Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska

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ABSTRACT: The potential for competition for food among zooplanktivorous species of gelatinous zooplankton and fishes has been the subject of much speculation. Here, we evaluate the dietary overlaps among 2 scyphomedusan species, *Aurelia labiata* and *Cyanea capillata*, 1 ctenophore species, *Pleurobrachia bachei*, 1 hydromedusan species, *Aequorea aequorea* var. *albida*, and juveniles (Age-0) of 4 forage fish species, walleye pollock *Theragra chalcogramma*, Pacific sandlance *Ammodytes hexapterus*, Pacific herring *Clupea pallasi*, and pink salmon *Oncorhynchus gorbuscha*. Zooplankton samples collected in July–August 1995 to 1998 showed great similarity among years (86 to 96%), which allowed valid dietary comparisons between pelagic coelenterates and fishes collected in different years during that period. The predators fell into 2 groups, one that ate primarily crustacean prey (*A. labiata*, *P. bachei*, juvenile walleye pollock, sandlance, and herring), and another that ate mostly larvaceans (*C. capillata*, *A. aequorea*, and juvenile pink salmon). Species within the first group showed significant positive selection for crustacean prey and significant negative selection for larvaceans. The opposite trends were observed in the second group. Dietary overlaps were higher among crustacean-eating species (63 ± 13%) and larvacean-eating species (66 ± 10%) than when comparing crustacean- with larvacean-eating species (24 ± 14%). Dietary overlaps among pelagic coelenterate species (41 ± 21%) and among fish species (42 ± 25%) were similar, while overlaps between pelagic coelenterate and fish species averaged 50 ± 21%. These pelagic coelenterate and fish species were collected together in 45 purse seine sets taken in Prince William Sound in July 1999. We conclude that the diets of pelagic coelenterate and forage fish species overlap substantially, and that the species co-occur spatially and temporally. Therefore, the potential for competition for prey exists for these zooplanktivores in Prince William Sound.

KEY WORDS: *Aurelia* · Competition · Ctenophore · *Cyanea* · Herring · Pollock · Salmon · Sandlance · Zooplankton

INTRODUCTION

The relationships of jellyfish and ctenophores (grouped here as 'pelagic coelenterates') with fishes have

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been of particular interest because of the potential effects on commercially important fisheries. These interactions include predation on ichthyoplankton by pelagic coelenterates (reviewed by Purcell 1985, 1997, Arai 1988, Purcell & Arai 2001), potential competition for prey between pelagic coelenterates, zooplanktivorous fishes and fish larvae (reviewed by Arai 1988, Purcell & Arai 2001), predation by fishes on pelagic coe-

lenterates (reviewed by Arai 1988, Ates 1988, Harbison 1993, Purcell & Arai 2001), pelagic coelenterates as intermediate hosts of fish parasites (reviewed by Arai 1988, Purcell & Arai 2001), and commensal associations between fishes and medusae (reviewed in Mansueti 1963, Purcell & Arai 2001). Generally, the importance of these interactions to fish or pelagic coelenterate populations is unknown.

Although several authors have speculated on the potential importance of competition among zooplanktivorous pelagic coelenterates and fishes (e.g. Möller 1980, van der Veer 1985, Arai 1988, Bailey & Houde 1989, Shiganova 1998), virtually no direct comparisons of diet and co-occurrence have been made. Although 2 recent studies reached different conclusions, any results probably would be specific to a particular situation. Purcell & Grover (1990) directly compared the diets of post-yolksac herring with those of 7 co-occurring medusa species. The prey of larval herring (copepod nauplii and eggs, shelled protozoans, and bivalve veligers) were abundant (41 l^{-1}) in the environment, and predation on those prey by the gelatinous species was estimated to be only 0.2% d^{-1} of the standing stocks. The authors concluded that competition among the fish larvae and pelagic coelenterates was not occurring at that time. Vinogradov et al. (1996) estimated the consumption of mesozooplankon by the ctenophore *Mnemiopsis leidyi* and zooplanktivorous fishes (European anchovy *Engraulis encrasicolus*, European sprat *Sprattus sprattus*, and Mediterranean horse mackerel *Trachurus mediterraneus*) 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. Competition for food among the ctenophores and fishes was inferred.

The diets of various jellyfish species have been quantified in recent years, and prey selection has been determined for some species. Among hydromedusae, groups of species have similar diets—a group that eats hard-bodied prey, such as crustaceans (most anthomedusae other than pandeids, trachymedusae), a second group that eats soft-bodied prey, such as other gelatinous organisms (narcomedusae, pandeid anthomedusae), and a third that eats both hard- and soft-bodied prey (leptomedusae, including *Aequorea* spp.) (Purcell & Mills 1988, Purcell 1997). The diets of fewer species of scyphomedusae have been examined. These include *Pelagia noctiluca*, *Pseudorhiza haeckeli*, *Cyanea capillata*, *Chrysaora quinquecirrha*, *Stomolophus meleagris*, and *Aurelia aurita*, which all consume a mixture of hard- and soft-bodied prey (Malej 1982, Fancett 1988, Brewer 1989, Larson 1991, Purcell 1992, Sullivan et al. 1994). Studies of prey selection by jellyfish, defined as the consumption of prey types in dispropor-

tion to their abundance in the environments, illustrated that *C. capillata*, *C. quinquecirrha*, and *Aequorea victoria* show positive selection for ichthyoplankton (Fancett 1988, Purcell 1989, Purcell et al. 1994), but that those species and *A. aurita* show negative selection for copepods (Fancett 1988, Purcell 1989, Purcell et al. 1994, Sullivan et al. 1994).

