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Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska

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ABSTRACT: Large jellyfish are conspicuous members of many coastal plankton communities. They are potentially important as competitors for zooplankton prey with fish larvae and zooplanktivorous fish, as well as being predators of fish eggs and larvae. Nevertheless, few data exist on predation effects of large medusae on zooplankton *in situ*. Biovolumes and densities of *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea* medusae combined, measured in fishing seines, were generally low (<1 l per 1000 m³ and <10 medusae 1000 m⁻³) at 24 to 44 stations during July in 1998 and 1999 in Prince William Sound (PWS), Alaska. Their diets contained mainly copepods, larvaceans and cladocerans, and also a variety of meroplankton. Few fish eggs and larvae were eaten. Multiple regression analyses showed that the numbers of the main prey taxa in the gut contents usually were significantly correlated with medusa diameter and prey density. Digestion rates for copepods and cladocerans at 14°C averaged 3 h for *A. labiata*, 2 h for *C. capillata* and 1.5 h for larvaceans by both predators. Calculations using the above data indicated that individual medusa consumed 100s to 1000s of prey daily. Because of high prey densities and low medusa densities, predation effects on small copepods were low (mean $\leq 0.3\%$ of the standing stock d⁻¹). Larvaceans experienced greater predation at an average of $\leq 8.3\%$ of the standing stock d⁻¹. These predation effects were underestimated in 1998, because sampling did not include the numerous aggregations of *A. labiata*, and also in 1999, when small hydromedusae were abundant (mean 59 medusae m⁻³). During this study, predation by medusae probably did not reduce prey availability to Age 0 sandlance, herring and walleye pollock, with diets consisting primarily of small copepods; however, medusa predation may have affected larvacean availability to Age 0 pink salmon, which consume them extensively.

KEY WORDS: Appendicularia · Copepoda · Cladocera · Scyphozoa · Hydrozoa · Fish eggs · Fish larvae · Competition · Larvaceans · Salmon

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INTRODUCTION

Interest in the importance of jellyfish as consumers in aquatic ecosystems has increased over the past 3 decades as outbreaks of jellyfish populations attract public and scientific attention (reviews in Arai 2001, Mills 2001, Purcell et al. 2001). Little information exists on jellyfish populations in Alaskan waters; however, recent analyses show dramatic increases in the Gulf of Alaska and Bering Sea, possibly resulting from climate regime shifts (Anderson & Piatt 1999, Brodeur et al.

1999, 2002) or reduction of fish populations by over harvesting (Parsons & Lalli 2003). The only prior study on the trophic importance of jellyfish in Alaskan waters did not estimate predation directly, but used the daily rations from a different species (*Cyanea capillata*) at a similar temperature to estimate that *Chrysaora melanaster* medusae consumed approximately 32% of the zooplankton standing stock in the Bering Sea (Brodeur et al. 2002).

Species in the genera *Aurelia*, *Cyanea* and *Aequorea* have global distributions and often occur in great

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abundance in the world's oceans (e.g. Fancett 1988, Purcell & Grover 1990, Fearon et al. 1992, Boltovskoy 1999, Purcell et al. 2000, Dawson & Martin 2001, Graham 2001, Sparks et al. 2001). *Aurelia aurita* undoubtedly is the most studied medusa in the world and has a circumpolar distribution, possibly due to introductions in various locations (see Dawson & Martin 2001, Mills 2001). *Aurelia* medusae have attracted attention because they form dramatic aggregations (Purcell et al. 2000 and references therein). The specific identities of *Aurelia* in the north Pacific Ocean have recently been questioned (Greenberg et al. 1996) and 3 species are now recognized, i.e. *A. aurita*, *A. limbata* and *A. labiata* (Wrobel & Mills 1998), with possible misidentifications of the other species as *A. aurita* in Alaskan and British Columbia waters in earlier studies. Species identification of *Aequorea* medusae is also in question, with 3 species names, i.e. *A. aequorea* var. *albida*, *A. forskalea* and *A. victoria*, in recent use in Alaskan and British Columbia waters for possibly the same species (Hamner & Schneider 1986, Purcell 1989, Brodeur et al. 1999, 2002, Purcell et al. 2000, Purcell & Sturdevant 2001). *Cyanea capillata* also has a global distribution (e.g. Fancett 1988, Brewer 1989, Martinussen & Båmstedt 1995, Purcell et al. 2000).

Aurelia, *Cyanea* and *Aequorea* medusae are potentially very important as predators of zooplankton and ichthyoplankton. *Aurelia aurita* has been shown to decrease populations of zooplankton (summarized in Schneider & Behrends 1998) and herring larvae (Möller 1980) in Kiel Bight, Germany and zooplankton in Tokyo Bay, Japan (Omori et al. 1995, Ishii & Tanaka 2001). Diets and prey selection also are reported for *A. aurita* (e.g. Sullivan et al. 1994, Graham & Kroutil 2001) and *A. labiata* (Purcell & Sturdevant 2001). Other recent studies have examined feeding in the laboratory (e.g. Stoecker et al. 1987, Båmstedt 1990, Båmstedt et al. 1994), and population dynamics and life history (reviewed in Lucas 2001). In spite of its wide distribution, *Cyanea capillata* has received less attention than *Aurelia* spp., perhaps because it does not form aggregations. It is known to feed on zooplankton, ichthyoplankton and gelatinous zooplankton (Fancett 1988, Fancett & Jenkins 1988, Brewer 1989, Båmstedt et al. 1994, 1997, Hansson 1997, Purcell & Sturdevant 2001). However, its feeding rates *in situ* have been estimated previously only in Port Phillip Bay, Australia (Fancett & Jenkins 1988) and in a Norwegian fjord (Martinussen & Båmstedt 1995). Diets and prey selection of *Aequorea victoria* feeding on ichthyoplankton, zooplankton and gelatinous zooplankton have been reported from northeast Pacific coastal waters (Purcell 1989, 1990, 1991, Purcell & Grover 1990, Purcell & Sturdevant 2001, Costello & Colin 2002). However, feeding rates have been reported previously only on

fish larvae (herring) in British Columbia (Purcell 1989, 1990, Purcell & Grover 1990, Purcell & Arai 2001).

The dual role of soft-bodied plankton as predators and competitors of fishes has been suggested many times (e.g. Purcell 1985, Arai 1988), but rarely evaluated directly (existing studies are Purcell & Grover 1990, Baier & Purcell 1997). Jellyfish predation on both zooplankton and ichthyoplankton may affect the larvae of numerous fish species, many of which are commercially important (e.g. herring, rockfish, cod, flatfish, see Fancett 1988, Purcell 1989, 1990), as well as the juveniles and adults of zooplanktivorous fish species (e.g. herring, walleye pollock, sandlance, pink salmon, see Purcell & Sturdevant 2001) that are important as forage fish of marine vertebrates, specifically piscivorous fish, sea birds and marine mammals.

The possibility of competition for zooplankton prey between jellyfish and fish has been directly examined in only a few studies. Substantial dietary overlap was shown between medusae and first-feeding herring larvae and hydromedusae (Purcell & Grover 1990) and between age-0 forage fish and 4 gelatinous species (Purcell & Sturdevant 2001). When the principle prey were copepod nauplii, the potential for competition was thought to be low due to the great abundance of copepod nauplii consumed by the larvae (Purcell & Grover 1990, Baier & Purcell 1997). When the main prey were copepodites, however, chaetognaths consumed significant percentages of the same prey as fish larvae (Baier & Purcell 1997). Vinogradov et al. (1996) estimated the consumption of mesozooplankton by the introduced ctenophore, *Mnemiopsis leidyi* and zooplanktivorous fishes (anchovy, sprat and horse mackerel) in the Black Sea. Biomass of zooplankton and fishes, and prey consumption by fishes were high until 1988, but decreased dramatically during the outbreak period of *M. leidyi* that began in 1989, and the authors concluded that competition occurred for food among the ctenophores and fishes.

Prince William Sound (PWS), Alaska has been the location of intensive ecological research since the 'Exxon Valdez' oil spill in 1989. It is a complex fjord-type estuary (Schmidt 1977) located on the northern margin of the Gulf of Alaska at 60° N, 146° W, covering about 8800 m² and having 3200 km of shoreline (Grant & Higgins 1910) (see Fig. 1). Many of the marine birds and mammals, whose populations were injured by the oil spill, feed on forage fish, the small, schooling, zooplanktivorous fishes (Springer & Speckman 1997), including juvenile walleye pollock, Pacific sandlance, Pacific herring, capelin and pink salmon. The research presented here is part of the multi-investigator project, Alaska Predator Ecosystem eXperiment (APEX). A goal of the APEX project was to determine if the zooplankton foods available to forage fish limited their

populations, and thereby have inhibited the recovery of piscivorous marine bird and mammal populations injured by the oil spill. Large zooplanktivorous jellyfish, the scyphomedusae *Aurelia labiata* and *Cyanea capillata*, and the hydromedusan *Aequorea aequorea* var. *albida*, are conspicuous members of the plankton community in PWS and show marked dietary overlap with forage fish species (Sturdevant & Willette 1999, Purcell & Sturdevant 2001). To evaluate the potential of jellyfish to limit zooplankton populations, I present data on zooplankton and jellyfish abundance, jellyfish diets and digestion rates, and estimate the feeding rates and effects on zooplankton populations of *A. labiata*, *C. capillata* and *A. aequorea* var. *albida* during summer in PWS.

