79 ml µg C <sup>-1</sup> d <sup>-1</sup>		Tiselius et al. (2003)
							31 ml µg C <sup>-1</sup> d <sup>-1</sup>	~180% body C d <sup>-1</sup>	
							3 ml µg C <sup>-1</sup> d <sup>-1</sup>	<360% body C d <sup>-1</sup>	
<i>Oikopleura fusiformis</i>	10	0.47 (LB)	Natural seston	10–45 µg C	0.6	0.036		247% body C d <sup>-1</sup>	Maar et al. (2004)
		0.165 (LB)	Beads	~150 µg C	0.1	0.0017			Fernandez et al. (2004)
		0.347 (LB)	Beads	~150 µg C	0.1	0.01			
		0.698 (LB)	Beads	~150 µg C	0.1	0.19			
		0.734 (LB)	Beads	~150 µg C	0.1	0.06			
	24	0.4–1.0 (LB)	Natural seston (eukaryotes)	15 µg C	0.265	0.912	190 ml µg C <sup>-1</sup> d <sup>-1</sup>	290% body C d <sup>-1</sup>	Scheinberg et al. (2005)

(Continued)

**Table 6** (Continued)

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance (l <sup>-1</sup> )	Container size (l)	Clearance rate (l ind. <sup>-1</sup> d <sup>-1</sup> )	Specific clearance rate	Ingestion rate ('ration')	Reference
<i>Oikopleura longicauda</i> , <i>O. fusiformis</i>	24	0.4–1.0 (LB) 0.4–1.0 (LB)	Natural seston (bacteria) Natural seston	3–9 µg C 19–25 µg C	0.265 0.265	0.6 0.87 (0.29–1.56)	125 ml µg C <sup>-1</sup> d <sup>-1</sup>	80% body C d <sup>-1</sup> 460% body C d <sup>-1</sup>	
<i>Oikopleura longicauda</i>	24	0.4–0.9 (LB)	Natural seston (eukaryotes)	~15 µg C	0.265	0.816	293 ml µg C <sup>-1</sup> d <sup>-1</sup>	370% body C d <sup>-1</sup>	
<i>Oikopleura</i> spp., <i>Fritillaria</i> spp.	9–20	0.4–0.9 (LB) 0.4 (LB)	Natural seston (bacteria) Natural seston	3–9 µg C 0.05–16.3 µg Chl. a	0.265 <i>in situ</i> (GC)	0.29 Min.=0.005–0.1	104 ml µg C <sup>-1</sup> d <sup>-1</sup>	80% body C d <sup>-1</sup>	Lopez-Urrutia et al. (2003)
<i>Fritillaria borealis</i>	15	0.7(LB) 1 (LB)	Natural seston Natural seston	0.05–16.3 µg Chl. a 0.05–16.3 µg Chl. a	<i>in situ</i> (GC)	Min.=0.01–0.4 Min.=0.05–0.6			Fernandez et al. (2004)
<i>Oikopleura vanhoeffeni</i>	–1.6 to 4.5	0.4–4.5 (LB)	Beads Beads	~150 µg C ~150 µg C	0.1 0.1	0.0024–0.0036 0.024–0.055			Deibel (1988)
			Bead tracer	80–130 µg POC	0.45	0.192–7.752	4–300 ml µg C <sup>-1</sup> d <sup>-1</sup>	Med.=64% body C d <sup>-1</sup> 12–982% body C d <sup>-1</sup>	
	1	2.5–3.0 (LB) 3.0–4.0 (LB) 4.0–5.0 (LB)	Natural seston Natural seston Natural seston	0.08–15 mg Chl a 0.08–15 mg Chl a 0.08–15 mg Chl a	0.45 0.45 0.45	0.48 ~1.32 ~2.9			Bochdansky et al. (1998)
Class Thaliacea									
<i>Thalia democratica</i>	20	2.7 (L) 3.3 (L) 4.2 (L)	Cultured phytoplankton Cultured phytoplankton Cultured phytoplankton	0.2–0.7 mm <sup>3</sup> 0.2–0.7 mm <sup>3</sup> 0.2–0.7 mm <sup>3</sup>	2.5	0.045 0.088 0.192	7 ml µg C <sup>-1</sup> d <sup>-1</sup> 9 ml µg C <sup>-1</sup> d <sup>-1</sup> 12 ml µg C <sup>-1</sup> d <sup>-1</sup>	60% body C d <sup>-1</sup>	Deibel (1982b)
	30–32	2–10 (L)	Radiolabeled phytoplankton and bacteria	69–200 µg POC	~5	~0.024–1.20		86–200% body C d <sup>-1</sup>	Mullin (1983)
	20–23	4.4–6.6 (L)	Natural seston	0.05–1.2 mm <sup>3</sup>	2	0.17 (0.05–0.30)	13 (2.7–35) ml µg C <sup>-1</sup> d <sup>-1</sup>	48% body C d <sup>-1</sup>	Deibel (1985a)
<i>Dolioletta gegenbauri</i> gonozooids oozooids	20	1.7–4.9 (L) 1.4 (L) 2.5 (L) 3.4 (L)	Cultured phytoplankton Cultured phytoplankton Cultured phytoplankton Cultured phytoplankton	0.2–0.7 mm <sup>3</sup> 0.2–0.7 mm <sup>3</sup> 0.2–0.7 mm <sup>3</sup> 0.2–0.7 mm <sup>3</sup>	2.5	0.014–0.335 0.012 0.094 0.294	3–30 ml µg C <sup>-1</sup> d <sup>-1</sup> 8 ml µg C <sup>-1</sup> d <sup>-1</sup> 17 ml µg C <sup>-1</sup> d <sup>-1</sup> 28 ml µg C <sup>-1</sup> d <sup>-1</sup>	132% body C d <sup>-1</sup>	Deibel (1982b)
	12–14	10–20 (L)	Radiolabeled phytoplankton and bacteria	460–1156 µg C	0.275, 0.5	0.225			Crocker et al. (1991)

(Continued)

**Table 6** (Continued)

Predator	Temperature (°C)	Predator size (mm)	Prey	Prey abundance ( $l^{-1}$ )	Container size (l)	Clearance rate ( $l \text{ ind.}^{-1} d^{-1}$ )	Specific clearance rate	Ingestion rate ('ration')	Reference
phorozoids		2 (L)	Radiolabeled phytoplankton and bacteria			0.0024			
gonozoids		10–20 (L)				0.104			
trophozoids	29	2 (L)				0.0096			
phorozoids		1.3–2.9 (L)	2.5 µm microspheres	0.07–0.18	0.5, 1	0.06			Tebeau and Madin (1994)
gonozoids		1.1–2.2 (L)	2.5 µm microspheres	0.07–0.18	0.5, 1	0.065			
		5–10 (L)	2.5 µm microspheres	0.07–0.18	0.5, 1	0.139			
	20	5 µg C ind. $^{-1}$	Cultured phytoplankton	20–390 µg C	2	<0.120	<24 ml µg C $^{-1} d^{-1}$	60–156% body C d $^{-1}$	Gibson and Paffenhofer (2000)
		15 µg C ind. $^{-1}$	Cultured phytoplankton	20–390 µg C		0.040–0.360	3–24 ml µg C $^{-1} d^{-1}$	52–173% body C d $^{-1}$	
		35 µg C ind. $^{-1}$	Cultured phytoplankton	20–390 µg C		0.1–0.58	3–17 ml µg C $^{-1} d^{-1}$	30–198% body C d $^{-1}$	
	16.5	5 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C	2	~0.1	20 ml µg C $^{-1} d^{-1}$	92% body C d $^{-1}$	
		15 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C		~0.2	13 ml µg C $^{-1} d^{-1}$	59% body C d $^{-1}$	
		35 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C		~0.27	8 ml µg C $^{-1} d^{-1}$	43% body C d $^{-1}$	
	26.5	5 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C	2	~0.10	20 ml µg C $^{-1} d^{-1}$	~100% body C d $^{-1}$	
		15 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C		~0.50	33 ml µg C $^{-1} d^{-1}$	147% body C d $^{-1}$	
		35 µg C ind. $^{-1}$	Cultured phytoplankton	60 µg C		~1.4	40 ml µg C $^{-1} d^{-1}$	179% body C d $^{-1}$	

<sup>a</sup>Freshwater.<sup>b</sup>CEPEX incubations.<sup>c</sup>Calculated.

All values represent means and/or range unless specified otherwise; M, maximum; Min., minimum; Med., median; DW, dry weight; WW, wet weight; AFDW, ash-free dry weight; C, carbon; POC, particulate organic carbon; VO, visual observation; GC, gut content analysis; ind., individual; TL, total length; OA, oral–aboral length, without lobes; D, diameter; CD, central disc diameter; LB, length of body; L, length; H, height; N, nauplii; Co, copepodites; A, adults.

on laboratory measurements using algal monocultures and small volumes are highly variable and likely to be underestimates of actual  $F$  in the field (Deibel, 1982b).

An alternative approach is to enumerate the gut contents from field-collected predators, identify and enumerate the prey available to the predators, and experimentally determine the digestion time for relevant prey types and quantities. For grazers, usually gut pigment is measured as the gut contents (Madin and Cetta, 1984), and ambient pigment for the prey concentration. The strength of this approach is that prior to collection, the predator has not been confined, but has been in a natural feeding environment with realistic prey types and concentrations. The approach can be time consuming and tedious, however, requiring large sample sizes from representative times and sites. There also may be artifacts associated with confining predators to determine the digestion time. Furthermore, the results are limited to the time and place of the collection, unless ingestion rates are combined with ambient prey stocks to calculate  $F$  and are then compared with laboratory-derived rates and applied to other environments. Another important aspect of quantifying feeding rates using the gut content approach is the measurement of digestion times that are relevant to the prey type, number ingested, and ambient temperature (Martinussen and Båmstedt, 1999; Martinussen and Båmstedt, 2001; for *C. capillata*, *A. aurita*, and *Bolinopsis infundibulum*).

Although a few studies of gelatinous zooplankton have used both approaches (Sullivan and Reeve (1982) for the ctenophore *Pleurobrachia*; Purcell and Kremer (1983) for the siphonophore *Sphaeronectes*; Kremer et al. (1986) for the ctenophore *Bolinopsis*; Daan (1989) for the hydromedusae *Clyta* (=*Phialidium*); Purcell and Nemazie (1992) for the hydromedusa *Nemopsis*; and Kremer (2005) for the scyphomedusa *Linuche*), a third, hybrid approach has been suggested which estimates ingestion by combining *in situ* gut contents with laboratory measurements of clearance and egestion (Chandy and Greene, 1995). A clear advantage of this approach is that it is not based solely on laboratory measurements of feeding rates in containers. It also sidesteps the uncertainties of measuring the prey concentration in the field as the approach assumes that the predators are in steady state with their prey field and egestion rates are constant over the range of *in situ* prey concentrations. Preliminary results for the tentaculate ctenophore *Pleurobrachia bachei* were encouraging (Chandy and Greene, 1995); however, this approach has not been widely adopted.