Forage fishes, are small, schooling, zooplanktivorous fishes that form a critical trophic link between zooplankton and vertebrate consumers (Springer & Speckman 1997). The diets of commercially important forage fishes, such as juvenile walleye pollock *Theragra chalcogramma*, Pacific herring *Clupea pallasi*, and pink salmon *Oncorhynchus gorbuscha*, have been examined for many locations and life stages. Diets of noncommercial forage species, such as Pacific sandlance *Ammodytes hexapterus*, are less well-known. All these species feed principally in the water column on zooplankton despite widely different life-history strategies and periods of nearshore residence in shallow water. Calanoid copepods are universally important prey (e.g. Manzer 1969, Kamba 1977, Field 1988, Coyle & Paul 1992), with different species selected in different areas by the same predators. The fish generally and gradually select larger prey with growth and sometimes a change in habitat. A wide variety of mesozooplankton, macrozooplankton and nekton is consumed by juveniles during the spring and summer, including, occasionally, fish larvae; piscivory becomes more common among the larger juveniles and adults (e.g. Juanes 1994, Landingham et al. 1998, Mittelbach & Persson 1998, Persson & Hansson 1999, Willette et al. 1999).

Prince William Sound (PWS) 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 m^2 and having 3200 km of shoreline (Grant & Higgens 1910) (Fig. 1). Many of the marine birds and mammals whose populations were injured by the oil spill feed on forage fishes, including the species mentioned above, as well as the capelin *Mallotus villosus*. The research presented here is part of the multi-investigator project, Alaska Predator Ecosystem eXperiment (APEX). PWS was surveyed to examine forage fish distribution and abundance along transects using acoustics and aerial mapping, with seining, trawling and underwater video for target verification. Additionally, the diets of forage fishes and pelagic coelenterates, and the abundance of their zooplankton prey were quantified (Sturdevant et al. 1997, 1998, Purcell 1999). A goal of the APEX project is to determine if the zooplankton foods available to forage fishes is limiting their populations and thereby inhibiting the recovery of piscivorous marine bird and mammal populations injured by the oil spill.

Dietary overlap among the pelagic coelenterates and juveniles of zooplanktivorous fish species that we consider here (the scyphomedusae *Aurelia labiata* and *Cyanea capillata*, the ctenophore *Pleurobrachia bachei*, the hydromedusan *Aequorea aequorea* var. *albida*, and Age-0 walleye pollock, Pacific sandlance, Pacific herring, and pink salmon) is potentially of broad ecological importance. Species in the gelatinous genera *Aurelia*, *Pleurobrachia*, *Cyanea*, and *Aequorea* often occur in great abundance in the world's oceans (e.g. Hirota 1974, van der Veer 1985, Fancett 1988, Purcell & Grover 1990, Båmstedt et al. 1997, Dawson & Martin 2001, Purcell et al. 2001, Sparks et al. 2001). Walleye pollock, Pacific herring and pink salmon are highly abundant fish species that support important commercial fisheries in various areas of the North Pacific Ocean; similarly, species of sandlance and herring are fished in several northern oceans (FAO 1999a,b, National Marine Fisheries Service 1999). Fisheries researchers are particularly interested in biological processes, such as trophic interactions, that occur in the early life history of these fishes and that affect their abundance and recruitment to multi-billion-dollar fisheries. In the present study, we present zooplankton data and dietary data for these species during summer in PWS, as well as examine prey selection by each coelenterate and fish species and dietary overlap among

all the species. We then discuss the potential for competition among pelagic coelenterates and fishes for zooplankton prey in PWS.

MATERIALS AND METHODS

Sampling locations and dates. Three regions in PWS were established (northeast, central, southwest) (Fig. 1). Sampling for fishes and zooplankton occurred in daylight; schools were located and successfully sampled in 1995 and 1996. In 1997 and 1998, 4 stations were selected to represent each region. Sampling for pelagic coelenterates and zooplankton occurred in both daylight and darkness in 1997 and 1998. Sampling dates were 26 July to 10 August 1995, 16 to 28 July 1996, 29 July to 8 August 1997, and 14 to 20 July 1998. During fish sampling in 1995, interest in jellyfish developed due to obervations that they often were abundant in trawl catches, and large aggregations of jellyfish were observed by sea and air (Purcell et al. 2001). Fish dietary sampling was completed before funding for jellyfish was instated, which resulted in fishes and pelagic coelenterates being sampled in different years.