MATERIALS AND METHODS

Sampling locations and dates. Three regions in PWS were established (northeast, central and southwest, NE, C and SW, respectively) and 8 stations were chosen in each region (Fig. 1). Sampling for medusae and zooplankton occurred in both daylight and darkness in 1997 and 1998, but only in daytime in 1999. Sampling dates were 29 July to 8 August 1997, 14 to 20 July 1998 and 1 to 6 July 1999. All 24 stations were sampled in each year.

Abundance of zooplankton and jellyfish. Zooplankton samples were collected at the same stations in vertical tows, from 20 to 60 m depth to the surface in 1997 and 1998, from 20 m to the surface in 1999, using a 0.2 m diameter bongo plankton with 243 μ m mesh. Formalin was added to the samples to create a 5% solution. In the laboratory, small hydromedusae (≤ 1 cm in diameter) were enumerated from whole samples. For mesozooplankton, the samples were split using a Folsom plankton splitter, and all organisms in $1/4$ to $1/16$ splits were identified to general taxon and counted with the aid of a dissecting microscope. Small calanoid copepods were defined as those ≤ 2.5 mm total length. Copepods (Stages C4 and C5) were identified to species in 1997. Numbers of each taxon were standardized to 1 m^3 .

To determine the abundance of large jellyfish (*Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*), samples were taken with an anchovy purse seine, 250 m long by 34 m deep with 25 mm stretch mesh. In 1998 and 1999, the seine was set at each of 24 stations. An additional 21 seine sets were made in the same regions between 10 and 19 July 1999. The samples were processed on board the ship; the medusae were identified, counted and live biovolumes of each species measured. Densities and biovolumes of the large jellyfish were standardized to 1000 m^3 by dividing the

numbers and volumes of each species in a catch by volume of water filtered by the seine ($57\,642 \text{ m}^3$; Purcell et al. 2000). The average volume of individual medusae in each seine set was determined by dividing the total volume by the total number of medusae for each species. The average medusa diameter at each station was estimated for each species from regressions of medusa diameter to wet weight or volume, which are roughly equivalent (Papathanassiou et al. 1987, Brewer 1989, Purcell 1990).

Predation estimates of jellyfish feeding on zooplankton. Medusae for gut content analysis were scooped up from the near surface with a net on a 3.7 m pole. They were immediately preserved individually in 5% formalin solution in 32 μ m filtered seawater. The jellyfish were dissected in the laboratory and all tissue and liquid examined for prey organisms, which were identified to general taxon, as above. Preserved medusa diameters were measured. Large specimens, particularly of *Cyanea capillata*, which had apparently completed sexual reproduction and had large infestations of hyperiid amphipods, contained few prey items, and may have been senescent; therefore, such individuals were eliminated from the analyses. The relationships of medusa diameter and prey density to the number of prey in the gut contents were analyzed in multiple linear regressions (Sigma-

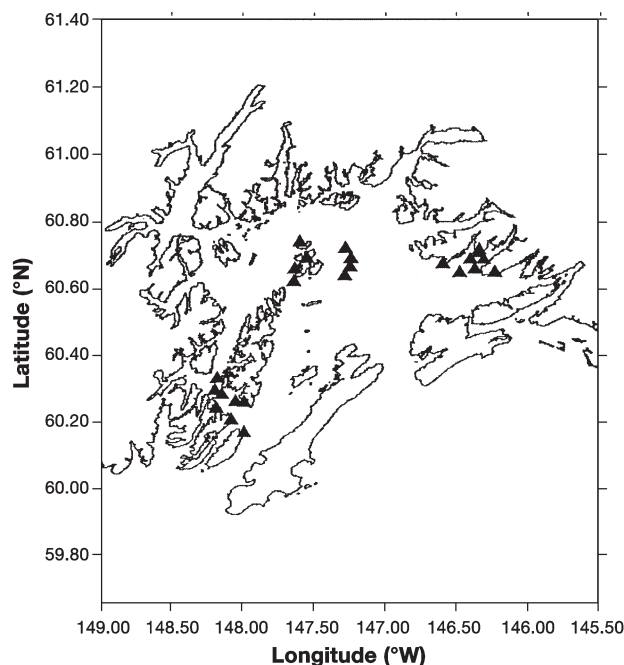


Fig. 1. Prince William Sound in south-central Alaska and sampling stations for zooplankton and jellyfish in 1997, 1998 and 1999. Eight stations (▲) were sampled in each of 3 regions (northeast, central and southwest) each year. North is towards the top of the figure

Table 1. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Frequency of occurrence of medusae in gut collections and in seine hauls at stations in 3 regions (northeast, central and southwest) of Prince William Sound, Alaska. Numbers represent the number of stations where medusae were collected/total stations. Numbers of medusae analyzed for gut contents are in parentheses. nd = no data

Predator Year	Northeast		Central		Southwest	
	Gut	Seine	Gut	Seine	Gut	Seine
<i>A. labiata</i>						
1997	0/8 (0)	nd	2/11 (8)	nd	0/8 (0)	nd
1998	1/8 (1)	6/8	1/8 (2)	7/8	6/8 (23)	8/8
1999	4/8 (15)	10/14	2/8 (6)	6/14	3/9 (8)	4/14
<i>C. capillata</i>						
1997	0/8 (0)	nd	9/11 (26)	nd	9/12 (26)	nd
1998	2/8 (8)	8/8	7/8 (25)	8/8	3/8 (5)	8/8
1999	8/8 (36)	14/14	7/8 (20)	14/14	9/10 (30)	16/16
<i>A. aequorea</i>						
1997	0/8 (0)	nd	0/11 (0)	nd	0/8 (0)	nd
1998	1/8 (1)	8/8	4/8 (14)	8/8	0/8 (0)	8/8
1999	7/8 (24)	14/14	3/8 (4)	14/14	1/8 (1)	16/16

Stat). Assumptions of normality and constant variance generally were not met until data were \log_{10} -transformed. One individual of each taxon was added to data from all stations to remove 0 values from these analyses before transformation.

To measure the gut passage times of zooplankton prey in 1998, individual medusae were collected in dip nets and maintained at ambient surface water temperature (14°C) in 94 l coolers filled with filtered (32 μm) seawater with low densities of *Artemia* nauplii to promote continuous digestion. One or more medusae were preserved immediately, and then one or more medusae were preserved at 1 or 2 h intervals for up to 8 h. The gut contents of the medusae were analyzed later in the laboratory for partly digested prey. The length of time when the different prey types were no longer recognized in the gut contents were used in calculations of feeding rates. Digestion experiments were conducted for *Cyanea capillata* (11 experiments), *Aurelia labiata* (4 experiments) and *Aequorea aequorea* (2 experiments). These methods were used because no controlled laboratory conditions were available on board ship or at port.

Individual feeding rates (numbers of prey eaten per medusa per d) were calculated by 2 methods. First, feeding rates on copepods, cladocerans and larvaceans were calculated directly from the number of prey in the gut contents divided by digestion times (h) and multiplied by 24 h d^{-1} . This method was used to average stations within regions where several gut content specimens were collected at most stations (*Aurelia labiata* SW 1998, *Cyanea capillata* C 1998 and all regions in 1999, *Aequorea aequorea* NE 1999). Second, because insufficient medusae were collected for gut contents at several stations (Table 1) to obtain good estimates of feeding, data on medusa diameter and prey densities (copepods and larvaceans) from each station were entered into the multiple regression equations, divided by digestion times and multiplied by 24 h d^{-1} to calculate feeding rate. For both methods, continuous feeding over 24 h was assumed. Individual feeding rates were multiplied by medusa densities and divided by prey densities at each station to estimate the effects of the medusae on the prey populations (% prey standing stock consumed d^{-1}). Individual feeding rates were divided by prey densities to estimate clearance rates.