Experimental studies have found that generally both ctenophores and medusae do not satiate when exposed to ecologically reasonable or even high concentrations of prey. Unlike copepods, that exhibit a plateau in their ingestion rate at high food concentrations, several experimental studies with gelatinous predators have documented a direct relationship between ingestion rate and prey concentration (Clifford and Cargo, 1978; Reeve et al., 1978; Kremer, 1979; Daan, 1986; Kremer, 2005; Møller and Riisgård, 2007b). Clearance rate, measured as the equivalent volume removed completely of prey, remains constant over a wide range of prey concentrations. Ctenophores have been observed to continue to feed (destroy prey) even as their assimilation efficiency decreases and prey are not completely digested (Reeve et al., 1989). It should be noted that not all studies have measured constant clearance rates for all experimental prey concentrations. At high

prey levels, the ingestion rate for two genera of ctenophores, *Pleurobrachia* spp. and *Bolinopsis* spp., has been measured to drop off even though ingestion does not reach a clear plateau (Reeve et al., 1978; Kremer et al., 1986; Kasuya et al., 1994; Båmstedt, 1998).

In contrast to these findings for ctenophores and medusae, the clearance rate of appendicularians has been measured to drop appreciably with increased food concentration (Tiselius et al., 2003), indicating that these animals satiate. Gonozooids of the doliolid *D. gegenbauri* were also measured to decrease their clearance rate in higher phytoplankton concentrations (Gibson and Paffenhöfer, 2000). Salps (i.e., *Thalia* spp.) have not been studied enough to determine if they too satiate at high food concentrations. Given their mode of feeding, which utilizes a mucous net to capture prey, one would hypothesize that they too would follow the same pattern as appendicularians and doliodids.

Although all gelatinous animals demonstrate higher ingestion and clearance rates per individual with increased size, the specific clearance rate per unit weight has been measured to decline with increased size for both ctenophores and medusae (Kremer, 1979; Kremer and Reeve, 1989; Finenko and Romanova, 2000; Finenko et al., 2003; Kremer, 2005). This pattern is what would be expected from conventional scaling properties. In contrast to this, appendicularians, doliodids, and the small salp, *T. democratica*, have been measured to keep an approximately constant or even increased specific clearance rate as they grow (Deibel, 1982b; Mullin, 1983; Gibson and Paffenhöfer, 2000).

Several studies have focused on the effect of different prey types on ingestion rates for gelatinous zooplankton. For ctenophores, ingestion rates generally increase with the size and activity level of the prey (Greene et al., 1986; Larson, 1987; Chandy and Greene, 1995) until the prey are too large and strong to be ingested efficiently (Greene et al., 1986). By contrast, clearance rates for medusae were higher on less active prey, perhaps as a result of their entrainment mode of feeding (Olesen et al., 1996; Jankowski et al., 2005; Møller and Riisgård, 2007b). For filter-feeding pelagic tunicates, the issue is more the size spectrum of the prey rather than swimming behavior. If particles are too small, they are less efficiently retained in the feeding net of salps (Harbison and McAlister, 1979; Kremer and Madin, 1992). Likewise, appendicularians have lower clearance rates on bacteria than on larger eukaryotes (Scheinberg et al., 2005).

There have been surprisingly few studies of the effect of temperature on feeding rates of gelatinous zooplankton. It is difficult to tease out the effect of temperature from the presentation in Table 6, given other variables such as predator size, type of prey, and prey concentration. There are preliminary findings for the ctenophore *M. leidyi* (Kremer, 1979) that feeding rates are increased at warmer temperatures. A more rigorous study of the effect of temperature (Gibson and Paffenhöfer, 2000) showed that higher temperature increased the clearance, ingestion, and growth rates of doliodids, and was much more pronounced in the larger doliodids (35 µg C) than the smaller ones (5 µg C). Diel patterns in feeding and ingestion have also received little attention. The few studies that have measured day and night clearance rates report no significant diel patterns in feeding (Fancett and Jenkins, 1988; Sullivan et al., 1994; Martinussen and Båmstedt, 1995; Kremer, 2005). However, several studies have reported diel differences in diet composition as a result of changes in available prey (Arkett, 1984; Pitt et al., 2008). Major changes in available prey result from the emergence of nocturnal demersal

zooplankton, including amphipods and cumaceans, into the water column at night. The consumption of these large prey items has also been suggested to significantly contribute to total ingestion (Pitt et al., 2008).

### 6.06.6 Grazing and Predation Impact

If gelatinous zooplankton abundance (Table 4) is combined with measurements of clearance or ingestion rates (Table 6), it is possible to calculate an estimate of the rate of prey removal. Various investigators have made estimates of this kind (Table 7). One is tempted to infer from these estimates that high removal rates implies large impacts of gelatinous predators on prey stocks. Naturally, a removal rate of  $20\% \text{ d}^{-1}$  would have a greater impact on the prey population than a removal rate of  $5\% \text{ d}^{-1}$ . However, these estimates do not take

into account the growth potential of the prey, which can significantly dampen the presumed rate of removal. This consideration is of particular importance when the prey are fast growing, such as the seston ingested by pelagic tunicates ( $\mu_{\text{phytoplankton}} = >0.60 \text{ d}^{-1}$ ; Landry and Calbet, 2004). In this case, a removal rate of a few percent per day is likely to be insignificant. By contrast, if the prey are slower growing ( $\mu_{\text{copepods}} = <0.35 \text{ d}^{-1}$ ; Kiørboe and Sabatini, 1995) or growth rates are reduced because of food limitation or other factors, removal rates of a few percent per day can have severe results on the abundance of prey in relatively short periods of time. The important parameter for the population dynamics of the prey is the difference between the growth rate of the prey and the combined mortality from all sources, not simply predation by gelatinous zooplankton. If gelatinous zooplankton are numerous and dominant, however, they may have a major influence on the decrease in prey abundance.

**Table 7** Predation impact of gelatinous zooplankton in coastal marine systems

Predator	Location	Season	Prey	Field impact ( $\text{d}^{-1}$ )	Reference
<b>Phylum Ctenophora</b>					
Order Cydippida					
<i>Pleurobrachi bachei</i>	CEPEX (Saanich Inlet, BC, CN)	S	Copepods	<4%	Reeve and Walter (1976)
<i>Pleurobrachia pileus</i>	Mejillones, Chile	Sp	Copepods	0.05–4.5%	Pavez et al. (2006)
	Southwestern Nova Scotia	Sp	Mesozooplankton	0.2–28%	Frank (1986)
	North-west Norwegian coast	S	Mesozooplankton	0.4–8.4%	Båmstedt (1998)
<i>Pleurobrachia rhodopis</i>	Mediterranean Sea	S	Copepods	<1%	Buecher and Gasser (1998)
Order Lobata					
<i>Bolinopsis infundibulum</i>	Malangen, Norway	S	Mesozooplankton	0.4–1% (depth integrated) 2–7% (surface)	Falkenhaug (1996)
<i>Bolinopsis mikado</i>	Tokyo Bay, Japan	S, F	Copepods	$M=24\%$	Kasuya et al. (2000)
<i>Mnemiopsis leidyi</i>	Narragansett Bay, RI, USA	S	Copepods	<1–26% (5 year seasonal var.)	Deason (1982)
larvae larvae	Chesapeake Bay, USA	S	<i>Achoa mitchilli</i> eggs	0–36%	Purcell et al. (1994)
	Northeast Black Sea	S	Fish larvae	7–74%	Tsikhon-Lukanina et al. (1994)
	Black Sea	S	Mesozooplankton	7–>50%	Vinogradov et al. (1996)
	Sevastopol Bay, Black Sea	Yr	Mesozooplankton	0–40%	Finenko and Romanova (2000)
	Sevastopol Bay, Black Sea	S	Mesozooplankton	4–16%	Finenko et al. (2003)
	Chesapeake Bay, USA	Sp, S	Copepods	0–208%	Condon and Steinberg (2008)
	Baltic Sea	W	Microplankton	0.5–1.5%	Viitasalo et al. (2008)
	Sevastopol Bay, Black Sea	S	Microzooplankton	$M=4\%$	Finenko et al. (2003)
	Narragansett Bay, RI, USA	S, Sp	Microzooplankton	<1–60%	Sullivan and Gifford (2004)
Order Beroida					
<i>Beroe cucumis</i>	Malangen, Norway	S	<i>Bolinopsis infundibulum</i>	6–50%	Falkenhaug (1996)
<i>Beroe ovata</i>	Northeast Black Sea	S, F	<i>Mnemiopsis leidyi</i>	4–30%	Shiganova et al. (2000)
	Sevastopol Bay, Black Sea	F	<i>Mnemiopsis leidyi</i>	$M=60\%$	Finenko et al. (2003)
<b>Phylum Cnidaria</b>					
Class Hydrozoa					
<i>Aequorea aequorea</i>	Prince William Sound, AK, USA	S	Copepods	$M=0.2\%$	Purcell (2003)
<i>Aglantha digitale</i>	Hardangerfjord, Norway	Sp	Copepods	0.2–1.5%	Pagès et al. (1996)
<i>Craspedacusta sowerbyi</i>	Pine Lake, WI, USA	F	Mesozooplankton	$M=0.6\%$	Dodson and Cooper (1983)
	Lake Kainui, New Zealand	S	Mesozooplankton	$A=0.5\%; M=3.4\%$	Boothroyd et al. (2002)
	Lake Alsdorf, Germany	S	Mesozooplankton	0.9%–2.4%	Jankowski et al. (2005)
Class Scyphozoa					
<i>Aurelia labiata</i>	Prince William Sound, AK, USA	S	Copepods	$M=0.08\%$	Purcell (2003)

(Continued)