Zooplankton. Zooplankton was sampled during the day at the same times and locations that predators were
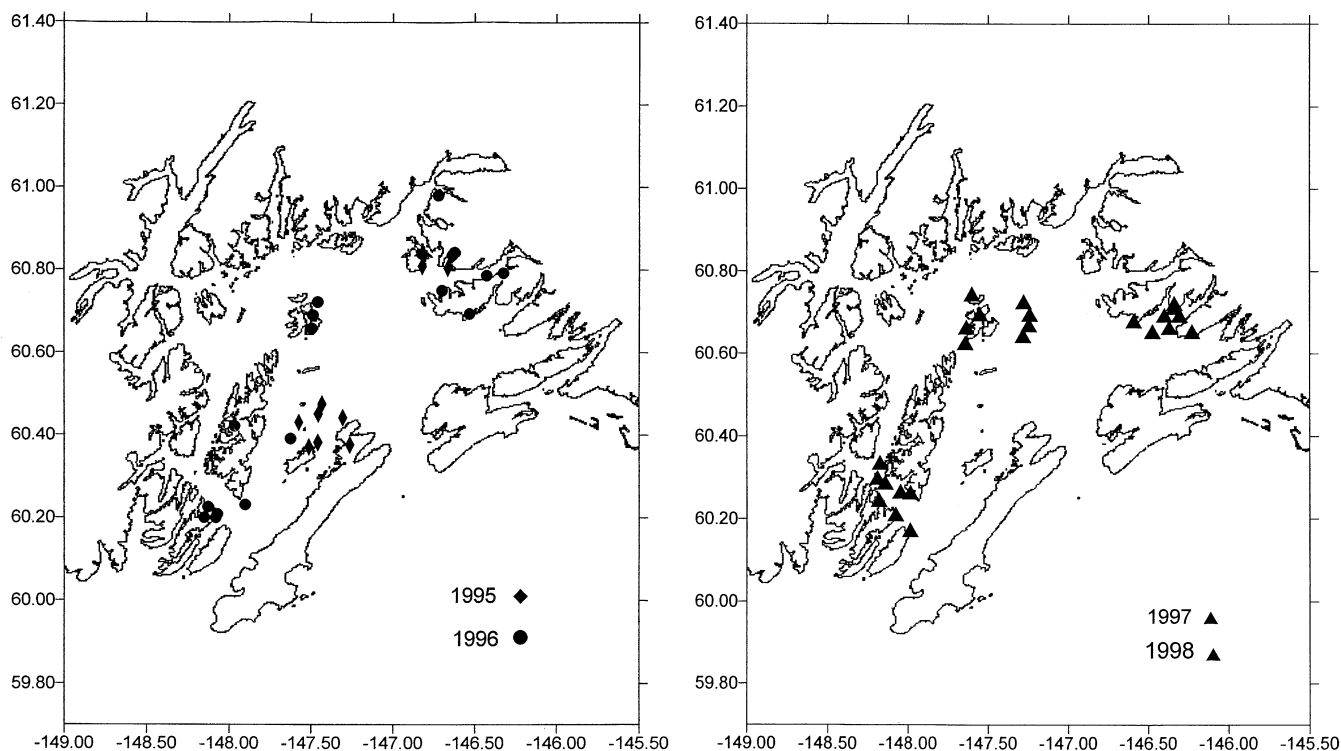

Fig. 1. Prince William Sound (PWS), south-central Alaska, USA. Locations of sampling stations for fishes and zooplankton in 1995 and 1996, and for pelagic coelenterates and zooplankton in 1997 and 1998

collected for gut-content analysis in 1995 to 1998. Zooplankton samples were collected in vertical tows of plankton nets of 243 µm mesh (from 20 m depth using a 0.5 m diameter Norpac net in 1995 and 1996, and from 60 m using a 0.2 m diameter bongo net in 1997 and 1998). Additional zooplankton samples from 1995 taken with a 303 µm mesh Norpac net were used only for calculation of juvenile walleye pollock prey selection, because no 243 µm mesh samples were available at those stations. Zooplankton percent composition did not differ among 243 and 303 µm mesh samples (Sturdevant & Willette 1999); therefore, calculations should not have been affected. Samples were preserved in 5% formalin solution. In the laboratory, the samples were split using a Folsom plankton splitter, and organisms were identified to general taxon and counted with the aid of a dissecting microscope. Large calanoid copepods were defined as those >2.5 mm total length (TL); cyclopoid copepods were pooled with small calanoids, defined as those ≤2.5 mm TL. Numbers of each taxon were standardized to 1 m^3 water volume, and grouped by general taxon. Minor components (primarily bivalve veligers and invertebrate eggs) were grouped as 'other'.

Pelagic coelenterates. Pelagic coelenterates for gut-content analysis were dipped from near surface with a net on a 3.7 m pole. They were immediately preserved individually in 5% formalin solution made from 32 µm filtered seawater. The pelagic coelenterates were dissected in the laboratory and all tissue and liquid examined for prey organisms, which were identified to general taxon as above.

Fishes. Forage fishes were collected during population surveys in PWS during 1995 and 1996, using fishing gear that was operated from chartered commercial fishing vessels (trawl and purse seine) and a 5 m (16′) skiff (beach seine) (Haldorson et al. 1997, 1998, Sturdevant & Hulbert 2000, Sturdevant & Willette 1999). In 1995 and 1996, a midwater trawl (mouth opening 50 m^2, 5 to 1 cm mesh net with 0.3 cm liner and 500 µm mesh cod-end) was fished for 20 to 35 min per haul at 2.5 to 3.0 knots. In 1996, a purse seine (200 m long by 20 m deep, 25 mm stretch mesh) was fished in shallow water and a beach seine (37 m long, tapering from 5 m to 1.5 m deep, 20 mm to 10 mm stretch mesh) was fished on shore. Additional fish samples from surface aggregations were sampled with cast nets and dipnets. Subsamples of forage species were retained for diet studies by preserving 10 to 15 specimens in 10% buffered formalin-seawater solution in the field for later stomach analysis in the laboratory. After a minimum of 6 wk in formalin solution, fish samples were transferred to 50% isopropanol for ≥10 d before stomach analysis was performed. Ten specimens of each species and size class were measured (mm standard fork length, FL; mg wet weight) per haul. Stomachs

were excised, weighed and the contents removed. For this study, prey organisms were identified to general taxon and enumerated (see Sturdevant & Hulbert 2000, Sturdevant & Willette 1999).

Analyses. Zooplankton taxa in numbers m^{-3} were averaged among stations within each region and across regions for each year, and the percentages of the taxa were calculated from the means. Gut-content data (numbers of each prey taxon predator^{-1}) were averaged for each predator species among stations for each year, and percentages were calculated from the means. Then Schoener's (1974) percent similarity index (PSI) was used to compare zooplankton among regions each year, and among years, and the prey consumed among pelagic coelenterates and fish species. PSI is computed by summing the minimum percentages of all taxa shared between 2 species or years:

$$\text{PSI}_{jk} \;=\; 1 - 0.5\left(\sum |P_{ij} - P_{ik}|\right)$$

where P is the numerical proportion of the ith prey taxon in n taxonomic categories consumed by Species j and k, for example.