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RESULTS

Abundance of zooplankton and jellyfish

During the summers in PWS, zooplankton populations were comprised mainly of small copepods, larvaceans, and cladocerans (Table 2). Data for individual stations are in Purcell (2000); therefore, here, we present combined data for the 24 stations. Small copepods were greater than 70% of the total zooplankton sampled, except in the northern region in 1998, where bivalve veligers were extremely abundant. The species composition of copepods (C4 and C5) in 1997 averaged among stations was *Calanus marshallae* 0.01 \pm

Table 2. Zooplankton densities (no. m^{-3} ; 243 μm mesh net) during July and August in Prince William Sound, Alaska. Numbers are means \pm SD from plankton tows at 24 stations

Year	Copepods	Cladocerans	Larvaceans	Copepod nauplii	Decapod larvae	Barnacle larvae	Gastropods	Bivalve veligers	Total
1997	834.2 \pm 415.0	20.7 \pm 32.0	96.7 \pm 78.2	6.3 \pm 7.9	11.6 \pm 9.5	7.5 \pm 8.4	85.1 \pm 64.0	7.6 \pm 6.7	1115.1 \pm 504.6
1998	1727.8 \pm 1340.1	65.5 \pm 114.3	173.7 \pm 243.9	24.0 \pm 34.1	7.2 \pm 8.2	35.9 \pm 38.8	0.7 \pm 2.4	276.4 \pm 232.8	2396.6 \pm 1413.3
1999	1974.3 \pm 1850.6	205.3 \pm 230.2	159.2 \pm 170.5	8.0 \pm 8.6	6.4 \pm 10.2	40.0 \pm 50.8	70.3 \pm 88.0	33.4 \pm 35.4	2398.3 \pm 1227.6

0.4%, *Oithona similis* $4.1 \pm 2.7\%$, *C. pacificus* $0.7 \pm 0.8\%$, *Acartia longiremis* $7.3 \pm 4.6\%$, *Metridia lucens* $11.8 \pm 15.8\%$ and *Pseudocalanus minutus* $54.3 \pm 12.3\%$, and unidentified copepodites $21.6 \pm 8.1\%$. Larvaceans averaged from 1.2 to 27.2% and cladocerans from 1.3 to 15.3% of the total mesozooplankton in each region.

Zooplankton populations were similar among years. Zooplankton taxonomic composition was very similar (86.0 to 95.6%; Schoener 1974, percent similarity index) among years (1995 to 1998; Purcell & Sturdevant 2001). Densities of the major zooplankton groups (copepods, cladocerans and larvaceans) were also very similar in 1998 and 1999 (Table 2); however, mean copepod densities in 1997 were about half of those in 1998 or 1999. Meroplanktonic larvae (bivalve and gastropod veligers, barnacle larvae and crab zoeae) were common and showed considerable variation among years (Table 2). Ichthyoplankton was not sampled adequately in the plankton tows to estimate densities.

Biovolumes and densities of the 3 large jellyfish species sampled with a purse seine were generally low at stations in PWS (Table 3). Total medusa biovolumes were about 5 times greater in 1998 than in 1999. In 1998, the 3 large species had similar biovolumes overall: 258, 136 and 102 ml 1000 m⁻³ *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, respectively). *C. capillata* had greatest biovolumes in the NE

region in both years. Biovolumes of *A. aequorea* also were greatest in the NE region and were very low in the SW region. The average sampled *A. labiata* biovolumes in 1998 were as much as 100 times the biovolumes in 1999. Densities of medusae (Table 3) showed that *C. capillata* were about 4 times more abundant in 1999 than in 1998, but that *A. labiata* medusae were $1/2$ to $1/100$ as numerous in 1999. Total densities sampled were generally <10 medusae 1000 m⁻³, with species maxima of 16.5 and 132 medusae 1000 m⁻³ for *C. capillata* and *A. aequorea*, respectively. The ratios of biovolume to number of medusae were much greater in 1998, showing that medusae in each species were larger in 1998 than in 1999. The data show great variation, due in large part to the contagious distributions of *A. labiata* and *A. aequorea* medusae. These biomass and density values are probably underestimates due to some breakage and loss from the seine, and the exclusion of aggregations of *A. labiata*.

Predation on zooplankton by jellyfish

Diets

The main prey of the large medusae in PWS during the summer were small copepods, larvaceans and cladocerans. Together, these prey made up 24 to 82% of the

Table 3. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Live biovolumes (ml 1000 m⁻³) and densities (no. 1000 m⁻³) of large jellyfish collected in anchovy seine sets at 8 stations in each region (northeast, central and southwest) in Prince William Sound (PWS) from 14 to 20 July 1998 and 1 to 6 July 1999. In 1999, PWS overall, 18 additional seine sets were included from 10 to 19 July. *A. labiata* data do not include aggregations and so are underestimates. Numbers are means \pm SD

Year Region	<i>A. labiata</i>	<i>C. capillata</i>	<i>A. aequorea</i>	Total
Biovolumes				
1998				
Northeast	10.7 \pm 13.6	205.4 \pm 133.6	132.4 \pm 109.1	352.0 \pm 231.8
Central	371.2 \pm 908.9	123.9 \pm 100.2	111.8 \pm 59.8	561.6 \pm 829.0
Southwest	309.9 \pm 429.9	77.6 \pm 46.4	63.1 \pm 25.8	451.7 \pm 442.3
PWS	257.8 \pm 555.1	136.4 \pm 102.5	102.5 \pm 71.0	458.1 \pm 508.1
1999				
Northeast	1.0 \pm 1.4	568.8 \pm 436.3	402.4 \pm 379.3	972.2 \pm 572.2
Central	0.6 \pm 0.9	105.9 \pm 45.0	32.6 \pm 50.3	139.1 \pm 81.4
Southwest	2.0 \pm 6.2	76.2 \pm 115.3	6.3 \pm 8.3	84.6 \pm 120.0
PWS	2.0 \pm 300.2	76.3 \pm 337.5	6.4 \pm 915.8	84.6 \pm 1067.3
Densities				
1998				
Northeast	0.1 \pm 0.2	0.5 \pm 0.5	19.4 \pm 18.8	20.1 \pm 19.2
Central	1.5 \pm 3.4	0.5 \pm 0.3	5.1 \pm 1.9	7.0 \pm 2.4
Southwest	2.2 \pm 2.8	1.0 \pm 0.7	3.4 \pm 1.0	6.6 \pm 3.6
PWS	1.4 \pm 1.7	0.7 \pm 0.4	9.3 \pm 7.6	11.2 \pm 7.4
1999				
Northeast	0.05 \pm 0.1	3.4 \pm 1.6	19.6 \pm 21.2	23.0 \pm 21.2
Central	0.01 \pm 0.03	2.0 \pm 1.2	2.0 \pm 3.1	4.0 \pm 3.3
Southwest	0.02 \pm 0.05	2.6 \pm 5.2	0.3 \pm 0.4	3.1 \pm 5.6
PWS	0.4 \pm 2.3	2.9 \pm 2.9	7.7 \pm 21.2	10.8 \pm 21.0

Table 4. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Percentages of zooplankton taxa in the gut contents of medusae from July and August in Prince William Sound, Alaska. Numbers are means \pm SD. nd = no data

Predator Year	No. of medusae	Medusa size (mm)	Total prey	Copepods (%)	Cladocerans (%)	Larvaceans (%)	Copepod nauplii (%)	Decapod larvae (%)	Barnacle larvae (%)	Gastropods (%)	Bivalve veligers (%)	Fish eggs (%)	Fish larvae (%)	Other (%)
<i>A. labiata</i>														
1997	8	262.5 \pm 101.5	3585	59.0	16.7	4.6	1.6	0.03	0.3	13.1	4.6	0	0	0
1998	34	106.3 \pm 21.7	15651	10.2	12.2	1.0	nd	0.08	4.3	3.4	65.1	0.1	0	3.4
1999	30	74.3 \pm 24.4	5665	28.6	4.6	4.5	20.4	0.10	1.8	5.2	29.1	1.1	0	4.4
<i>C. capillata</i>														
1997	44	129.2 \pm 58.4	6707	7.6	5.2	82.6	0.2	0.6	1.3	1.7	0.5	0.1	0.06	0.1
1998	57	81.0 \pm 39.2	2622	16.2	14.7	43.2	nd	0.07	4.8	2.6	17.5	0.3	0.04	0
1999	97	73.9 \pm 22.5	13823	40.3	4.4	41.4	1.6	0.1	1.8	3.1	4.4	0.05	0.02	0.9
<i>A. aequorea</i>														
1997	8	55.2 \pm 21.0	164	9.8	0	77.4	3.7	0.6	1.2	4.9	0	1.2	0	1.2
1998	23	53.5 \pm 17.7	318	10.4	6.6	42.7	nd	0	1.6	0	16.4	2.2	0	16.7
1999	32	73.4 \pm 15.8	2250	36.3	1.0	43.7	12.8	0	0.1	0.5	4.7	0.8	0	0.7

prey in the gut contents of *Aurelia labiata*, 49 to 96 % of the prey of *Cyanea capillata* and 60 to 91 % of the prey in *Aequorea aequorea* (Table 4). Variations in the proportions of consumed prey roughly reflected variations in the availability of zooplankton *in situ*. For example, in 1998, bivalve veligers were more abundant *in situ* than in either 1997 or 1999 (Table 2), and were found in great numbers in the medusa diets; thereby, reducing the apparent contribution of the main prey taxa to the diet in 1998 (Table 4). *A. labiata* ate mainly crustaceans and bivalve veligers (92 to 94 %), while *C. capillata* and *A. aequorea* contained large percentages of larvaceans (42 to 83 %), as well as other soft-bodied prey (hydromedusae, ctenophores and ichthyoplankton; Table 4). Few fish eggs or larvae were found in the gut contents of medusae, only up to 2.2 % of the total prey items of *A. aequorea* (Table 4). Therefore, it appears that in July, when ichthyoplankton were not numerous, the jellyfish did not consume many of them.