**Table 7** (Continued)

Predator	Location	Season	Prey	Field impact ( $d^{-1}$ )	Reference
<i>Aurelia aurita</i>	Kiel Bight, Baltic Sea	S	Meso and Microzooplankton	8–34%	Schneider (1989)
	Raunefjorden, Norway	S	Mesozooplankton	$A=23\%$	Martinussen and Båmstedt (1995)
	Inland Sea of Japan	S	Meso and Microzooplankton	$A=26\%, M=98\%$	Uye and Shimauchi (2005)
<i>Chrysaora quinquecirrha</i>	Tapong Bay, Taiwan	W, Sp	Mesozooplankton	$A=27\%$	Lo and Chen (2008)
	Pamlico River, NC, USA	Sp, S	<i>Mnemiopsis leidyi</i>	$M=51\%$	Miller (1974)
	Chesapeake Bay, USA	S, F	Copepods	1.1–2.8% (main stem) 2.0–94% (tributary)	Purcell (1992)
	Chesapeake Bay, USA	S	<i>Achoa mitchilli</i> eggs	8–20%	Purcell et al. (1994)
			<i>Achoa mitchilli</i> larvae	10–54%	
	Chesapeake Bay, USA	F	<i>Mnemiopsis leidyi</i>	0–60% (main stem) 0.16–99% (tributary)	Purcell and Cowan (1995)
	Chesapeake Bay, USA	Sp, S	<i>Mnemiopsis leidyi</i>	<1–242%	Condon and Steinberg (2008)
			Copepods	<1–26%	
<i>Chrysaora fuscescens</i>	Northern California Current	S, F	Euphasid eggs	33–60%	Suchman et al. (2008)
		S, F	Other zooplankton	<1–12%	
<i>Cyanea capillata</i>	Port Phillip Bay, Australia	W	Copepods	0.6–1.6%	Fancett and Jenkins (1988)
		W	Fish eggs and larvae	$M=2.4\%$	
	Raunefjorden, Norway	S	Mesozooplankton	$M=1.1\%$	Martinussen and Båmstedt (1995)
	Prince William Sound, AK, USA	S	Copepods	$M=0.11\%$	Purcell (2003)
<i>Nemopilema nomurai</i>	Tsushima Island, Japan	S	Mesozooplankton	$M=24\%$	Uye (2008)
Phylum Chordata					
Class Appendicularia					
<i>Oikopleura dioica</i>	CEPEX (Saanich Inlet, BC, CN)	S	Bacterioplankton	$M=5\%$	King et al. (1980)
	Gulf of California	S	Particulate organic carbon	1–38%	Alldredge (1981)
<i>Oikopleura longicauda</i>	Skagerrak	S, F	Natural seston	$A=7\%$	Maar et al. (2004)
<i>Oikopleura fusiformis</i>	Kaneohe Bay, HI, USA	W, Sp	Bacterioplankton	>60%	Scheinberg et al. (2005)
<i>Oikopleura</i> spp., <i>Fritillaria</i> spp.	Kaneohe Bay, HI, USA	W, Sp	Bacterioplankton	>50%	
<i>Oikopleura vanhoeffeni</i>	Coastal England; Cantabrian Sea, Spain	Sp, F	Natural seston	<1–10%	Lopez-Urrutia et al. (2003)
	Logy Bay, Newfoundland	Sp, S	Particulate organic carbon	<1–13%	Deibel (1988)
Class Thaliacea					
<i>Dolioletta gegenbauri</i>	Coastal Georgia, USA	Sp	Natural seston	<1–120%	Deibel (1985b)
	Seto Inland Sea, Japan	S	Natural plankton	$A=14\%; M=63\%$	Nakamura (1998)
	San Miguel Island, CA, USA	Sp	Bacteria and diatoms	$M=10\%$	Crocker et al. (1991)

Sp, spring; S, summer; F, Fall; W, winter; Yr, year; A, average; M, maximum.

Although clearance rates of gelatinous zooplankton can be extremely high (Table 6), low abundance often results in little to no observable predation impact (e.g., *C. capillata*: Martinussen and Båmstedt (1995); *B. infundibulum*: Falkenhaug (1996); *P. rhodopis*: Buecher and Gasser (1998)). Gelatinous predators in coastal marine environments are regularly reported to remove less than 10% of their prey standing stocks per day (Table 7). Although these estimates are low when integrated over the entire water column, higher impacts have been calculated in surface waters where gelatinous zooplankton abundance is often highest (Falkenhaug, 1996; Båmstedt, 1998). Additionally, even small daily impact,  $1–10\% d^{-1}$ , can act to control prey composition through selective feeding (Pavez et al., 2006). For slower-growing prey, such as fish eggs and larvae, predation can add up over the duration of the planktonic stage to significantly impact prey abundance (Fancett and Jenkins, 1988). Small impacts from

a single species, when combined with other consumers, may also add up to strong predation pressure on prey populations (Fancett and Jenkins, 1988; Pagès et al., 1996).

Significant impact on mesozooplankton, specifically copepods, has been demonstrated in some locations where gelatinous predators reach high densities (Table 7). Gelatinous zooplankton abundance is often inversely correlated with prey abundance in locations where predation impact is estimated to exceed 20%, including Narragansett Bay, USA (*M. leidyi*: Deason and Smayda (1982)), Browns Bank, Nova Scotia (*P. pileus*: Frank (1986)), Kiel Bight, Germany (*A. aurita*: Behrends and Schneider (1995)), Chesapeake Bay, USA (*M. leidyi*: Condon and Steinberg (2008)), and the northern California Current, USA (*C. fuscescens*: Suchman et al. (2008)) (Figure 3). Additionally, significant predation on crustacean zooplankton reduces grazing pressure and can indirectly increase

phytoplankton populations (Greve, 1981; Deason and Smayda, 1982; Jankowski et al., 2005; Møller and Riisgård, 2007c). The impact of gelatinous zooplankton on prey populations has received a lot of attention in the Black Sea after the introduction of the ctenophore *M. leidyi* in the early 1980s (reviewed by Purcell et al. (2001)) (Figure 3). Due to the low abundance of fish (as the result of overfishing) and gelatinous predators/competitors, *M. leidyi* has thrived in its new habitat and has expanded to several other locations in the Mediterranean basin. Sharp decreases in mesozooplankton following the introduction have been attributed to direct predation by *M. leidyi*. The reported decreases in mesozooplankton abundance and species composition have also contributed to a reduction in diet compositions and daily rations of planktivorous fish, reducing growth and production of these potential competitors (Shiganova and Bulgakova, 2000).

Although many authors have claimed the importance of gelatinous predators as consumers of fish eggs and larvae, there are relatively few studies that clearly demonstrate the importance of gelatinous zooplankton to fish stocks. Predation by the ctenophore *M. leidyi* has been implicated in the decline of ichthyoplankton in the Black Sea following its introduction (reviewed by Purcell et al. (2001)) (Figure 3). Estimates of the predation impact of *M. leidyi* in the Black Sea exceed 70% per day during periods of peak abundance (Tsikhon-Lukanina et al., 1994). High predatory impacts of *M. leidyi* on ichthyoplankton have also been reported in its native habitat. In Chesapeake Bay, USA, *M. leidyi* and *C. quinquecirrha* were responsible for 21% of the daily *in situ* mortality of bay anchovy (*Anchoa mitchilli*) eggs and the medusae alone were responsible for 41% of the daily *in situ* larval mortality (Purcell et al., 1994) (Figure 3). High abundance of the scyphomedusa *A. aurita* has also been correlated to declines in the abundance/survival of larval herring (*Clupea harengus*) in Kiel Bight, Germany (Möller, 1984) and the North Sea (Lynam et al., 2005a) (Figure 3).

Secondary consumers, including the ctenophore *Beroe* spp. and the scyphomedusa *C. quinquecirrha*, also exert significant predation pressure (Table 7). Estimated predation impacts of these species are frequently greater than 50% per day. This is significantly higher than the growth rates of their gelatinous prey, with the exception of some early life history stages (Table 3). High predation pressure by *Beroe* spp. has been linked to declines of its ctenophore prey in several locations, including Narragansett Bay, USA, (*M. leidyi*: Kremer and Nixon (1976)), Chesapeake Bay, USA (*M. leidyi*: Burrell and Van Engel (1976)), Helgoland Bight, Germany (*P. pileus*: Greve (1981)), Malangen fjord, Norway (*B. infundibulum*: Falkenhaug (1996)), and the Black Sea (*M. leidyi*: Shiganova et al. (2001b) and Finenko et al. (2003)) (Figure 3). A subsequent rebound in mesozooplankton abundance following the depletion of ctenophore prey has been observed in most of these locations. Predation by *B. ovata* on *M. leidyi* has been of particular importance in the recovery of the Black Sea ecosystem (Shiganova et al., 2001b; Finenko et al., 2003; Mutlu, 2009). Following the introduction of *B. ovata* into the Black Sea in 1997, populations of *M. leidyi* decreased. The decline in *M. leidyi* released mesozooplankton from feeding pressure and resulted in increases in zooplankton abundance. Planktivorous fish, which compete with *M. leidyi* for zooplankton prey, have also increased. In its native habitats, predation by *C. quinquecirrha* has more commonly been observed to control populations of the ctenophore *M. leidyi*

(Miller, 1974; Feigenbaum and Kelly, 1984; Purcell and Cowan, 1995; Condon and Steinberg, 2008). In Chesapeake Bay, USA, peaks in *C. quinquecirrha* abundance coincide with summer declines in *M. leidyi* (Feigenbaum and Kelly, 1984; Condon and Steinberg, 2008), specifically in tributaries where *C. quinquecirrha* abundance is highest (Purcell and Cowan, 1995) (Figure 3). Increases in herbivorous zooplankton have also been observed following declines in ctenophore abundance that resulted from predation by *C. quinquecirrha* (Feigenbaum and Kelly, 1984; Purcell et al., 1994; Purcell and Decker, 2005).

The estimated feeding rates of gelatinous grazers (e.g., appendicularians, salps, and doliolids), although higher than those of gelatinous predators, have rarely been shown to influence prey populations. Despite their low impacts, gelatinous grazers contribute significantly to the total mesozooplankton grazing in many locations (Deibel, 1988; Nakamura, 1998; Lopez-Urrutia et al., 2003). Even when grazing rates exceed 20% per day, the growth rates of their prey are significantly higher than the mesozooplankton prey of gelatinous predators. As a result, only the highest abundances have been observed to impart significant impacts on prey populations (Table 4). Extreme abundances of pelagic grazers have been inversely correlated to pico/nanoplankton abundance (*D. gegenbauri*: Deibel (1985b); *Paffenhofer* et al. (1995), and Nakamura (1998); *O. longicauda*: Nakamura (1998)). High abundances of doliolids have also been inversely correlated to copepod abundance (Deibel, 1985b; Paffenhofer et al., 1995). This may result from competition for prey or direct consumption of copepod eggs and nauplii by the doliolids. In addition to the direct effects of grazing, changes in phytoplankton composition resulting from higher consumption of small particles selectively favor larger cells (Deibel, 1985b). Consequently, high abundances of the appendicularian *O. dioica* have been positively correlated to the biomass of large phytoplankton in both field and laboratory observations (Fernandez and Acuña, 2003).