Pearre's (1982) electivity index, C, was used to test for significant predator selection from available zooplankton using chi-square analyses with 1 degree of freedom. Electivity indices were calculated for each predator species using data on the numbers of prey in the diets relative to those available in the plankton samples at each station:

$$\chi^2 \;=\; \frac{n(|a_d b_e - b_d a_e| - n/2)^{0.5}}{abcd}$$

where a is the number of individuals in species a and b is the number of individuals in all other taxa in the diet (subscripts d) and in the environment (subscripts e), respectively; $a = a_d + a_e$; $b = b_d + b_e$; $c = a_d + b_c$; and $d = a_c + b_e$; and $n = a + b + c + d$. This was repeated for each taxon of interest:

$$C \;=\; \pm(\chi^2 \div n)^{0.5}$$

We present the data as the percentages of significant (p < 0.05) electivity values relative to the total number of stations where zooplankton and dietary data were collected together for each predator species.

RESULTS

Zooplankton

Mean total zooplankton density in all regions of PWS ranged from 791 to 6117 organisms m^{-3} in the upper 20 to 60 m water column in all years of the study; however, for the purposes of the prey selection

and diet similarity analyses, the relative numerical composition of the suite of zooplankton taxa is critical, rather than abundance. The percentages of the various zooplankton taxa were very similar among regions and years (Fig. 2). The zooplankton samples were dominated by small calanoid and cyclopoid copepods, *Pseudocalanus* sp., *Oithona similis*, *Acartia* spp., and *Centropages abdominalis* (Sturdevant & Willette 1999), larvaceans, cladocerans, and bivalve larvae. Comparisons of the zooplankton (243 µm mesh) population compositions showed great similarity in each year among regions (northeast, central, southwest). PSI values averaged 85 ± 11% in 1995 to 1998 (Table 1). In 1998, the northeastern region was least similar compared with the other regions due to high densities of bivalve larvae. The high degree of similarity

Table 1. Percent similarity indices (PSI) comparing zooplankton population composition (243 µm mesh) by regions during summer in different years in Prince William Sound (PWS), Alaska. –: no data

Regions	PSI (%)			
	26 Jul–10 Aug 1995	16–28 Jul 1996	29 Jul–8 Aug 1997	14–20 Jul 1998
North vs Central	81.9	92.0	86.3	72.8
North vs South	–	92.0	95.4	60.7
Central vs South	–	96.8	88.7	87.7

among zooplankton samples allowed us to combine regions for further analyses. Zooplankton composition was very similar among years when regions were combined, with PSI values averaging 90.3 ± 3.6% (Table 2), which allowed us to make valid comparisons among fish and pelagic coelenterate diets from different years.
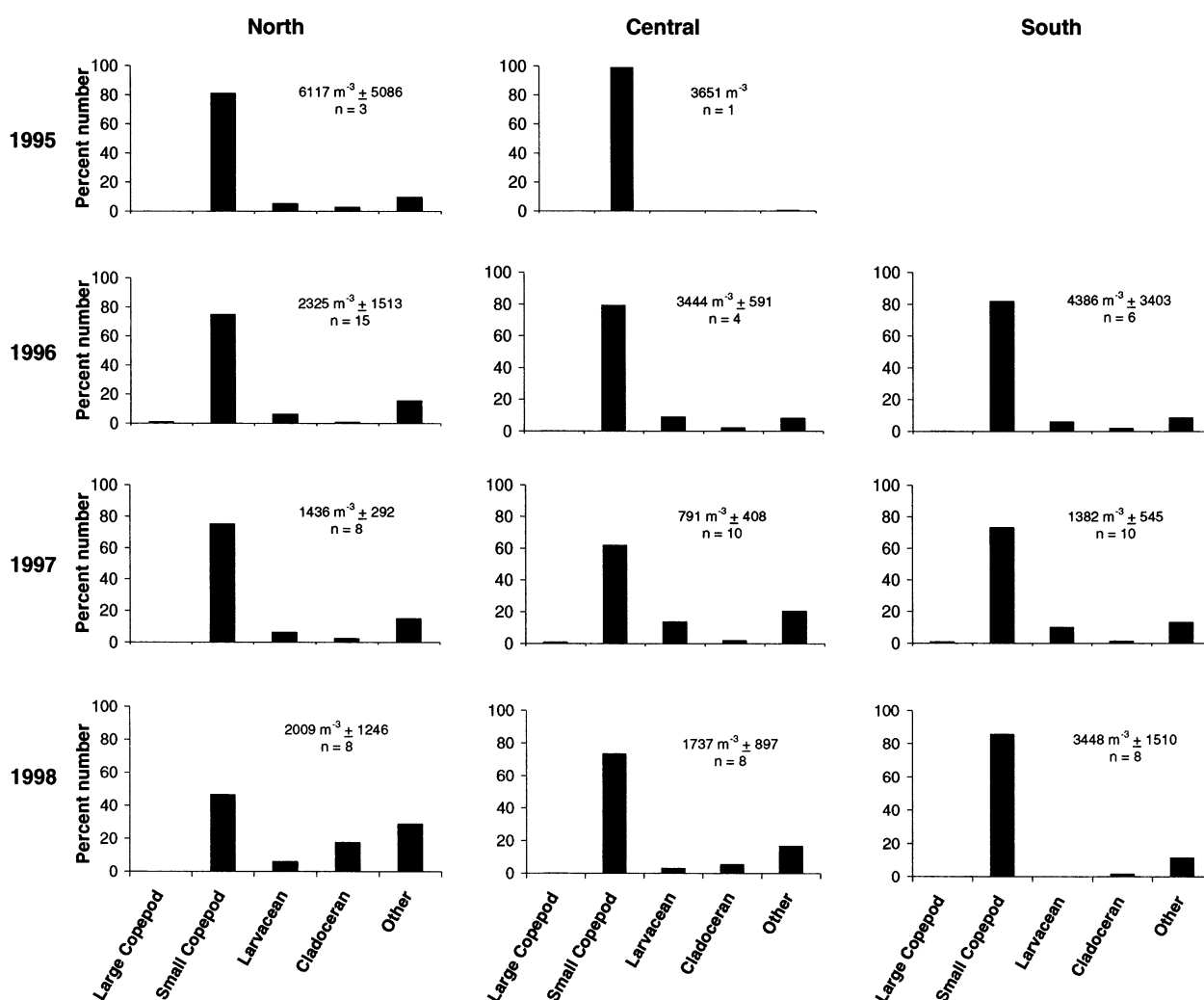