Relationships of medusa diameter and prey density to feeding

The numbers of prey captured were significantly correlated (Table 5) with prey density and medusa diameter (Figs. 2, 3 & 4) for each medusa species. Multiple linear regressions with \log_{10} -transformed data from all years combined showed that medusa diameter had a greater effect on feeding than did prey density in each regression (Table 5). Relationships were stronger for copepods and larvaceans than for cladocerans (Table 5). Even though there was considerable variation in these data, these regressions can be used to approximate feeding rates of medusae from data on medusa size and prey density.

Digestion rates

The numbers of small copepods and cladocerans in the gut contents of medusae declined rapidly between t_0 (t is time in hours) and 3 h for *Aurelia labiata*, and had nearly disappeared from *Cyanea capillata* medusae in only 2 h (Fig. 5). The linear regression for *A. labiata* was: number of prey per medusa = $88.14 - 28.11t$, $r^2 = 0.995$. The linear regression for *C. capillata* was: number of prey per medusa = $20.30 - 8.66t$, $r^2 = 0.946$. Solving the equations for 0 prey yielded 3.1 h for *A. labiata* and 2.3 h for *C. capillata*. Mean diameters of medusae in the digestion experiment were 110.6 ± 30.4 mm for *A. labiata* and 102.6 ± 37.5 mm for *C. capillata*. These medusa diameters did not differ significantly among the hourly sampling times (1-way ANOVA) and were similar to those col-

Table 5. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Results of multiple linear regression analyses evaluating the relationships of medusa size (preserved diameter) and prey density with numbers of prey captured. Large medusae with <10 prey were omitted from these analyses. Numbers examined are in parentheses. PPM = prey medusa⁻¹; D = diameter in mm; PA = prey m⁻³; p = probability; ns = not significant

Predator Prey	Multiple R ²	p for diameter	p for prey m ⁻³	p overall	Predictive equation
<i>A. labiata</i> (56)					
Copepods	0.434	<0.001	<0.001	<0.001	Log ₁₀ PPM = 1.83 Log ₁₀ D + 0.62 Log ₁₀ PA - 4.14
Cladocerans	0.423	<0.001	0.603	<0.001	Log ₁₀ PPM = 2.37 Log ₁₀ D + 0.07 Log ₁₀ PA - 3.66
Larvaceans	0.547	<0.001	<0.001	<0.001	Log ₁₀ PPM = 1.31 Log ₁₀ D + 0.38 Log ₁₀ PA - 2.66
<i>C. capillata</i> (163)					
Copepods	0.289	<0.001	<0.001	<0.001	Log ₁₀ PPM = 1.26 Log ₁₀ D + 0.69 Log ₁₀ PA - 3.30
Cladocerans	0.202	<0.001	0.056	<0.001	Log ₁₀ PPM = 1.09 Log ₁₀ D + 0.09 Log ₁₀ PA - 1.67
Larvaceans	0.535	<0.001	<0.001	<0.001	Log ₁₀ PPM = 1.49 Log ₁₀ D + 0.63 Log ₁₀ PA - 2.54
<i>A. aequorea</i> (29)					
Copepods	0.575	<0.001	0.467	<0.001	Log ₁₀ PPM = 3.32 Log ₁₀ D + 0.14 Log ₁₀ PA - 5.39
Cladocerans	0.170	0.198	0.140	0.089	ns
Larvaceans	0.199	0.053	0.098	0.056	Log ₁₀ PPM = 2.71 Log ₁₀ D + 0.62 Log ₁₀ PA - 5.24

lected *in situ* for gut content analysis (Table 4). Therefore, differences in medusa size should not have affected our experimental results, or use of these results in the following calculations of feeding rates. In calculations of feeding rates, the digestion times of crustacean prey used for *A. labiata* was 3 h and for *C. capillata* was 2 h, measured at 14°C, which was the surface water temperature measured in PWS in July in each year.

Digestion of larvaceans was more rapid than copepods. In the digestion experiments, 35 larvaceans were in *Aurelia labiata* medusae at t_0 , but no larvaceans were found in medusae at subsequent hourly sampling intervals. At t_0 , 160 larvaceans were found in 8 *Cyanea capillata* medusae and only 5 larvaceans in 1 specimen at 1 h. Therefore, 1.5 h was used as the digestion time of larvaceans for both *A. labiata* and *C. capillata* medusae at 14°C.

Aequorea aequorea medusae, which are predisposed to gut evacuation when handled, contained only 4 prey at the start of the experiments; therefore, no digestion rates could be measured directly. Earlier data on digestion times of large copepods by *A. victoria* (mean 5.4 h, $n = 7$; unpubl.) and 9 to 14 mm herring larvae (mean 3.0 h, $n = 204$; Purcell 1989) at 8 to

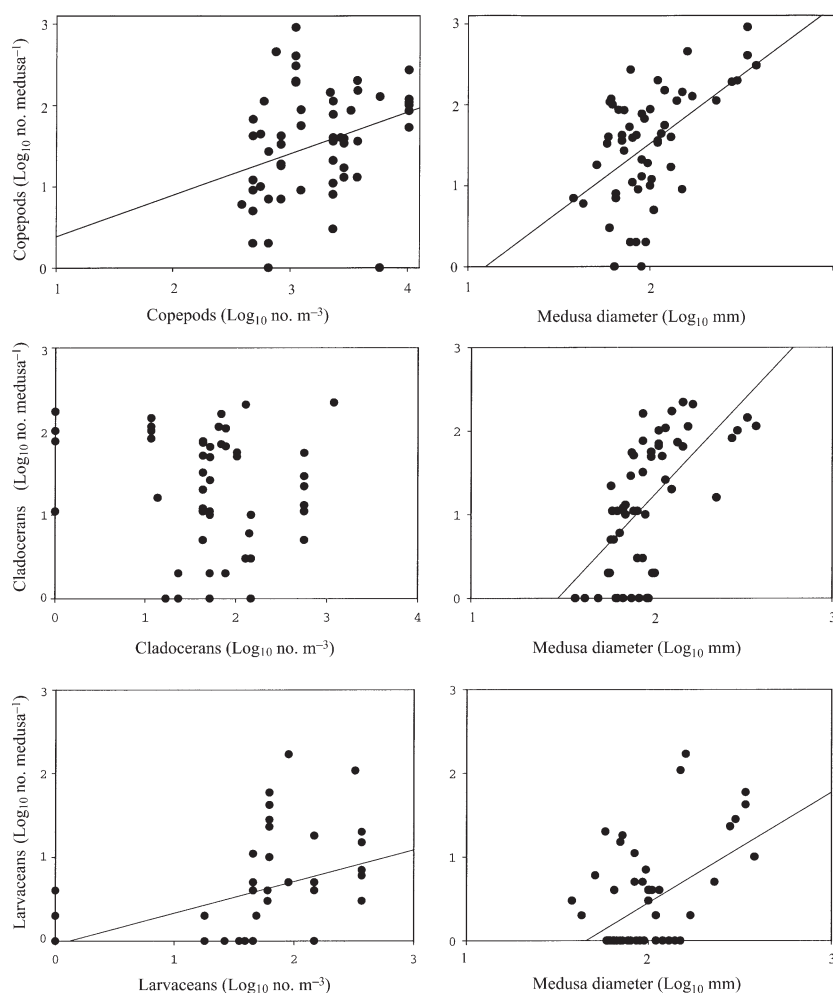


Fig. 2. *Aurelia labiata*. Relationship of prey density and medusa diameter to the numbers of prey in the gut contents for small copepods, cladocerans and larvaceans in 1997 to 1999. Multiple regression equations are in Table 5