Estimates of predation impact vary greatly among taxa and locations as the result of differences in clearance rates, abundance, and spatial/temporal overlap with prey (Table 7). Gelatinous predators in coastal marine environments generally remove between 1% and 10% of their prey standing stock per day; however, impacts greater than 50% per day are often associated with peaks in abundance (Table 7). To better understand the potential of gelatinous zooplankton to control prey populations, future studies should compare estimates of predation impact with *in situ* growth rates of their prey. Additionally, attempts should be made to quantify feeding impacts over consecutive years to better correlate predation impact with prey abundance, and to consider additional sources of mortality such as other potential predators.

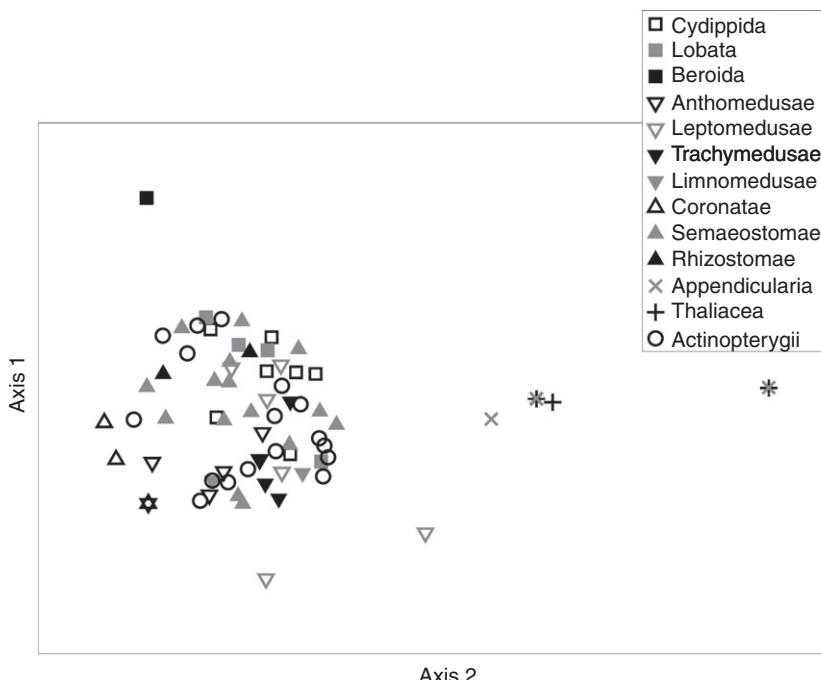
### **6.06.7 Competitors**

In addition to direct impacts on pelagic food webs that result from consumption, gelatinous zooplankton are commonly implicated as important competitors in coastal marine ecosystems (e.g., Vinogradov et al., 1996; Shiganova and Bulgakova, 2000; Lynam et al., 2005b; Oguz et al., 2008). Diet similarity between gelatinous zooplankton taxa (Table 5) and with planktivorous fish, class Actinopterygii (Table 8) are presented

**Table 8** Diet composition of planktivorous fish from coastal marine systems

Species	Location	Season	Copepods	Copepod nauplii	Amphipods	Cladocerans	Cumaceans	Barnacle larvae	Euphausiids	Isopods	Ostracods	Myiids	Crab larvae	Insect larvae	Polychaete larvae	Veiger larvae	Chaetognaths	Ascidian larvae	Scyphomedusae	Hydromedusae	Siphonophores	Ctenophores	Appendicularians	Invertebrate eggs	Fish larvae	Fish eggs	Rotifers	Microzooplankton	Microphytoplankton	Nanoplankton	Picoplankton	Method n	Reference
Class Actinopterygii																																	
Order Clupeiformes																																	
<i>Clupea pallasi</i> (Pacific herring)	San Francisco Estuary, USA	Sp	x	x										x																GC	1270	Bollens and Sanders (2004)	
<i>Sardinops melanostictus</i> (J. sardine) L	Kuroshio Current, Japan	Sp	x	x																											GC	947	Nakata (1988)
<i>Sardinops sagax</i> (Pacific sardine)	Pacific Northwest, USA	S	x	x	x			x	x									x	x	x	x									GC	184	Emmett et al. (2005)	
<i>Sardinops sagax</i> (Pacific sardine) L	California Current, USA	Sp, S	x	x														x	x	x	x									GC	10408	Arthur (1976)	
<i>Engraulis anchoita</i> (A. anchovy)	Argentine Sea, Argentina	Sp	x	x	x			x			x		x	x			x	x	x	x									GC	532	Capitanio et al. (2005)		
<i>Engraulis encrasicolus</i> (E. anchovy) L	Adriatic Sea, Italy	S	x	x	x									x			x	x	x	x									GC	999	Conway et al. (1998)		
<i>Engraulis mordax</i> (N. anchovy) L	California Current, USA	Sp, S	x	x										x			x	x	x	x									GC	2350	Arthur (1976)		
Order Osmeriformes, smelt																																	
<i>Hypomesus transpacificus</i> (Delta) L	San Francisco Estuary, USA	Sp	x	x	x									x						x									GC	1474	Norbriga (2002)		
<i>Hypomesus transpacificus</i> (Delta)	San Francisco Estuary, USA	Yr	x	x	x									x	x														GC	679	Moyle et al. (1992)		
Order Perciformes																																	
<i>Scomber scobrus</i> (A. mackerel) L	Celtic Sea, Ireland	S	x	x														x	x										GC	1177	Hillgruber and Kloppmann (2001)		
<i>Trachurus mediterraneus</i> (H. mackerel)	Black Sea, Bulgaria	Sp, S	x	x	x			x		x	x	x	x				x												GC	1042	Yankova et al. (2008)		
<i>Trachurus symmetricus</i> (J. mackerel) L	California Current, USA	Sp, S	x	x	x		x	x									x		x										GC	750	Arthur (1976)		
<i>Morone saxatilis</i> (Striped bass) L	Hudson River, USA	S	x	x	x														x										GC	480	Limburg et al. (1997)		
<i>Morone saxatilis</i> (Striped bass) L	San Francisco Estuary, USA	F	x	x	x				x	x				x	x														GC	320	Stevens (1966)		
Order Pleuronectiformes, flatfish																																	
<i>Platichthys bicoloratus</i> (S. flounder) L	Mutsu Bay, Japan	Sp	x	x	x									x	x			x	x			x	x				GC	277	Takatsu et al. (2007)				
Order Salmoniformes, salmon																																	
<i>Oncorhynchus gorbuscha</i> (Pink) J	Hecate Strait, BC, Canada	S	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	GC	1982	Healey (1991)					
<i>Oncorhynchus keta</i> (Chum) J	Hecate Strait, BC, Canada	S	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	GC	826	Healey (1991)					
<i>Oncorhynchus nerka</i> (Sockeye) J	Hecate Strait, BC, Canada	S	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	GC	208	Healey (1991)					

Sp, spring; S, summer; F, fall; W, winter; Yr, Year; x, present; n, sample size; GC, gut contents; L, larvae; J, juvenile.



**Figure 4** Similarity of diet composition between gelatinous zooplankton and planktivorous fish. The graph was constructed with nonmetric multidimensional scaling (MDS) from a similarity matrix of prey presence/absence data based on the Sørensen similarity measure (Primer v6). Stress = 0.15. The axes of MDS plots do not have units.

in Figure 4 (nonmetric multidimensional scaling, MDS) (Primer v6). MDS plots are graphic representations of the degree of similarity between samples. The more similar samples are to one another, the closer they appear in the plot. Diet overlap was also examined with a one-way analysis of similarities (ANOSIM) (Primer v6). ANOSIM is a nonparametric multivariate permutation procedure analogous to a multivariate analysis of variance (Clarke and Green, 1988). It tests for differences between groups of samples using a nonparametric permutation procedure applied to a similarity matrix, based in this case on the Sørensen similarity measure.

Significant dietary overlap was observed between ctenophores, hydromedusae, scyphomedusae, and planktivorous fish (1-way ANOSIM,  $r=0.31$ ,  $p>0.05$ ). Not surprisingly, the diet of pelagic tunicates differed significantly from all other groups (1-way ANOSIM,  $r=0.31$ ,  $p<0.01$ ). Through the consumption of phytoplankton, this group competes instead with other primary consumers, such as copepods. Finer-scale differences between taxonomic groups could not be examined because of small sample sizes. However, from Table 5 and Figure 4, it is apparent that the diet of beroid ctenophores differs significantly from most other gelatinous zooplankton as they consume almost exclusively other gelatinous zooplankton. Additionally, the hydromedusae *Obelia* spp. differs from most other gelatinous zooplankton because of its limited diet (copepod nauplii and microzooplankton). The diet limitations of this species are due, in part, to its extremely small size (<1 mm).

Examination of the diet composition of both gelatinous zooplankton (Table 5) and planktivorous fish (Table 8) suggests competition both among gelatinous zooplankton and between gelatinous zooplankton and fish. However, diet

composition depends on both prey availability, which can vary over short space- and timescales, and prey vulnerability, which is influenced by predator size, feeding mechanisms, and behavior. As a result, the potential for competition is extremely difficult to assess without a simultaneous examination of predators in the same locale. Only a handful of studies regarding gelatinous zooplankton have met this criterion (Purcell, 1991a; Purcell and Sturdevant, 2001; Costello and Colin, 2002).

As discussed above (Section 6.06.4, Prey), not all components of the planktonic community are used equally by predatory gelatinous zooplankton, even within specific taxonomic groups. Niche partitioning/separation is most obvious between the two major feeding guilds, ambush and cruising predators, resulting from differences in the mechanical traits that govern their predation processes. Ambush foragers (e.g., tentaculate ctenophores and prolate hydromedusae) feed primarily on fast-swimming crustacean zooplankton, while cruising predators (e.g., lobate ctenophores, oblate hydromedusae, and most coastal scyphomedusae) feed more effectively on slow-moving soft-bodied prey (Costello and Coverdale, 1998; Costello and Colin, 2002). However, among these groups, particularly cruising predators, dietary overlap can be significant resulting in direct competition for food resources (Costello and Colin, 2002). Intraguild predation is also frequently observed in larger members of this group (Purcell, 1991a, 1991b; Costello and Colin, 2002). For example, *Aequorea victoria* commonly consumes other pelagic hydrozoans that compete with it for the same mesozooplankton prey (Purcell, 1991a). By eating species that use similar, often limiting, resources, intraguild predators reduce the abundance of competitors and at the same time gain direct nutritional benefits (Polis et al., 1989).