Fig. 2. Percentage composition of zooplankton taxa by region (northeast, central, southwest) and year (1995 to 1998). Total zooplankton densities (mean no. m^{-3} ± 1 SE) and the numbers of samples are shown in each panel

Table 2. Percent similarity indices (PSI) comparing zooplankton population composition (243 µm mesh) in July and August by year in Prince William Sound (PWS), Alaska

Years	PSI (%)
1995 vs 1996	90.4
1995 vs 1997	86.6
1995 vs 1998	86.0
1996 vs 1997	95.6
1996 vs 1998	91.0
1997 vs 1998	92.3

Diets of pelagic coelenterates and fishes

Because of the lower PSI values for zooplankton in 1998 compared with other years and the standard use of 243 µm mesh nets after 1995, we focused on comparisons between fish in 1996 and pelagic coelenterates in 1997. The pelagic coelenterate diet data presented here were from 1997 for *Aurelia labiata*, *Pleurobrachia bachei*, and *Cyanea capillata*, and from 1998 for *Aequorea aequorea*, for which dietary data were unavailable in 1997 (Fig. 3, Table 3). Of the gelatinous species, only *P. bachei* consumed almost exclusively crustacean prey. The other species ate crustaceans, larvaceans, and bivalve veligers; however, *A. labiata* consumed primarily hard-bodied prey (95%), while *C. capillata* and *A. aequorea* consumed high percentages of larvaceans (83 and 77%, respectively). The species of prey could not consistently be identified in the gut contents, and so are not reported here.

The diets of the fish species presented here were from 1996, except for juvenile walleye pollock, which were collected only in 1995 (Fig. 4, Table 3). The dietary trends were similar to those of the pelagic coelenterates. All fish species consumed some of each zooplankton taxon, but juvenile walleye pollock, sandlance, and herring consumed mostly small copepods (45 to 85%), while juvenile pink salmon consumed mostly larvaceans (85%).

Prey selection by pelagic coelenterates and fishes

Prey selection analyses for pelagic coelenterates provided insight into the trends apparent in the dietary comparisons. All pelagic coelenterate species selected against large (>2.5 mm TL) calanoid copepods (Fig. 5), which were rare in the zooplankton samples (Fig. 2). Selection for small copepods was significantly positive for *Aurelia labiata* at 60% of the stations where they were collected. For *Pleurobrachia bachei*, selection of small copepods was significantly negative at 60% of their stations, due to the strong positive selection for
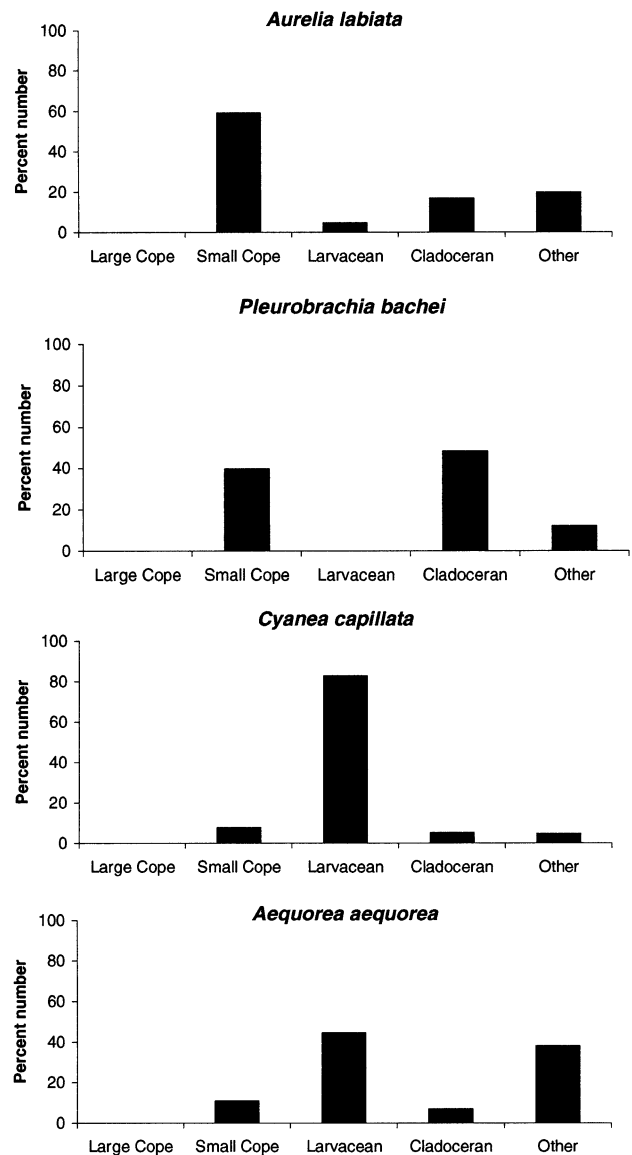