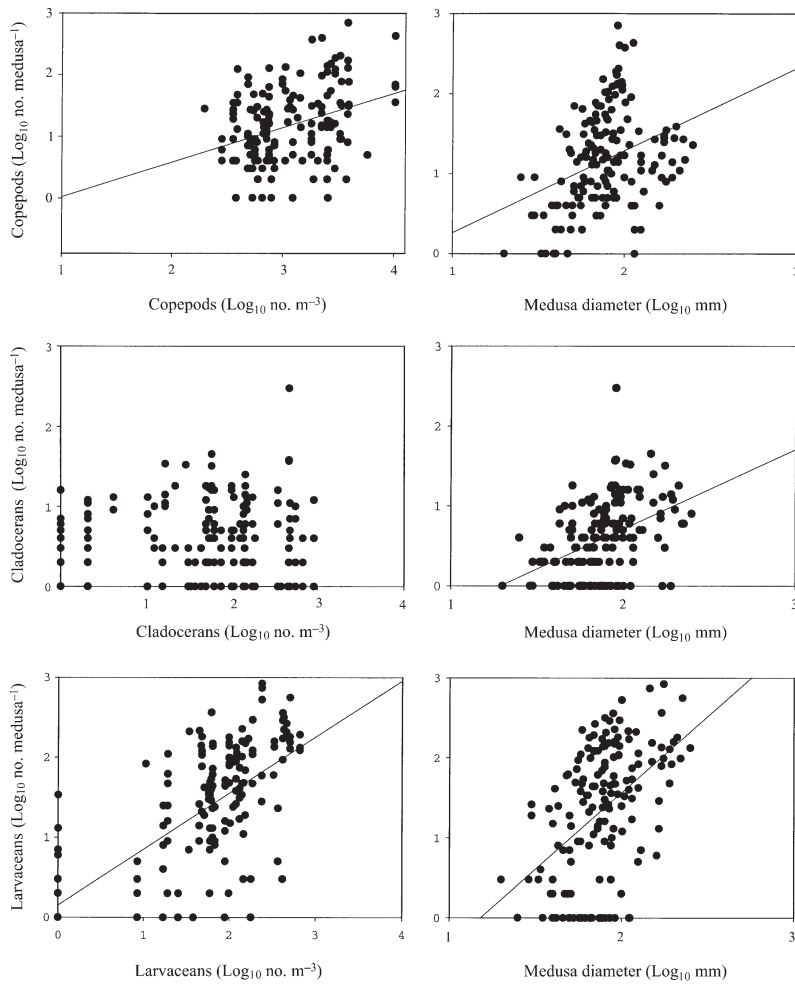


Fig. 3. *Cyanea capillata*. Relationships of prey density and medusa diameter to the numbers of prey in the gut contents for small copepods, cladocerans and larvaceans in 1997 and 1999. Multiple regression equations are in Table 5

12°C suggest that approximate digestion times of 4 h for small copepods and 1.5 h for larvaceans (0.5 to 0.75 mm trunk length) would be reasonable and conservative at the higher summer temperatures (14°C) in PWS.

Feeding effects of large medusae in PWS

Direct estimates of the percentages of zooplankton prey populations (small copepods, cladocerans and larvaceans) consumed daily were made from gut contents, digestion rates, and densities of jellyfish and prey at stations where gut content collections were adequate. Individual medusae were estimated to consume 10s to 100s (cladocerans) and 100s to 1000s (copepods and larvaceans) of prey daily (Table 6). However, due to high abundance of these prey (Table 7) and low

medusa abundance (Table 3), the effects on crustacean prey populations were small, generally $\leq 0.3\% \text{ d}^{-1}$ (Table 6). In each region, *Cyanea capillata* consumed $\leq 0.3\% \text{ d}^{-1}$ of the crustaceans on average. Regional estimates were also low for consumption of crustaceans by *Aurelia labiata* ($\leq 2.3\% \text{ d}^{-1}$) and *Aequorea aequorea* ($\leq 0.3\% \text{ d}^{-1}$). Predation effects were greater for medusae eating larvaceans, with regional averages of $\leq 3.4\% \text{ d}^{-1}$ for *C. capillata* and $8.3\% \text{ d}^{-1}$ for *A. aequorea*. *C. capillata* medusae consumed 2 to 5 times more prey in 1999 than in 1998 in the C region, where direct comparison was possible.

Insufficient medusae were available to estimate feeding at many stations (Table 1); therefore, the statistically significant multiple regression equations (Table 5) were used to estimate feeding on copepods and larvaceans. Even so, low occurrence of *Aurelia labiata* in 1999 prevented meaningful calculations at most stations; hence, those results were not presented. Because of the high copepod densities, medusa predation removed only $\leq 0.1\% \text{ d}^{-1}$ of the copepod populations (Table 7). Larvacean densities (generally $< 200 \text{ m}^{-3}$) were considerably less than copepod densities (~ 900 to 3000 m^{-3}) and medusa predation removed greater percentages (mean $\leq 4.2\% \text{ d}^{-1}$) of the larvacean populations in some regions. At some stations, predation of larvaceans was as great as $13\% \text{ d}^{-1}$. Regional means of total consumption showed that $\leq 0.3\% \text{ d}^{-1}$ of the copepod standing stock and $\leq 6.9\% \text{ d}^{-1}$ of the larvacean standing stock were consumed by the 3 species of medusae combined, with the greatest effects generally in the NE region (Table 8).

DISCUSSION

Zooplankton and jellyfish abundance

Zooplankton and large jellyfish (*Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*) populations showed regional and interannual variation in PWS. *C. capillata* and *A. aequorea* medusa populations were largest at the NE stations. Seine data for *A. labiata* showed that the population was much larger in 1998 than in 1999 (Table 3). Mean *A. labiata* biovolumes in

1999 were only 1% of those in 1998 and medusa densities in 1999 were 30% of those in 1998. The seine hauls in both years did not include any aggregations of *A. labiata*, because the samples could not be hauled on ship-board due to the great weight. The estimated biovolumes, densities and predation effects of *A. labiata* would be greater if aggregations could have been sampled. Aerial and acoustic observations of *A. labiata* aggregations concur with the seine data. Aerial surveys of PWS showed that in 1998, a larger number of aggregations (770) of *A. labiata* was observed (Brown et al. 1999) than previously reported for 1995, 1996 or 1997 (94, 493 or 28, respectively; Purcell et al. 2000). Only 2 *A. labiata* aggregations were encountered (not sampled) along the cruise track (1 to 19 July) in 1999, during which fish and jellyfish concentrations were continuously monitored.

The explanations for interannual differences in medusa populations are unknown, but may relate to differences in environmental conditions or prey abundance. (L. Haldorson et al. unpubl. data). Zooplankton populations at the same stations in PWS were larger in 1998 than in 1997 (Table 2), which was related to greater water column stability and shallower deep chlorophyll maximum in 1998 (L. Haldor-

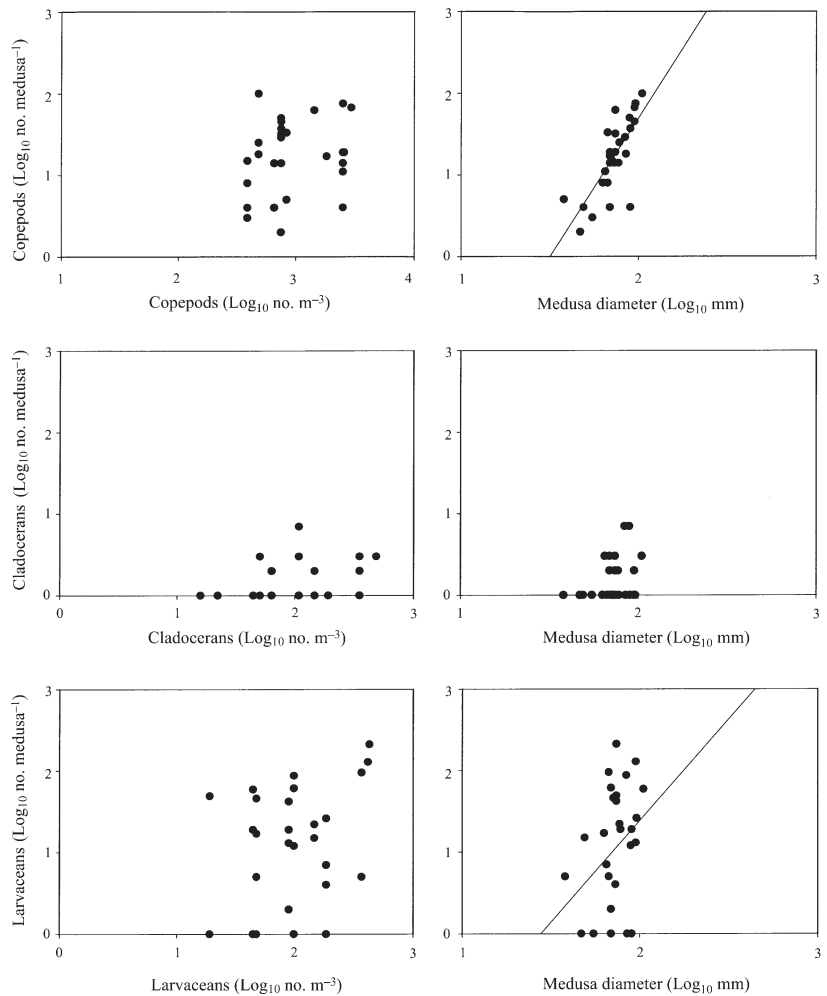


Fig. 4. *Aequorea aequorea*. Relationships of prey density and medusa diameter to the numbers of prey in the gut contents for small copepods, cladocerans and larvaceans in 1999. Multiple regression equations are in Table 5