Purcell and Sturdevant (2001) examined the diet overlap of co-occurring jellyfish and juvenile forage fish species in Prince William Sound, AK, USA (Figure 3). Higher dietary overlap was observed between gelatinous zooplankton and fish (50%) than among these predator groups (~40%). They also grouped these predators by their preferred prey (crustacean zooplankton and appendicularians). Within these groupings, dietary overlap was high (>60%), regardless of predator type. In addition to significant dietary overlap, they confirmed spatial and temporal overlap and concluded that the potential for competition for prey between planktivorous fish and gelatinous zooplankton existed within their study site. Additional such studies, including spatial-temporal overlap as well as dietary overlap, are clearly needed to understand the magnitude of the importance of gelatinous zooplankton as competitors with planktivorous fish in coastal marine systems.

Differences in feeding mechanisms may act to reduce diet overlap between gelatinous zooplankton and fish in some habitats. As visual predators, planktivorous fish feed more efficiently under high light availability and at low prey density (Sørnes and Aksnes, 2004) and prey selection is strongly influenced by size (Hunter, 1981). Conversely, predation by gelatinous zooplankton (=tactile predators) is not affected by light (Eiane et al., 1999; Sørnes and Aksnes, 2004), feeding rates often increase in proportion to prey concentration (Reeve and Walter, 1978; Kremer, 1979), and prey selection is more strongly influenced by behavior (Gerritsen and Strickler, 1977). As a result of these differences, the degree of competition among these predators may be strongly mitigated by the characteristics of the particular environment.

### 6.06.8 Predators

Gelatinous zooplankton have historically been considered poor-quality prey and, therefore, trophic dead ends, but increasing evidence suggests that this is not the case. Although they have a low carbon content, gelatinous zooplankton have been documented as important prey items for a wide variety of organisms including other gelatinous zooplankton, crustaceans, squid, fish, turtles, birds, and marine mammals (Ates, 1988; Purcell, 1997; Arai, 2005). The many predators of gelatinous zooplankton take advantage of different aspects of the biology of their gelatinous prey. Birds, fish, and marine mammals utilize gelatinous zooplankton as a seasonally abundant prey source (Harrison, 1984; Oviatt and Kremer, 1977; Blanco et al., 2006). Slow-moving predators, such as sea turtles and ocean sunfish, take advantage of the slow-swimming speeds and reduced escape capabilities of gelatinous zooplankton (Thys, 1994; Bjorndal, 1997). As a result, the diet of these predators often consists solely of gelatinous zooplankton and their migration cycles revolve around the distribution and population dynamics of their prey (James et al., 2005; Houghton et al., 2006; Hays et al., 2009).

Despite the quantity and diversity of predators, their quantitative impact on populations of gelatinous zooplankton remains unknown and the actual contribution of gelatinous zooplankton to the diets of their predators is poorly understood. The high water content and ephemeral nature of gelatinous zooplankton have resulted in a paucity of quantitative data documenting their consumption. Gut content

analysis is the most commonly used method to quantify the composition of the diet of large consumers. The high water content and soft body tissue of gelatinous zooplankton limit this kind of analysis because they are often digested too rapidly to be observed and/or identified in consumer guts. Thus, historically there has been a lack of scientific interest in gelatinous zooplankton as potentially important prey items and a bias toward hard-bodied prey, which are more easily observed and identified in gut contents. To compensate for the rapid digestion of gelatinous prey, some researchers have used the presence of nematocysts to confirm consumption (Den Hartog, 1980; Van Nierop and Den Hartog, 1984). By identifying the types of nematocysts present in consumer guts, it is possible to determine the taxonomic groups consumed, sometimes even to the species level (Russell, 1938, 1939, 1940; Östman, 2000). The presence of both crustacean and noncrustacean parasites of gelatinous zooplankton in the guts of consumers has also been used to infer consumption (Oviatt and Kremer, 1977; Harrison, 1984). Some parasites, such as hyperiid amphipods, can serve as a reliable indicator of ingestion because they are parasitic on gelatinous zooplankton rather than free living (Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980).

To avoid the problems associated with rapid digestion, several other techniques have also been used to investigate predation on gelatinous zooplankton. Direct observations of feeding events are commonly used to confirm feeding by birds and sea turtles (Heithaus et al., 2002; Suazo, 2008). These observations are limited to surface-feeding events, however, and provide limited quantitative data. To capture feeding underwater, consumer-mounted video cameras have been employed to supplement direct observations, but costs and technological limitations restrict the amount of data collected and processed (Salmon et al., 2004). Although incubation experiments are commonly used to quantify feeding by gelatinous predators on other gelatinous species, these experiments are limited by the necessary large container size (Larson, 1986c; Purcell and Cowan, 1995). As most adult consumers are large, incubation experiments have predominantly been used to study early life history stages (Constantino and Salmon, 2003; Båmstedt et al., 1997) or small predators (Oviatt and Kremer, 1977; Runge et al., 1987). Chemical signatures provide an additional approach for investigating feeding. Fatty acid composition (Hooper et al., 1973; Holland et al., 1990) and stable isotope analysis (Wallace et al., 2009) have confirmed the consumption of gelatinous zooplankton by fish and sea turtles. Although these techniques provide information about the importance of gelatinous zooplankton to the diets of their consumers, they are not useful for quantifying predation rates.

Beyond the technical restrictions mentioned above, the ephemeral nature of gelatinous zooplankton populations and their patchiness limit our ability to accurately estimate consumption. Gelatinous plankton populations are characterized by seasonal blooms that result in populations that are highly localized in both time and space. Consequently, gelatinous zooplankton often contribute only a fraction of the diet of their predators, with peaks in consumption associated with their maximum seasonal abundance. As many of the consumers of gelatinous zooplankton, including birds, turtles, and marine mammals, are endangered or threatened, the chances of encountering such feeding events, regardless of technique,

are extremely rare. Furthermore, federal regulations make it increasingly difficult to collect samples or observations in the vicinity of these protected species.

Numerous invertebrates have been reported to consume gelatinous zooplankton in coastal marine systems. Besides gelatinous zooplankton discussed above, other invertebrate predators include copepods, shrimp, crabs, nudibranchs, and squid. Most of the information regarding invertebrate predators is based on qualitative observations and very little quantitative data are available about the importance of gelatinous zooplankton in the diets of these consumers. Some copepods from the family Candaciidae appear to specialize in feeding on appendicularians (Ohtsuka and Onbe, 1989; Ohtsuka and Kubo, 1991), and a variety of copepods have been documented to feed on appendicularian eggs and juveniles, although ingestion decreases with increasing appendicularian size (Lopez-Urrutia et al., 2004). Results from a mesocosm study suggest that common calanoid copepods may control appendicularian population dynamics (Sommer et al., 2003). Although copepods have slower somatic and population growth rates than appendicularians, they can terminate a bloom of appendicularians through selective predation on eggs and juveniles (Lopez-Urrutia et al., 2004). Copepods have also been reported to colonize the internal surfaces and feeding filters of discarded appendicularian houses, presumably gleaning food from their surfaces (Alldredge, 1976a; Ohtsuka et al., 1993). Although this is not predation *per se*, appendicularians are still the source of the food for these copepods. In addition to copepods, grass shrimp (*Palaemonetes pugio*) have been observed to consume adult and larval ctenophores in laboratory incubations (Sullivan, unpublished) and the shore crab (=European green crab), *Carcinus maenas*, frequently feeds on stranded medusae, *A. aurita* (Rasmussen, 1973).

In addition to predation on the pelagic stages, invertebrate consumption of the benthic polyp stages of some cnidarians may also be important. Although very limited data are available on the predation of polyps, the few available studies suggest a potential to influence gelatinous zooplankton populations. For example, predation by the nudibranch, *Coryphella verrucosa*, on polyps has been implicated in the regulation of population development for *A. aurita* in Gullmar Fjord, Western Sweden (Hernroth and Grondahl, 1985) and *C. quinquecirrha* in Chesapeake Bay, USA (Cargo and Schultz, 1967) (Figure 3). Conversely, the importance of consumption of polyps by nudibranch predators is better understood. It has been suggested that many eolid nudibranchs sequester and maintain nematocysts from their cnidarian prey to provide protection against predators (Edmunds, 2009) and that they can modulate nematocyst incorporation in response to the presence of predators (Frick, 2003). The limpet, *Diado cayenensis*, has also been observed to feed on the polyps of hydromedusae and scyphomedusae, but its impact on gelatinous zooplankton populations has not been examined (Phillips et al., 1969).

Several species of fish also consume gelatinous zooplankton (Ates, 1988; Purcell and Arai, 2001; Arai, 2005). Fish that feed primarily on medusae and ctenophores, including butterfish and ruff, possess protruding lower jaws and enlarged stomachs or intestines (Harbison, 1993). The underslung jaw allows fish to envelop large prey by expanding its reach and creating

powerful suction. Extended digestive tracts increase gut capacity for processing large volumes of watery prey. Although these fish are specialized to feed on gelatinous zooplankton, a wide variety of life history stages, body types, and feeding guilds consume gelatinous zooplankton, including ctenophores, cnidarians, and salps (Table 9). Most of these generalists take advantage of peaks in the abundance of gelatinous zooplankton associated with hydrographic events (Hobson and Chess, 1988) or reproductive cycles (Mianzan et al., 1996; King and Beamish, 2000; Laptikhovsky and Arkhipkin, 2003). This temporally and spatially localized consumption may sustain growth and survival during periods when the abundance of other prey items is low (Mianzan et al., 1996; Mianzan et al., 2001).

Appendicularians have also been shown to be an important part of the diet of many fish species (reviewed in Purcell et al. (2004)), especially early life history stages (Landingham et al., 1998; Sampey et al., 2007; Takatsu et al., 2007) and planktivorous fish (Capitanio et al., 1997, 2005). A small mouth size limits the type of prey consumed by planktivorous fish (Pepin and Penney, 1997; Gill, 2003). As appendicularians are generally small, planktivores are likely predators. For larval fish, copepods often dominate the diet, but many appendicularians have a trunk length approximately the same size as copepods. The presence of the larger house, however, may provide a refuge for appendicularians from small fish larvae. Although appendicularians exhibit extremely fast-swimming speeds while outside of their houses ( $>500 \text{ cm s}^{-1}$ ), inside their houses they move at much slower rates ( $1.4 \text{ cm s}^{-1}$ ) and may be easily preyed upon by planktivorous fish if the fish's mouth is large enough to consume the whole house (Alldredge, 1976b).