Fig. 3. *Aurelia labiata, Pleurobrachia bachei, Cyanea capillata and Aequorea aequorea.* Percentage composition of zooplankton prey in the gut contents of medusae and ctenophores in Prince William Sound. All data were from July and August 1997, except those for *A. aequorea*, which were from July 1998. See Table 3 for dates of collection, number of stations, number of pelagic coelenterates examined, and number of prey

cladocerans. For *Cyanea capillata*, selection was strong and significantly negative for small copepods and positive for larvaceans at all stations, and positive for cladocerans at most stations. *Aequorea aequorea* showed relatively weak selection; selection was significantly negative for copepods at 45% of the stations and signficantly positive for larvaceans at 20% of the stations. Selection of 'other' prey types, primarily

Table 3. Numbers of specimens examined, sizes (means ± 1 SD), prey items and stations for gut-content analysis of pelagic coelenterates and forage fishes (Age-0) from Prince William Sound during July and August. All pelagic coelenterate data are from 29 July to 8 August 1997, except those for *Aequorea aequorea* (14 to 20 July 1998), and all fish data are from 16 to 28 July 1996, except those for walleye pollock (26 July to 10 August 1995). Walleye pollock: *Theragra chalcogramma*; Pacific sandlance: *Ammodytes hexapterus*; Pacific herring: *Clupea pallasi*; pink salmon: *Oncorhynchus gorbuscha*

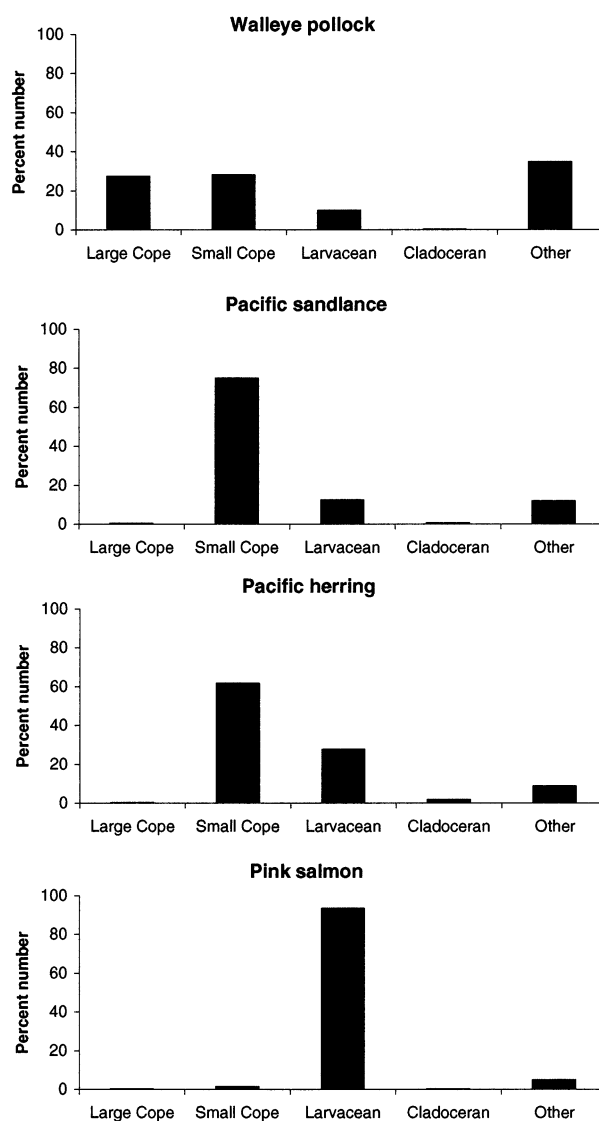|	*Aurelia labiata*	*Pleurobrachia bachei*	*Cyanea capillata*	*Aequorea aequorea*
No. of pelagic coelenterates	8	57	44	35
Preserved diameter (mm)	104 ± 31	<10	68 ± 26	55 ± 19
No. of prey	3585	116	6706	315
No. of stations	3	14	16	11
	Walleye pollock	Pacific sandlance	Pacific herring	Pink salmon
No. of fish	100	110	80	70
Fork length (mm)	58 ± 4	78 ± 10	41 ± 7	87 ± 14
No. of prey	10, 299	5899	2162	2846
No. of stations	12	15	13	7

bivalve larvae, was neutral or generally negative for the pelagic coelenterate species.

Of the fish species, 2 showed marked trends in selection, but 2 others did not (Fig. 6). Juvenile walleye pollock showed significant positive selection for large copepods at 50% of the stations, and for other prey at most stations. Walleye pollock also showed significant negative selection for small copepods at all stations, and significant positive selection for larvaceans and negative selection for cladocerans at about 25% of the stations. Juvenile pink salmon showed significant negative selection for small copepods and significant positive selection for larvaceans at all stations. In contrast, sandlance and herring were not strongly selective. Prey selection by sandlance was especially weak and mixed for all prey taxa. Herring showed somewhat stronger, but generally weak prey selection.