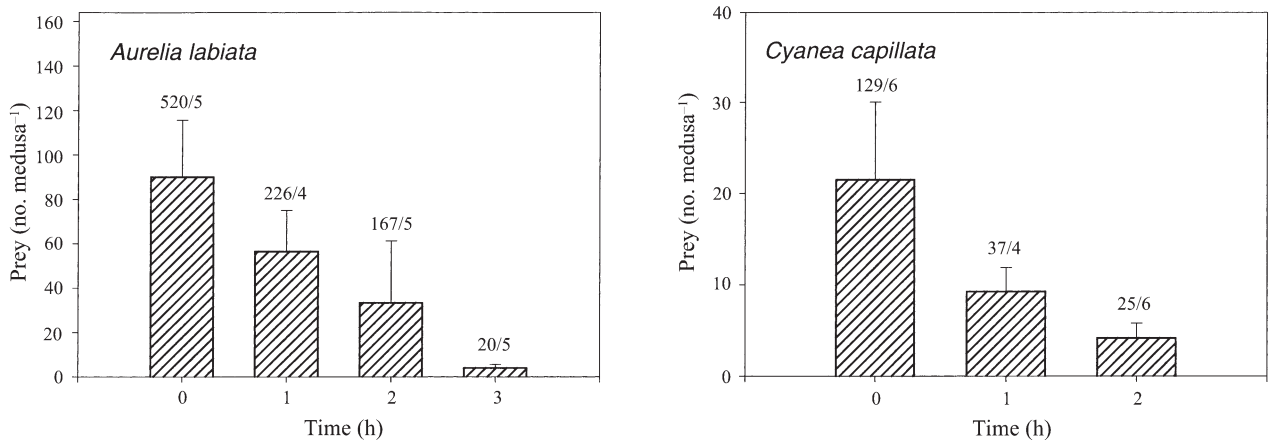


Fig. 5. *Aurelia labiata* and *Cyanea capillata*. Results of digestion experiments during July 1998. Crustacean prey (copepods and cladocerans) ingested *in situ* disappeared from the gut contents over time. Numbers of prey items/numbers of jellyfish at each time interval appear above the SE bars

Table 6. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Prey consumption (numbers of prey medusa⁻¹ d⁻¹, percentages of prey consumed d⁻¹ and clearance rates) calculated directly from gut contents for each station averaged by region (northeast, central and southwest) in Prince William Sound, Alaska in July 1998 or 1999. Only regions and years when medusae were collected at most stations were used (see Table 1). Digestion times used for crustaceans were 4 h (*A. aequorea*), 3 h (*A. labiata*) and 2 h (*C. capillata*), and for larvae, 1.5 h for all predators. Mean medusa sizes for gut contents are in Table 4. Numbers are means ± SD

Predator, year Region	Copepods medusa ⁻¹ d ⁻¹	Cladocerans medusa ⁻¹ d ⁻¹	Larvaceans medusa ⁻¹ d ⁻¹	Copepods (% d ⁻¹)	Cladocerans (% d ⁻¹)	Larvaceans (% d ⁻¹)	Copepods (l cleared medusa ⁻¹ d ⁻¹)	Cladocerans (l cleared medusa ⁻¹ d ⁻¹)	Larvaceans (l cleared medusa ⁻¹ d ⁻¹)
<i>A. labiata</i> , 1998 Southwest	506 ± 252	634 ± 258	nd	0.05 ± 0.06	2.3 ± 2.7	nd	176 ± 98	8556 ± 2970	nd
<i>C. capillata</i> , 1998 Central	128 ± 77	91 ± 51	668 ± 555	0.01 ± 0.01	0.1 ± 0.2	0.8 ± 0.9	166 ± 145	2274 ± 4077	14 743 ± 16 560
<i>C. capillata</i> , 1999 Northeast	781 ± 738	156 ± 301	1241 ± 732	0.2 ± 0.1	0.2 ± 0.2	3.4 ± 2.9	641 ± 431	681 ± 639	15 500 ± 10 007
Central	509 ± 418	25 ± 1	2069 ± 1706	0.2 ± 0.2	0.3 ± 0.5	1.8 ± 2.0	360 ± 312	950 ± 1852	4378 ± 4607
Southwest	1066 ± 823	31 ± 30	302 ± 463	0.1 ± 0.2	0.04 ± 0.05	1.0 ± 2.1	442 ± 452	161 ± 216	4392 ± 5966
<i>A. aequorea</i> , 1999 Northeast	140 ± 82	7 ± 7	397 ± 238	0.3 ± 0.4	0.05 ± 0.07	8.3 ± 8.2	191 ± 190	54 ± 67	5892 ± 6681

son et al. unpubl. data). Unfortunately, no seine sets were made for large jellyfish abundance in 1997. However, aerial surveys of PWS showed that aggregations of *Aurelia labiata* were much more numerous in 1998 (770) than in 1997 (28; Brown et al. 1999, Purcell et al. 2000), possibly reflecting prey availability. Zooplankton populations were very similar during sampling in 1998 and 1999, suggesting that factors other than food were responsible for the differences in medusa population size in those years. Climatic factors have been previously shown to affect scyphomedusa and ctenophore population sizes in the Mediterranean Sea (Goy et al. 1989), in Chesapeake Bay (Cargo & King 1990, Purcell et al. 1999), in the Bering Sea (Brodeur et al. 1999) and in Narragansett Bay (Sullivan et al. 2001). Effects of environmental conditions, such as temperature and salinity, on medusa production rates and timing can be direct (Purcell et al. 1999, X. Ma & J. E. Purcell unpubl. data) or indirect by affecting by the prey populations.

Numerous quantitative estimates of *Aurelia aurita* medusa populations exist. *A. aurita* medusa biomass and densities in restricted or eutrophic bodies of water were much greater (maxima of 20 to 70 ml m⁻³ and 1.5 to 300 medusae m⁻³; Möller 1980, Papathanassiou et al. 1987, Lucas & Williams 1994, Olesen et al. 1994, Berstad et al. 1995, Omori et al. 1995, Ishii & Båmstedt 1998) than measured in PWS for *Aurelia labiata* (maxima of 2.4 ml m⁻³ and 0.01 medusae m⁻³). It is important to emphasize that aggregations of *A. labiata* were avoided in sampling in PWS; therefore, their abundance was underestimated, especially in 1998. Aggregations were most common at the heads of the inlets in PWS. Densities of *A. aurita* in aggregations were estimated at 13.4 medusae m⁻³ in a Japanese inlet (Toyokawa et al. 1997). Numbers of medusae in the aggregations could be estimated through combined sampling for aggregation abundance (aerial), aggregation volume (acoustics or video) and medusa density (net sampling or video).