Most of the quantitative information regarding the consumption of gelatinous zooplankton is related to fish predators (Table 9). Interest in the diets of fish has been stimulated by their economic importance. Additionally, the consumption of appendicularians and salps is of particular ecological importance because it represents a very short food chain from small particles to fish (Mianzan et al., 1996, 2001; Capitanio et al., 1997, 2005; Takatsu et al., 2007). Diet has been quantified for many fish species and numerous studies have sampled either annually or seasonally. Most results have been reported as percent frequency of occurrence and/or percent diet composition that are both calculated using gut-content analysis (Table 9). Indices of relative importance also confirm the dietary significance of gelatinous zooplankton (Landingham et al., 1998; Sampey et al., 2007). The relatively large sample size and frequency has revealed several patterns about the role of gelatinous zooplankton in fish diets. Observations for different life history stages have shown life-stage-specific consumption (Laptikhovsky and Arkhipkin, 2003). Seasonal sampling confirms peaks in consumption associated with increased abundance of gelatinous zooplankton (King and Beamish, 2000; Laptikhovsky and Arkhipkin, 2003) and multiyear data show consistent consumption between years (Landingham et al., 1998). Large-scale patterns associated with hydrographic events have also been observed. Specifically, decreases in the consumption of gelatinous zooplankton have been reported during upwelling events when they are dispersed by wind-driven offshore currents (Hobson and Chess, 1988; Brodeur and Pearcy, 1992).

**Table 9** Predation of gelatinous zooplankton in coastal marine systems

Predator	Location	Rate/Method	Prey	Reference	
Sea turtles:		% predators (n)			
<i>Chelonia mydas</i> (green)	A J	Shark Bay, AU Florida current	82% (11) VO 3% (33) VO	Cnidaria & Ctenophora Ctenophora	Heithaus et al. (2002) Salmon et al. (2004)
<i>Caretta caretta</i> (loggerhead)	A A J	Gulf of Mexico Mediterranean North Atlantic: Selvagens Is. Azores	11% (82) GC <1% pDW (82) 1% (95) GC 100% (5) GC 80% (5) GC 40% (5) GC	Cnidaria Scyphomedusae Siphonophorae Scyphomedusae Hydromedusae	Plotkin et al. (1993) Casale et al. (2008) Van Nierop and Den Hartog (1984)
<i>Lepidochelys kempi</i> (Kemp's ridley)	A	South Texas	13% (101) GC <1% pDW (101)	Siphonophorae: <i>Physalia physalia</i>	Shaver (1991)
<i>Dermochelys coriacea</i> (leatherback)	J	Florida current	18% (34) VO 6% (34) VO	Scyphomedusae: <i>Aurelia aurita</i> Ctenophora	Salmon et al. (2004)
Seabirds:		% predators (n)			
Order Procellariiformes					
<i>Puffinus griseus</i> (shearwater)	North Pacific	30% (30) GC	Hydrozoa: <i>Vallela lata</i>	Ogi (1984)	
<i>Puffinus</i> spp. (shearwater)	Bering Sea:	25% (28) GC	Scyphozoa:	Harrison (1984)	
<i>Fulmaris glacialis</i> (fulmar)	St. Matthew and Pribilof Is.	42% (136) GC	<i>Chrysaora</i> sp.		
<i>Oceanodroma furcata</i> (petrel)		27% (55) GC	<i>Cyanea</i> sp.		
<i>Diomedea melanophris</i> (albatross)	Chile	27% (7) VO	Scyphozoa	Suazo (2008)	
<i>Diomedea exulans</i> (albatross)	South Georgia	22% (9) R 10% pWW (9)	Scyphozoa	Xavier et al. (2003)	
<i>Thalassarche chrysotoma</i> (albatross)	South Georgia	22% (13) R <1% pWW (13)	Appendicularia	Catry et al. (2004)	
Order Charadriiformes					
<i>Larus hyperboreus</i> (gull)	Bering Sea:	50% (2) GC	Scyphozoa:	Harrison (1984)	
<i>Rissa</i> spp. (kittiwake)	St. Matthew and Pribilof Is.	38% (34) GC	<i>Chrysaora</i> sp.		
<i>Uria</i> spp. (murre)		19% (32) GC	<i>Cyanea</i> sp.		
<i>Aethia cristatella</i> (auklet)		50% (2) GC			
<i>Cyclorrhynchus psitacula</i> (auklet)	Bering Sea	50% (8) GC 54% (52) GC 17% (52) GC	Scyphozoa Ctenophora	Harrison (1990)	
Fish:		% predators (n)			
Class Chondrichthyes					
Family Squalidae					
<i>Squalus acanthias</i> (spiny dogfish)	Argentina Falkland Is.	20% (221) GC W 36% (147) GC W	Ctenophora Ctenophora	Mianzan et al. (1996) Laptikhovsky and Arkhipkin (2003)	
	Oregon/Wash.	50% pWW (23) GC	Cnidaria	Brodeur and Pearcy (1992)	
Class Actinopterygii					
Family Clupidae					
<i>Alosa pseudoharengus</i> (alewife)	Inshore N. of Cape Hatteras	10% pWW (64) GC	Ctenophora	Bowman et al. (2000)	
Family Engraulidae					
<i>Engraulis anchoita</i> (anchovy)	Argentina Argentina	46% (321) GC 29% pNo (532) GC	Appendicularia Appendicularia	Capitanio et al. (1997) Capitanio et al. (2005)	
Family Congridae					
<i>Conger orbignianus</i> (eel)	Argentina	13% (133) GC S	Salpida	Mianzan et al. (1996)	
Family Macrouridae					
<i>Macrourus holotrachys</i> (grenadier)	Argentina	18% (54) GC Sp	Salpida	Mianzan et al. (1996)	
Family Centrolophidae					
<i>Seriola porosa</i> (choicy ruff)	Argentina	47% (133) GC S/Sp	Ctenophora	Mianzan et al. (1996)	

(Continued)

**Table 9** (Continued)

Predator	Location	Rate/Method	Prey	Reference
Family Scorpaenidae				
<i>Helicolenus dactylopterus lahillei</i> (scorpion fish)	Argentina	28% (273) GC S/Sp	Ctenophora	Mianzan et al. (1996)
<i>Sebastes melanops</i> (black rockfish)	Oregon/Wash.	17% (53) GC Sp 13% pWW (20) GC	Hydromedusae Ctenophora	Brodeur and Pearcy (1992)
<i>S. mystinus</i> (blue rockfish)	N. California	22% pVol (51) GC 22% pVol (73) GC 26% pVol (38) GC 35% pVol (85) GC 32% pVol (38) GC	Cnidaria Salpida	Hobson and Chess (1988)
Family Nototheniidae				
<i>Patagonotothen ramsayi</i> (rock cod)	A Argentina	21% (81) GC Sp	Ctenophora	Mianzan et al. (1996)
	A Falkland Is.	51% (81) GC S	Ctenophora	Laptikhovsky and Arkhipkin (2003)
	J and A	19% (159) GC W		
	J and A	31% (122) GC S/Sp	Salpida	
Family Salmonidae (salmon)				
<i>Oncorhynchus kisutch</i> (coho)	A Oregon/Wash.	15% pWW (33) GC	Cnidaria	Brodeur and Pearcy (1992)
<i>O. gorbuscha</i> (pink)	J SE Alaska/NW British Columb	35% (372) GC S	Appendicularia	Landingham et al. (1998)
<i>O. keta</i> (chum)	J British Columb	13% (580) GC	Ctenophora	Healey (1991)
	J British Columb	36% (260) GC	Ctenophora	King and Beamish (2000)
	J SE Alaska/NW British Columb	48% (699) GC S 10% (408) GC S		
		47% (176) GC S	Appendicularia	Landingham et al. (1998)
Family Pleuronectidae (flounder)				
<i>Platichthys bicoloratus</i> (stone)	L Japan	81% pNo (258) GC	Appendicularia	Takatsu et al. (2007)
Family Gadidae				
<i>Pollachius virens</i> (cod)	Scotland	17% (133) GC	Cnidaria	Hall et al. (1990)
Family Sciaenidae				
<i>Micropogonias furnieri</i>	Argentina	11% (350) GC Sp	Ctenophora	Mianzan et al. (1996)
Family Stromateidae				
<i>Peprilus triacanthus</i> (butterfish)	Inshore, N. of Cape Hatteras	9% pWW (327) GC	Cnidaria	Bowman et al. (2000)
<i>Stromateus brasiliensis</i> (b. butterfish)	Argentina	76% (285) GC S/Sp	Ctenophora	Mianzan et al. (1996)
Family Anoplopomatidae				
<i>Anoplopoma fimbria</i> (sablefish)	Oregon/Wash.	14% pWW (35) GC 19% pWW (16) GC 76% pWW (18) GC	Cnidaria Salpida	Brodeur and Pearcy (1992)
Squid:				
<i>Loligo opalescens</i> (market squid)	Oregon/Wash.	22% pWW (17) GC	Cnidaria	Brodeur and Pearcy (1992)

If multiple samples were taken, data were combined. n, number of predators examined; GC, gut contents; VO, visual observations; R, regurgitation; A, adult; J, juvenile; L, larvae; pVol, prey volume; pWW, prey wet weight; pDW, prey dry weight; pNo, prey number; Sp, Spring; S, Summer; W, Winter.

A few studies have examined fish feeding on gelatinous zooplankton using laboratory incubations. These studies demonstrate selective feeding (Runge et al., 1987) and report feeding rates (Oviatt and Kremer, 1977). Feeding rates can be combined with physiological data to examine the dietary importance of gelatinous zooplankton. Oviatt and Kremer (1977) estimated that consumption of the ctenophore *M. leidyi* by butterfish (*Peprilus triacanthus*) well exceeded basal metabolic requirements. Additionally, feeding rates and abundance information can be combined to estimate the impact of fish predators on their gelatinous prey. Oviatt and Kremer (1977)

estimated that butterfish, *P. triacanthus*, could consume up to 5% of the ctenophore population per day, which could potentially result in the seasonal decline in population levels of *M. leidyi* observed in Narragansett Bay, RI, USA, if the ctenophores were growing and reproducing slowly due to food limitation (Figure 3).