Dietary overlap among pelagic coelenterates and fishes

Dietary overlap among pelagic coelenterate species was generally below 60% (Table 4). The greatest dietary overlaps were among species that ate mostly crustaceans, *Aurelia labiata* and *Pleurobrachia bachei* (68%), and among species that ate mostly larvaceans,

Fig. 4. Walleye pollock *Theragra chalcogramma*, sandlance *Ammodytes hexapterus*, herring *Clupea pallasi*, and pink salmon *Oncorhynchus gorbuscha*. Percentage composition of zooplankton prey in the gut contents of juvenile fishes in Prince William Sound. All data are from July 1996, except those for walleye pollock (July and August 1995). See Table 3 for dates of collection number of stations, number of fishes examined, and number of prey
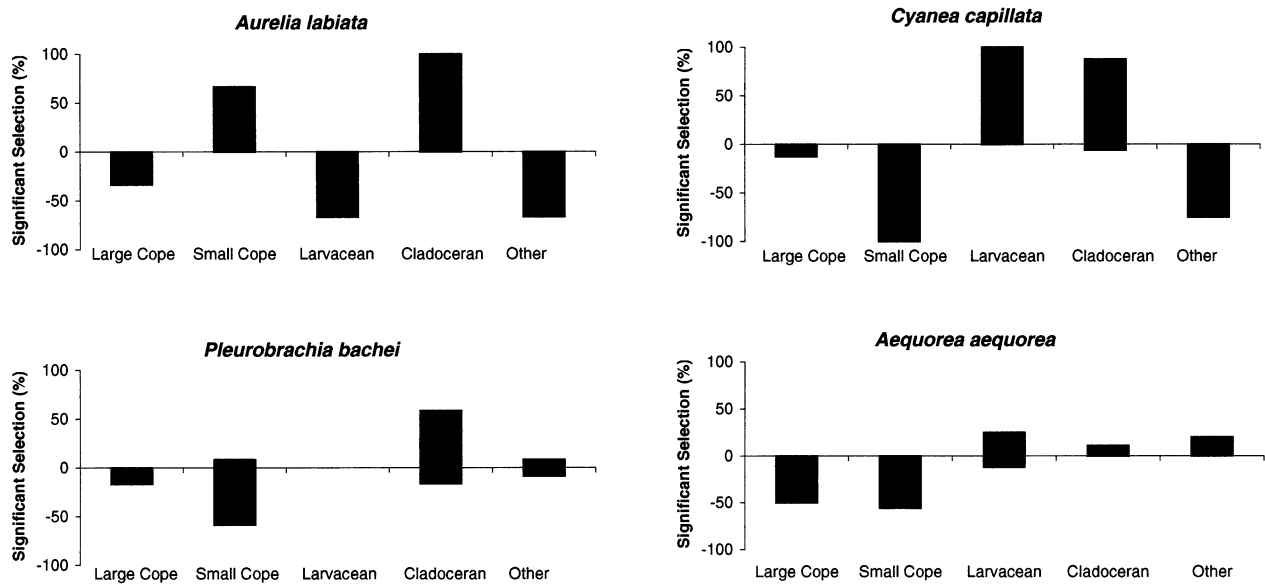
Fig. 5. *Aurelia labiata, Pleurobrachia bachei, Cyanea capillata* and *Aequorea aequorea.* Selection of zooplankton prey by medusae and ctenophores in Prince William Sound. Percentages represent the proportions of stations where prey selection was either significantly positive or negative relative to the total number of stations where each species was collected for gut-content analysis. All data were from July and August 1997, except those for *A. aequorea*, which were from July 1998. See Table 3 for dates of collection, number of stations, number of pelagic coelenterates examined, and number of prey

Cyanea capillata and *Aequorea aequorea* (62%). Dietary overlaps among crustacean-eating and larvacean-eating species were low (17 to 49%). The average overlap among all pelagic coelenterate species was 41 ± 21%.

Table 4. Percent diet similarities (PSI) among pelagic coelenterate and among forage fish species (Age-0) during summer in Prince William Sound. Dietary data for pelagic coelenterates are from July and August 1997, except those for *Aequorea aequorea* (July 1998), and data for fishes are from July 1996, except those for walleye pollock (July and August 1995). Specific names of fishes are given in Table 3 legend

	PSI (%)
Pelagic coelenterates	
Aurelia labiata vs *Pleurobrachia bachei*	68.4
Aurelia labiata vs *Aequorea aequorea*	49.1
Aurelia labiata vs *Cyanea capillata*	21.9
Aequorea aequorea vs *Pleurobrachia bachei*	29.7
Cyanea capillata vs *Aequorea aequorea*	61.8
Cyanea capillata vs *Pleurobrachia bachei*	17.4
Forage fishes	
95 walleye pollock vs 96 Pacific sandlance	50.4
95 walleye pollock vs 96 Pacific herring	47.1
95 walleye pollock vs 96 pink salmon	16.4
96 Pacific sandlance vs 96 Pacific herring	83.5
96 Pacific herring vs 96 pink salmon	34.2
96 sandlance vs 96 pink salmon	18.9

Dietary overlap among fish species showed similar trends to that for pelagic coelenterates, but overlaps were generally greater (Table 4). The greatest overlaps occurred between crustacean-eating species, juvenile walleye pollock, sandlance, and herring (47 to 84%). Juvenile pink salmon, which ate mostly larvaceans, showed low dietary similarity with the other fish species (16 to 34%). The average overlap among all fish species was 42 ± 25%.