There are few abundance data for *Cyanea capillata* or *Aequorea* spp. medusae. *C. capillata* were dispersed in PWS, with greater numbers and biomass in the inlets than in open water. The densities of *C. capillata* measured in PWS (<4 medusae 1000 m⁻³) were lower than those reported in semi-enclosed bays (Fancett & Jenkins 1988, Berstad et al. 1995). Sampling in a small bay on Vancouver Island, British Columbia, Canada showed 1000-fold variation among 5 yr in the densities of *Aequorea victoria* (Purcell & Arai 2001). Densities there typically were 1 to 500 medusae 1000 m⁻³ and were often higher than *A. aequorea* densities in PWS (<20 medusae 1000 m⁻³), with densities as great as 1 to 5 medusae m⁻³ in 1 yr. Shipboard surface counts off Namibia gave densities of <2 medusae 1000 m⁻²

Table 7. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Feeding rates (number of prey eaten medusa⁻¹ d⁻¹), densities of copepods and larvaceans (number m⁻³), and estimates of the percentages of prey standing stock removed daily during July and August from 3 different regions (northeast, central and southwest, NE, C and SE, respectively) in Prince William Sound, Alaska. Feeding rates were calculated from the regressions in Table 5, divided by the digestion times and multiplied by 24 h, assuming constant feeding. Digestion times used were 4 h (*A. aequorea*), 3 h (*A. labiata*) and 2 h (*C. capillata*) for copepods, and 1.5 h for all predators for larvaceans. Medusa densities are in Table 3. *A. labiata* data do not include aggregations, and so are underestimates. Data are presented as means \pm SD. Calculations were not made for *A. labiata* in 1999, due to low frequency of occurrence

Predator Year, region	Medusa diameter (mm)	Prey density (no. m ⁻³)		Prey standing stock consumed (% d ⁻¹)	
		Copepods	Larvaceans	Copepods	Larvaceans
<i>A. labiata</i>					
1998, NE	134 \pm 25	940.4 \pm 612.0	131.2 \pm 182.2	0.001 \pm 0.002	0.06 \pm 0.08
1998, C	146 \pm 25	1279.2 \pm 900.4	57.8 \pm 27.2	0.08 \pm 0.2	0.3 \pm 0.5
1998, SW	146 \pm 17	2963.9 \pm 1425.0	13.8 \pm 9.0	0.01 \pm 0.01	1.4 \pm 1.6
<i>C. capillata</i>					
1998, NE	181 \pm 29	940.4 \pm 612.0	131.2 \pm 182.2	0.03 \pm 0.02	1.9 \pm 1.9
1998, C	149 \pm 37	1279.2 \pm 900.4	57.8 \pm 27.2	0.02 \pm 0.1	0.9 \pm 0.8
1998, SW	104 \pm 17	2963.9 \pm 1425.0	13.8 \pm 9.0	0.03 \pm 0.01	1.8 \pm 1.0
1999, NE	127 \pm 23	1412.9 \pm 1235.1	98.7 \pm 54.3	0.11 \pm 0.06	4.2 \pm 2.3
1999, C	94 \pm 8	1441.2 \pm 357.7	357.7 \pm 36.2	0.04 \pm 0.02	1.3 \pm 1.1
1999, SW	73 \pm 8	3153.2 \pm 2648.8	42.0 \pm 47.7	0.03 \pm 0.05	2.3 \pm 3.9
<i>A. aequorea</i>					
1998, NE	47 \pm 6	940.4 \pm 612.0	131.2 \pm 182.2	0.06 \pm 0.06	1.9 \pm 2.2
1998, C	63 \pm 9	1279.2 \pm 900.4	57.8 \pm 27.2	0.04 \pm 0.03	0.9 \pm 0.5
1998, SW	62 \pm 7	2963.9 \pm 1425.0	13.8 \pm 9.0	0.01 \pm 0.005	0.9 \pm 0.3
1999, NE	67 \pm 12	1412.9 \pm 1235.1	98.7 \pm 54.3	0.2 \pm 0.3	2.7 \pm 3.0
1999, C	58 \pm 7	1441.2 \pm 357.7	357.7 \pm 36.2	0.01 \pm 0.01	0.1 \pm 0.2
1999, SW	58 \pm 7	3153.2 \pm 2648.8	42.0 \pm 47.7	0.001 \pm 0.002	0.1 \pm 0.1

(Sparks et al. 2001), but peak medusa abundance is generally deep. Biomass estimates of *A. aequorea* off Namibia were higher (2 to 7 ml m⁻³, Fearon et al. 1992) than in PWS (\leq 0.6 ml m⁻³).

Predation estimates of jellyfish eating zooplankton

The diets of *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea* are similar to diets previously reported for *A. aurita*, *C. capillata* and *A. victoria*, respectively, which contained a variety of holo- and merozooplankton (Fancett 1988, Brewer 1989, Purcell 1989, Sullivan et al. 1994, Behrends & Schneider 1995, Graham & Kroutil 2001, Ishii & Tanaka 2001). The 3 genera are known to eat ichthyoplankton and can remove substantial percentages of available fish eggs or larvae. In years of great medusa abundance, both *A. aurita* and *A. victoria* medusae appeared to have dramatically reduced herring larva populations (Möller 1980, Purcell & Grover 1990). The plankton sampling in PWS did not filter sufficient volumes of water to determine ichthyoplankton densities *in situ*; however, few fish eggs and larvae were in the samples and few were found in the medusa gut contents.

One species of jellyfish (*Aurelia labiata*) consumed predominantly hard-bodied prey (crustaceans and bivalve veligers) and 2 species (*Cyanea capillata* and

Aequorea aequorea) consumed many soft-bodied larvaceans in addition to crustaceans and veligers. This pattern is reflected by prey selection indices. Selection was positive for small copepods only by *A. labiata* and was strongly positive for cladocerans by *A. labiata* and *C. capillata*; selection for larvaceans was strongly positive by *C. capillata* and weakly positive by *A. aequorea* (Purcell & Sturdevant 2001). Those results were consistent with selection analyses for congeners (Fancett 1988, Purcell 1989, Sullivan et al. 1994, Costello & Colin 2002). Possible explanations for such dietary differences include medusa and tentacle morphology and

Table 8. *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*. Prey consumption (% consumed d⁻¹) calculated from multiple regressions (Table 5) for 3 species of large medusae combined and averaged (\pm SD) by region in Prince William Sound, Alaska in 1998 and 1999. *A. labiata* is not included in 1999 due to very low densities

Year, region	Copepods (% consumed d ⁻¹)	Larvaceans (% consumed d ⁻¹)
1998, NE	0.1 \pm 0.1	3.9 \pm 3.9
1998, C	0.1 \pm 0.2	2.0 \pm 1.4
1998, SW	0.05 \pm 0.02	4.0 \pm 2.2
1999, NE	0.3 \pm 0.3	6.9 \pm 3.9
1999, C	0.05 \pm 0.02	1.4 \pm 1.2
1999, SW	0.04 \pm 0.05	2.4 \pm 3.9

nematocyst composition (reviewed in Purcell 1997). Swimming-generated flow at the bell margin of *C. capillata* is approximately twice that of *A. aurita* for any given medusa size (J. Costello pers. comm.) and would not seem to explain the much greater difference between species in larvacean feeding because flows of both species exceed the speeds of larvaceans in houses and are much less than the speeds of free-swimming larvaceans, leading to the expectation of similar capture rates by both medusae. Differences in nematocyst composition are correlated with prey types ('soft-' vs 'hard-bodied') eaten by siphonophores and hydromedusae (Purcell 1984, Purcell & Mills 1988). Comparisons of nematocysts of medusae from PWS showed that tentacles and oral arms of *A. labiata* contained predominantly euryteles (54 to 87%), but that those of *C. capillata* contained mostly isorhizas (56 to 100%; unpubl. data). The nematocysts of *A. victoria* also were predominantly isorhizas (Purcell & Mills 1988). Thus, isorhizas predominate in species that feed heavily on larvaceans, as well as in other species that eat fish larvae and gelatinous prey (Purcell 1984, Purcell & Mills 1988).

The numbers of prey eaten by *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea* medusae increased with increasing medusa diameter and prey density. Similar results have been reported previously. Significant correlations of feeding with medusa size and prey densities were reported for *Chrysaora quinquecirrha* medusae feeding on copepods and on fish eggs (Purcell et al. 1994a,b). Graham & Kroutil (2001) found increasing prey in gut contents with diameter over a broad size range of *Aurelia aurita* (50 to 350 mm) from the Gulf of Mexico. No trend in ingestion rate with *A. aurita* medusa diameter (55 to 85 mm) was found at high prey densities in 90 l tanks; however, there was a clear effect of diameter on feeding by *C. capillata* (Båmstedt et al. 1994).

Medusa feeding rates vary among these studies, depending at least in part, on prey densities. *Aurelia aurita* medusae >45 mm diameter ate 2000 to 3500 prey medusa⁻¹ d⁻¹ at 100 prey l⁻¹ in the laboratory (Båmstedt 1990), which is similar to the consumption rates observed in PWS, albeit at much lower prey densities. This and the lack of a trend in ingestion with medusa size suggest that feeding by *A. aurita* medusae was saturated at high prey densities in laboratory containers. The regression of Graham & Kroutil (2001) for *A. aurita* in the Gulf of Mexico indicated that a medusa of the average size collected in PWS in 1998 (134 to 146 mm, Table 7) would contain only 75 to 80 prey; however, the gut contents of *A. labiata* of that size in PWS contained an average of 460 prey (Table 4). The small numbers of prey found in medusa gut contents from the Gulf of Mexico could be due to lower prey

densities (333 µm mesh, mean 332 zooplankton m⁻³) than in PWS (243 µm mesh, mean 2397 zooplankton m⁻³), and more rapid digestion in the warmer temperatures in the Gulf (>25°C) than in PWS (14°C). Results in Båmstedt et al. (1994) predict that a 75 to 80 mm diameter *Cyanea capillata* medusa feeding at their experimental prey density (25 prey l⁻¹) would consume 4764 zooplankton daily, which is more than twice the feeding rate calculated using the equations for copepods in Table 5 for the same medusa diameter and prey density.