Almost all sea turtles have been documented to consume gelatinous zooplankton. The one exception is the hawksbill, which uses its beak-like mouth to feed on corals and sponges (Bjorndal, 1997). Newly hatched green, loggerhead, and ridley sea turtles are pelagic and feed primarily on gelatinous

zooplankton (Table 9). When these turtles leave the pelagic environment as adults to forage in benthic habitats their diet changes from pelagic invertebrates to seagrasses and algae (green), or benthic invertebrates (loggerhead and ridley). Leatherback turtles, on the other hand, spend their entire lives as pelagic feeders consuming primarily gelatinous zooplankton, including scyphomedusae and pelagic tunicates (Holland et al., 1990; Grant and Ferrell, 1993; Bjorndal, 1997). This preference for gelatinous prey has been linked to their migratory cycles (James et al., 2005; Houghton et al., 2006; Hays et al., 2009) and the unintended consumption of plastics, which has been reported to cause gut blockages and, in some cases, death (Mrosovsky et al., 2009).

Data on sea turtle feeding have been constrained by their endangered status, making it difficult to collect observations. As a result, information on feeding has been limited to visual observations and gut-content analysis of beached remains, turtles caught as bycatch, and hatchlings reared in the laboratory. Most of these observations report the frequency of occurrence of gelatinous plankton consumption, and only a few observations include quantitative information regarding the contribution to the diet of sea turtles (Table 9). In both studies, where diet contribution has been quantified, the contributions were less than 1% of the diet by weight; however, these observations were for adult Kemp's ridley and loggerhead turtles that switch from pelagic to benthic feeders as adults (Shaver, 1991; Plotkin et al., 1993). Stable isotope analysis indicated that gelatinous zooplankton composed up to 25% of the diet of immature loggerheads (Wallace et al., 2009) and fatty acid composition confirmed the consumption of gelatinous zooplankton by adult leatherbacks (Holland et al., 1990). Two studies have also attempted to investigate the consequences of an all-gelatinous diet (Lutcavage and Lutz, 1986; Davenport, 1998). Their results suggest requirements greater than 65 kg jellyfish d<sup>-1</sup> for adult leatherback turtles, or the equivalent of six large medusae per day. No studies have estimated the impact of sea turtle predation on the population dynamics of gelatinous zooplankton, although some studies have correlated sea turtle abundance to the presence of gelatinous zooplankton (Grant et al., 1996; Houghton et al., 2006).

Two orders of seabirds, Procellariiformes and Charadriiformes, include all documented predators of gelatinous zooplankton (Table 9). The order Procellariiformes includes petrels, shearwaters, fulmars, and albatrosses, which possess tubular nasal passages associated with advanced olfactory capabilities (Prince and Morgan, 1987). The order Charadriiformes is much larger and highly varied, including most other seabirds (gulls, terns, murres, and auks). Tubenose seabirds are pelagic feeders adapted to long-distance and wide-range flight. They rely heavily on gliding as they travel far from shore and cover large areas in search of prey feeding primarily on continental shelves and slopes (Xavier et al., 2003; Catry et al., 2004). Members of the Charadriiformes have shorter wingspans and are confined more to nearshore feeding. With the exception of shearwaters, most marine birds rely on surface feeding or shallow diving to obtain prey, and many feed at night to take advantage of vertically migrating and bioluminescent prey (Prince and Morgan, 1987). The diets of seabirds are highly variable and dependent on the seasonal availability of prey. Their major prey items include fish, squid, and crustacean zooplankton (e.g.,

euphausiid, mysids, amphipods, isopods, and copepods). Gelatinous prey are also commonly observed, but they probably provide only a small portion of the diet, with peaks in consumption associated with seasonal increases in gelatinous zooplankton abundance (Harrison, 1984; Schneider et al., 1986).

As with turtles, most observations regarding the consumption of gelatinous zooplankton by birds were reported as frequency of occurrence, and were collected using visual observations and gut-content analysis (Table 9). Although sampling of birds is regulated, the unlisted status of most species and the ability to use regurgitation to examine gut contents result in higher sample sizes and increased frequency of observations. Nevertheless, sampling is still limited by bird behavior and most samples have been collected during the breeding or chick-rearing season when birds spend more time on shore and are easily captured (Xavier et al., 2003; Catry et al., 2004). Seasonal sampling shows peaks in consumption associated with increases in gelatinous zooplankton abundance (Harrison, 1984) and annual data show consistent consumption between years (Harrison, 1990). There is also some evidence that the consumption of the parasites and other associates of gelatinous zooplankton increases diet diversity of their bird predators (Harrison, 1984). Still, quantitative information on the contribution of gelatinous zooplankton is lacking and no studies have examined the impact of bird predation on the population dynamics of gelatinous zooplankton.

For many of the predators of gelatinous zooplankton, the absence of measurements for digestion rates prevents the calculation of feeding rates based on gut-content analysis (Arai, 1988). Therefore, even with the large number of observations that have been made of the gut contents of field-collected consumers, our ability to assess the impact of these predators on the populations of gelatinous prey remains very limited. Measurements of digestion times for gelatinous prey are needed for all predator groups. This information could then be used to calculate feeding rates from existing data. Additional observations would still be required, however, to quantify growth rates and survival of the predators on a range of prey types to fully understand the role of gelatinous zooplankton in the diets of these consumers. In the case of birds and turtles, increases in sample size and frequency combined with information on dietary contribution (percent of prey consumed) are also needed. Recent advances in biochemical analysis and genetic identification of prey from gut-content analysis may lead to more insights regarding dietary contributions and feeding rates. Once this information has been collected, concurrent data on predator and prey abundance can be used to evaluate the impact of these predators on their gelatinous prey.

### 6.06.9 Biological Associates

In addition to predator-prey relationships, gelatinous zooplankton are key participants in several other biological associations, including parasitism (+ -), commensalism (+ 0), and mutualism (+ +). Within these associations, the gelatinous zooplankton usually acts as a source of energy or provides some sort of service (e.g., transportation, shelter, or protection). The type of association and the role of gelatinous zooplankton are often flexible and vary throughout the duration of the

relationship. The definitions of these associations are broad and subtle differences between them are often difficult to assess in nature, as they can overlap or transition into one another. Additionally, these associations can change with life history stage (Mansueti, 1963; Laval, 1980) or as the result of food limitation (Laval, 1980). Consequently, although these associations have been well-documented and their occurrence often measured (Table 10), quantitative information regarding their trophic role is lacking.

Although examples of gelatinous parasites are rare (*Lampea pancerina*: Harbison et al., 1978), gelatinous zooplankton are hosts to a wide range of parasitic organisms. Hyperiid amphipods are almost exclusively associated with this group (e.g., Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980). In coastal marine systems, two species infest large

numbers of ctenophores (*Hyperoche*: Brusca (1970), Hirota (1974), and Sorarain et al. (2001)) and scyphomedusae (*Hyperia*: Bowman et al. (1963), Rasmussen (1973), Dittrich (1988), and Martinussen and Båmstedt (1995)) during summer (Table 10). Adult females of these species deposit their larvae directly into the tissue of their gelatinous host. Larvae then feed on prey caught by the host or directly on the host during periods of low prey availability. In some species, the larvae develop into adult predators/parasitoids that consume their host entirely. As a result, it has been suggested that hyperiid amphipods contribute to the seasonal decline of gelatinous zooplankton populations (Rasmussen, 1973; Möller, 1980); however, no quantitative data are available to support these claims. Additionally, although hyperiid amphipods have been considered obligate parasites of gelatinous zooplankton (Laval,

**Table 10** Occurrence of biological associations with gelatinous zooplankton in coastal marine systems

Associate	Host	Location	Peak occurrence	Reference
Parasites:	% (n) Season			
Order Amphipoda				
Suborder Hyperiidae				
<i>Hyperoche medusarum</i>	<i>Pleurobrachia bachei</i>	Northern California, USA	15% (135) Sp	Brusca (1970)
<i>Hyperoche mediterranea</i>	<i>Pleurobrachia bachei</i>	La Jolla Bight, CA, USA	>40% (NR) S	Hirota (1974)
<i>Hyperia galba</i>	<i>Aurelia aurita</i>	Islefjord, Denmark	~100% (NR) S	Rasmussen (1973)
	<i>Aurelia aurita</i>	Raunefjorden, Norway	12% (73) S	Martinussen and Båmstedt (1995)
	<i>Cyanea capillata</i>		33% (188) S	
Phylum Nematoda				
Family Anisakidae				
<i>Hysterothylacium aduncum</i>	<i>Pleurobrachia pileus</i>	Black Sea, Turkey	72% (17194) S	Mutlu and Bingel (1999)
Class Trematoda				
Subclass Digenea				
<i>Opechona bacillaris</i>	<i>Pleurobrachia pileus</i>	Galway Bay, Ireland	>50% (NR) S	Yip (1984)
Class Anthozoa				
Order Actiniaria				
<i>Peachia quinquecapitata</i>	<i>Phialidium gregarium</i>	Friday Harbor, WA, USA	63% (NR) S	Spaulding (1972)
<i>Edwardsia lineata</i>	<i>Mnemiopsis leidyi</i>	Woods Hole, MA, USA	78% (253) S/F	Crowell (1976)
Phylum Dinoflagellata				
Family Oodinidae				
<i>Oodinium</i> sp.	<i>Beroe abyssicola</i> <i>Bolinopsis infundibulum</i>	Friday Harbor, WA, USA	97% (28) F 100% (10) F	Mills and McLean (1991)
Commensals:				
Order Amphipoda				
Suborder Hyperiidae				
<i>Thermisto australis</i>	<i>Cyanea capillata</i>	Port Phillip Bay, Victoria	70% (105) S	Condon and Norman (1999)
Order Decapoda				
Family Scyllaridae				
<i>Scyllarus</i> sp.	<i>Aurelia aurita</i>	Bimini, The Bahamas	20% (402) F	Herrnkind et al. (1976)
Class Actinopterygii				
Family Gadidae				
<i>Theragra chalcogramma</i>	<i>Cyanea</i> sp.	Prince William Sound, AK, USA	~75% (50) S	Van Hyning and Cooney (1974)
Family Carangidae				
<i>Chloroscombrus meleagris</i>	<i>Aurelia aurita</i>	Tampa Bay, FL, USA	83% (53) S	Tolley (1987)

If multiple samples were taken, data were combined. n, number of individuals examined; NR, not reported; Sp, Spring; S, Summer; F, Fall.