The digestion times measured here on *Aurelia labiata* and *Cyanea capillata* agree with those measured for *A. aurita* medusae 4.5 to 13.5 mm in diameter, which digested small copepods in 3 to 4 h at 15°C, and for *C. capillata* medusae 37 to 106 mm in diameter, which digested small copepods in 1.5 to 2 h at 9.5°C (Martinussen & Båmstedt 1999). Both Dawson & Martin (2001) and Ishii & Tanaka (2001) reported digestion of very small copepods (*Oithona* spp.) of <1 h at 22 to 30°C. Digestion by jellyfish is more rapid at higher temperatures. Temperature has the greatest effect on jellyfish digestion rates, with jellyfish size and prey number having small effects (Purcell 1992, 1997, Martinussen & Båmstedt 1999, Ishii & Tanaka 2001). Martinussen & Båmstedt (1999) found great individual variability in digestion times for *A. aurita*. However, they concluded that the average digestion time in a physically and nutritionally stable environment is robust.

Most larvaceans disappeared from the gut contents during the first sampling interval (1 h) for both *Aurelia aurita* and *Cyanea capillata*. More precise measurements on the times required for digestion of larvaceans would be desirable. The only previous data indicate that the scyphomedusa *Stomolophus meleagris* required 1.5 h to digest larvaceans (Larson 1991). No direct measurements were possible for digestion by *Aequorea aequorea* medusae in this study, due to their tendency to purge their gut contents when disturbed. I used conservative digestion times estimated from previous results, but those rates should be interpreted only as approximations.

Weight-specific feeding rates (prey consumed g wet weight [WW]⁻¹ d⁻¹) and clearance rates (l cleared g WW⁻¹ d⁻¹) were similar among species of large medusae (scyphomedusae and the hydromedusan, *Aequorea aequorea*; Table 9). Feeding rates and clearance rates on copepods generally were under 10. Large *Cyanea capillata* medusae had greater rates. The high feeding rates of *Chrysaora quinquecirrha* were due to the great copepod densities in Chesapeake Bay (9841 ± 9484 m⁻³, Purcell 1992). A similar pattern was observed for cladocerans, except that *Aurelia labiata* had higher feeding and clearance rates

Table 9. Comparisons of size-specific (adjusted for wet weight, WW) feeding rates (prey consumed g WW⁻¹ d⁻¹) and clearance rates (l cleared g WW⁻¹ d⁻¹) on zooplankton prey determined from *in situ* data for large medusae. All species are scyphomedusae, except *Aequorea aequorea*. Numbers are means \pm SD, except for *Cyanea capillata*, which are ranges. Copepods are calanoid species

Predator	Diameter (mm)	WW (g)	Temperature (°C)	Prey	Feeding rate	Clearance rate	Source
<i>Aurelia labiata</i>	106	54	14	Copepods	9 \pm 5	3 \pm 2	This study
<i>Cyanea capillata</i>	75–81	26–34	14	Cladocerans	12 \pm 5	158 \pm 55	This study
				Copepods	5–31	6–19	
				Cladocerans	1–5	6–67	
<i>Chrysaora quinquecirrha</i>	40	5	25	Larvaceans	11–61	165–457	Purcell (1992)
				Copepods	90 \pm 48	3	
<i>Stomolophus meleagris</i>	55 ^a	110	28	Copepods	4	0.4	Larson (1991)
				Larvaceans	7	7	
<i>Aequorea aequorea</i>	73	31.5	14	Copepods	4 \pm 3	6 \pm 6	This study
				Cladocerans	0.2 \pm 0.2	2 \pm 2	
				Larvaceans	13 \pm 8	187 \pm 212	

^aBell height

than did the other species. Feeding and clearance rates on larvaceans by medusae were 10- and 100-times greater than for crustacean prey, except for *Stomolophus meleagris*, which had more similar rates for both prey types. Such comparisons illustrate that clearance rates for any medusa species differ greatly among different prey types (reviewed in Purcell 1997). Fancett & Jenkins (1988) showed similar clearance rates measured in 25 l containers for *C. capillata* 75 mm in diameter, but lower rates for 80 mm specimens than in the present study. The work of Martinussen & Båmstedt (1995) was not included in these comparisons because their plankton and gut content samples were from different locations, and rates were presented for all zooplankton types combined.

The predation estimates calculated directly from gut contents (Table 6) were quite similar to those estimated from the multiple regressions (Table 7). The multiple regressions allow rough estimates of predation effects when only data on medusa diameter and prey density are available, but estimates from gut contents are preferable. Although there was great variability in the gut content data and weaknesses in both methods, both types of predation estimates led to the same conclusion, specifically, that large medusae consumed small percentages of copepod standing stocks. Fancett & Jenkins (1988) also estimated low predation effects (average $\leq 0.3\%$ d⁻¹, maximum 1.6% d⁻¹) by *Cyanea capillata* at densities of 70 medusae 1000 m⁻³ in Port Philip Bay. It is likely that such rates do not seriously affect the copepod populations. Predation on larvaceans in PWS was considerably greater, up to 13% d⁻¹ at some stations. Even though larvaceans generally have a faster production rate than copepods (Sato et al. 1999 and references therein) and their production rate in PWS is unknown, it is possible that medusa predation may limit larvacean populations at times. Preda-

tion effects of medusae generally were greatest in the NE region of PWS, where medusae were most abundant. Greater overall predation effects did not accompany the markedly larger medusa biomass in 1998, perhaps because the small *Aurelia labiata* population in 1999 was offset by a large *C. capillata* population.

Consumption of zooplankton was underestimated in this study because predation by *Aurelia labiata* medusae in aggregations and by small hydromedusae was not included. Predation by the thousands of *A. labiata* medusae in numerous aggregations (770) in 1998 would have increased estimates, especially in the inlets of PWS. By contrast, small hydromedusae occurred in low numbers in 1998 (mean 5 m⁻³), but in great numbers in 1999 (mean 60 m⁻³; Table 10). The predominant species were *Euphysa* sp., *Clytia gregaria* (*Phialidium gregarium*), *Proboscoidactyla flavicirrata* and *Aglantha digitale*. Several other species occurred less abundantly, including *Sarsia* spp., *Hali-tholus* sp., *Catablema nodulosa*, *Obelia* sp., *Melicer-tum octocostatum*, *Leukartiara* sp., *Eperetmus typus*, *Aegina citrea* and *Eutonina indicans*. These predators are utilizing the same prey populations (Purcell & Mills 1988) as the large medusae (Table 2). Although

Table 10. Densities of small hydromedusae at 24 stations in Prince William Sound (PWS), Alaska. Hydromedusae were sampled along with zooplankton, and were counted from whole samples. Numbers are means \pm SD

Region	Hydromedusa density (no. m ⁻³)	
	14–20 July 1998	1–6 July 1999
Northeast	10.4 \pm 5.6	53.4 \pm 57.5
Central	1.4 \pm 0.9	8.5 \pm 5.5
Southwest	1.7 \pm 2.0	108.2 \pm 76.1
PWS overall	4.6 \pm 5.2	58.6 \pm 114.4

no prey consumption data were collected for these species in PWS, based on other studies (Larson 1987, Purcell & Mills 1988, Costello & Colin 2002), it is reasonable to speculate that hydromedusae may have been important consumers of zooplankton in July 1999. Therefore, predation effects of gelatinous species were underestimated in both 1998 and 1999.

This research presents one component of the information necessary to determine if zooplanktivorous fish and jellyfish were competing for food in PWS. Small copepods were the main prey of Age 0 herring, sand lance and walleye pollock, and larvaceans were the predominant prey of Age 0 pink salmon during summer in PWS, and dietary overlaps between fish and gelatinous species averaged 63% among the crustacean-eaters and 66% among the larvacean-eaters (Purcell & Sturdevant 2001). My results suggest that large medusae removed small percentages of the copepod populations and moderate percentages of the larvacean populations during summer in PWS. The possibility for competition may be greatest among the larvacean predators, *Cyanea capillata* and *Aequorea aequorea* medusae and pink salmon, because the larvacean populations were only 5 to 10% of the copepod populations. Of course, many more fish and invertebrate species also eat copepods and larvaceans (reviewed in Purcell et al. in press). Analyses of fish biomass, consumption rates and condition as well as prey production rates are necessary to further address the difficult question of competition for food among fish and jellyfish.

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