1980), there have been no investigations of the role these gelatinous hosts play in the life history of these hyperiid parasites.

Coastal species of gelatinous zooplankton are also common intermediate or transport hosts for nematodes (e.g., *Hysterothylacium aduncum*: Koie (1993) and Mutlu and Bingel (1999)) and trematodes (e.g., *Neopechona pyriforme*: Stunkard (1969); *Opechona bacillaris* = *O. retractilis*: Fraser (1970), Koie (1975), Yip (1984), and Bray and Gibson (1990)). These worm parasites (helminths) have extremely complicated life cycles involving numerous intermediate hosts and frequently infest predatory/piscivorous fish as their definitive hosts (Marcogliese, 1995). Even though none of the helminth species associated with gelatinous zooplankton have been reported to infect humans, transmission of these parasites to species such as cod, mackerel, and whiting may affect the population dynamics of these commercially important fish species. As with crustacean parasites, quantitative information regarding the effect of helminth parasites on their gelatinous hosts or the importance of gelatinous hosts to the life cycles of these parasites has not been reported. This is also true of the relationship between these parasites and their definitive fish hosts, making it almost impossible to fully assess the role of gelatinous zooplankton in these associations.

Some quantitative information is available regarding the impact of cnidarian parasites on growth and reproduction of their gelatinous hosts. The larvae of several species of anemones infest ctenophores (*Edwardsiella lineata* = *Edwardsia lineata*: Crowell (1976), Bumann and Puls (1996), Daly (2002), Reitzel et al. (2007), and Reitzel et al. (2009)), hydro-medusae (*Peachia quinquecapitata*: Spaulding (1972)), and scyphomedusae (*P. parasitica*: McDermott et al. (1982)) in large numbers during summer. Increased interest in this small group of parasites probably results from their conspicuous coloration (pinkish-brown), large size (~2–30 mm), and high frequency of occurrence (Table 10). The anemone larvae enter gelatinous zooplankton through direct consumption, the consumption of other infested hosts, or through penetration of the outer body wall. The larvae then burrow through the host's tissue, orient themselves with their mouths opening into the gastrovascular or reproductive systems, and consume prey caught by the gelatinous host or reproductive tissue. Bumann and Puls (1996) examined the effect of infestation by the larval anemone *E. lineata* on the ctenophore *M. leidyi*. They observed no difference in egg production between infested and noninfested individuals of similar size; however, they did observe significantly lower growth rates of infested individuals, even at low parasite loads. As reproduction of *M. leidyi* is positively correlated to size (Baker and Reeve, 1974; Finenko et al., 2006), differences in growth rates between infested and noninfested individuals could ultimately impact host population growth rates *in situ*.

The costs and benefits of commensal relationships are difficult to demonstrate because they are subtle and defined by the absence of an effect on one of the participants. Although evidence supporting commensalism on both sides of these examples (benefactor/unaffected partner) is lacking, commensals of gelatinous zooplankton reported in coastal marine systems include protists, crustaceans, and fish. Peritrichous ciliates (e.g., *Trichonina ctenophorii*) attach to the comb plates of the ctenophore *M. leidyi* (Estes et al., 1997; Moss

et al., 2001). Turbulent eddies produced by movement of the comb plates during swimming may increase prey encounters for ciliates, enhancing their feeding (Moss et al., 2001). Changes in the contour of the comb plates created by the attachment of these organisms appear to have little or no effect on the ctenophore, unlike parasitic protists (Mills and McLean, 1991; Moss et al., 2001) that damage their gelatinous hosts through direct consumption. The small size of these commensals compared to their hosts makes it difficult to confirm both the reported benefits to the ciliates and the lack of harm to the ctenophore.

Numerous crustaceans have also been observed clinging to the exterior surfaces (exumbrella and subumbrella) of medusae with no observable impact on the gelatinous hosts, including palaemonid 'cleaner' shrimp (*Periclimenes paivai*: Filho et al. (2008)), phyllosoma (*Scyllarus* sp.: Herrnkind et al. (1976)), spider crabs (*Libinia dubia*: Corrington (1927)), hyperiid amphipods (*Thermisto australis*: Condon and Norman (1999)), and copepods (*Paramacrochiron maximum*: Browne and Kingsford (2005)). These crustaceans may benefit from enhanced dispersal, protection from predation, increased feeding in the wake of medusa swimming, and/or the consumption of mucus generated by the host. However, these potential benefits have not been examined directly and evidence suggests that these piggyback rides might be detrimental to the gelatinous hosts. Marliave and Mills (1993) observed altered swimming behavior and reduced growth rates of hydromedusae transporting pandalid shrimp, and considered the relationship detrimental phoresy rather than commensalism.

Commensal relationships have most commonly been observed between gelatinous zooplankton, specifically scyphomedusae, and fish (Mansueti, 1963). In coastal environments, these associations are generally limited to juvenile fish, as the majority of reported commensals are free living as adults. Despite their high frequency of occurrence (Table 10), commensal relationships between fish and gelatinous zooplankton appear to be facultative, because only a fraction of the juveniles from any given species form these associations. Commensal fish are usually observed swimming in close proximity to the bell or among the tentacles and oral arms of medusae. They escape consumption or damage from their hosts by avoiding contact with the medusa's tentacles (Dahl, 1961; Phillips et al., 1969), inhibiting nematocyst discharge (Dahl, 1961; Phillips et al., 1969), and/or developing immunities to the nematocyst toxins (Phillips et al., 1969). Associations with medusae are suggested to provide shelter (Brodeur, 1998), protection (Dahl, 1961; Van Hyning and Cooney, 1974), and enhanced feeding (Mansueti, 1963; Phillips et al., 1969). By decreasing predation mortality or increasing growth rates during vulnerable life history stages, these associations may significantly influence the population dynamics of fish, including commercially important species such as whiting, pollock, and cod. Despite the potential economic importance of these associations, evidence confirming the actual benefits is lacking. In the case of these associations, the lack of information is probably due, in part, to the difficulties of working with multiple large and mobile organisms *in situ*.

Considerably more quantitative information is available regarding mutualistic associations with gelatinous zooplankton. Several species of scyphomedusae, specifically those from tropical coastal regions, harbor endosymbiotic algae called

'zooxanthallae'. Unfertilized eggs are released free of algal symbionts (Rahat and Adar, 1980; Montgomery and Kremer, 1995). Zooxanthellae are acquired by developing embryos, planula, or polyps, and then transmitted to medusae during asexual reproduction. Within the tissue of the host, zooxanthellae fix carbon through photosynthesis, and subsequently translocate a portion of the carbon to the host. Studies estimate that algal photosynthesis is capable of contributing carbon in excess of the host's daily metabolic carbon demand (*Cassiopea xamachana*: Verde and McCloskey (1998); *Linuche unguiculata*: Kremer et al. (1990); *Mastigias* sp.: McCloskey et al. (1994)). Algal photosynthesis has also been suggested to stimulate strobilation in polyps (Rahat and Adar, 1980; Hofmann and Kremer, 1981), supply growth requirements of medusae (Kremer et al., 1990; McCloskey et al., 1994), and influence carbon cycling in marine lakes (McCloskey et al., 1994). The algae, in turn, utilize nutrients excreted by the medusae that were originally obtained through the ingestion of zooplankton or environmental absorption (Muscatine and Marian, 1982; Wilkerson and Kremer, 1992). By preventing the loss of nutrients to the surrounding water, this association acts to conserve nutrients in oligotrophic waters, which can then be used to support growth of both algae and hosts (Muscatine and Marian, 1982; Wilkerson and Kremer, 1992; Pitt et al., 2005; Pitt et al., 2009; West et al., 2009).

Despite the large number of associations that have been identified and their high frequency of occurrence, the ecological significance of most of these associations is poorly understood. As intermediate or transport hosts, gelatinous zooplankton may control the distribution and abundance of their associates. Changes caused by gelatinous zooplankton can then indirectly influence the population dynamics of other hosts or future prey of their associates, which can include commercially important fish species. Conversely, these associates may negatively (parasitism) or positively (mutualism) affect the populations of their gelatinous hosts, many of which are important consumers of zooplankton in the coastal marine systems. Only through a concerted effort that combines field observations and carefully designed laboratory experiments will we better understand the role of these associations in coastal marine systems.

### **6.06.10 Conclusion**

Gelatinous zooplankton are highly adapted to succeed in coastal marine environments. They are large in size relative to their organic content. This dilute composition gives them an energetic advantage when converting ingested prey into somatic growth. Both ctenophores and medusae do not satiate, but continue to ingest zooplankton prey at high clearance rates even at high prey densities. Tunicate grazers are able to ingest even very small particles, which gives them access to the smallest but most abundant seston. Coastal species of gelatinous zooplankton grow quickly when environmental conditions (i.e., temperature and food availability) are suitable. As a result, the population dynamics of gelatinous zooplankton are characterized by high seasonal abundance and large interannual variability. Typically, populations of ctenophores and pelagic tunicates are not abundant throughout the year, but die back to low levels between blooms, which occur at different times

depending on the geographic location. Coastal cnidarians are not holoplanktonic, and instead leave the pelagic environment to overwinter as benthic polyps.

Several species of both gelatinous predators and grazers can grow and reproduce at a rate high enough to produce population densities sufficient for a large, but temporary, impact on the density of their prey, and provide an abundant ephemeral food source for their predators. Rates of ingestion, somatic growth, and reproduction have been quantified for several coastal species, but laboratory artifacts associated with confinement of animals compromised many of the results. Experimental studies with large or active species are especially problematic. Only a very few species have been studied sufficiently to allow even rough deterministic predictions of their peak population density and trophic impact. Although several predators have been identified, rates of predation on gelatinous zooplankton are generally poorly quantified, and most information is anecdotal and qualitative. The degree to which populations of gelatinous zooplankton are controlled by predation is generally poorly understood, but some examples (e.g., predation on lobate ctenophores by beroid ctenophores) have been documented. Many nongelatinous predators (e.g., turtles and fish) have declining populations, and thus are likely to exert less control over the abundance of gelatinous zooplankton than they did historically. The combination of declining populations of planktivorous fish and eutrophication (Arai, 2001; Mills, 2001) of coastal environments creates conditions especially well-suited to a variety of gelatinous zooplankton, and vulnerable to invasive populations. Climate change is likely to affect the distribution, timing, and abundance of gelatinous zooplankton as well. Some studies have already documented changes with broad ecological consequences (Sullivan et al., 2001; Costello et al., 2006).

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