Dietary similarities among pelagic coelenterate and fish species were greatest among crustacean-eating species and among larvacean-eating species (Table 5). The diets of *Aurelia labiata* and *Pleurobrachia bachei*

Table 5. Percent diet similarities (%) among pelagic coelenterate and forage fish (Age-0) species in Prince William Sound. Dietary data for pelagic coelenterates are from July and August 1997, except those for *Aequorea aequorea* (July 1998), and data for fishes are from July 1996, except those for walleye pollock (July and August 1995). Specific names of fishes are given in Table 3 legend

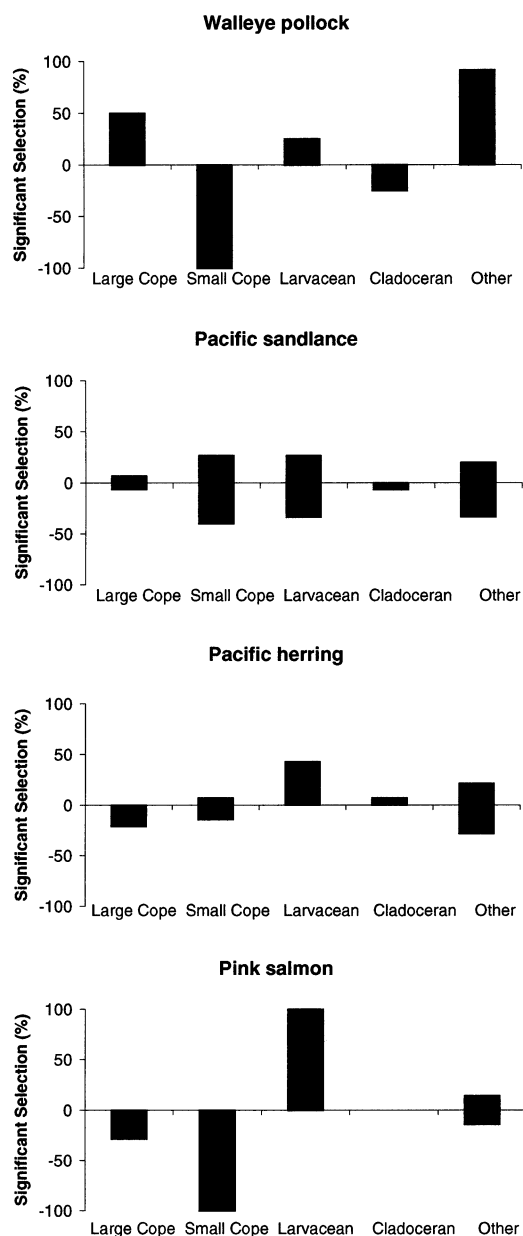|	Walleye pollock	Pacific sandlance	Pacific herring	Pink salmon
Aurelia labiata	67.2	75.1	73.3	18.7
Pleurobrachia bachei	41.1	63.4	62.0	5.3
Cyanea capillata	34.8	33.7	50.2	78.1
Aequorea aequorea	55.2	35.5	48.9	59.0

Fig. 6. Walleye pollock *Theragra chalcogramma*, sandlance *Ammodytes hexapterus*, herring *Clupea pallasi*, and pink salmon *Oncorhynchus gorbuscha*. Selection of zooplankton prey by juvenile (Age-0) fishes in Prince William Sound. Percentages represent the proportions of stations where prey selection was either significantly positive or negative relative to the total number of stations where each species was collected for gut-content analysis. All data are from July 1996, except those for walleye pollock (July and August 1995). See Table 3 for dates of collection, number of stations, number of fish examined, and number of prey

overlapped 67 to 75 and 41 to 63%, respectively, with diets of juvenile walleye pollock, sandlance and herring. The diets of *Cyanea capillata* and *Aequorea*

aequorea overlapped 78 and 59%, respectively, with diet of juvenile pink salmon. PSI comparisons among all pelagic coelenterate and fish species averaged 50 ± 21%. Thus, dietary overlaps between pelagic coelenterates and fishes were of similar magnitude as overlaps within each group.

DISCUSSION

The best dietary comparisons among fish and pelagic coelenterate species would be for specimens collected at the same times and locations, but this was not possible in the APEX study. Because zooplankton and predator abundances and distributions vary as much at small spatial and temporal scales as they do at large scales (e.g. Macer 1966, McGurk & Warburton 1992, Springer 1992, Brodeur & Wilson 1996, Brodeur et al. 1996, Fritz 1996, Incze et al. 1997, Schweigert 1997, Zheng 1997, Anderson & Piatt 1999, Foy 2000, Orsi et al. 2000, Stokesbury et al. 2000), and because the predator diets depend, in large part, on the availability of prey, we have taken a general approach to illustrate the degrees of similarity among the diets of pelagic coelenterate and fish predators. We show that the proportions of zooplankton taxa available were very similar in all years, which allowed us to compare diets among different years even though zooplankton densities may have varied among years. The proportional differences observed were due to occasional high abundance of 1 prey type (i.e. bivalve veligers, invertebrate eggs). We minimized the effect of variation by restricting our analyses to single years, as much as possible, and by using zooplankton data from 243 µm mesh nets only.

Diets of pelagic coelenterates and fishes

The diets of the pelagic coelenterates collected in PWS were generally similar to those reported from other locations, with some differences connected with the prey available. Such differences are generally due to the unusually high abundance of an easily captured (e.g. herring larvae) or a poorly digested prey type (e.g. bivalve veligers). For example, dietary differences observed between years in PWS were attributed to differences in the availability of bivalve veligers. Bivalve veligers constituted 0.7 and 12.0% of mesozooplankton organisms present in 1997 and 1998, respectively, and between 4.6 and 66.4% of the prey items in *Aurelia labiata* medusae, and 0.5 and 12.8% of the prey items in *Cyanea capillata* medusae in the 2 years.

The presence of bivalve veligers in the gut contents of medusae and fishes does not mean that they have been killed or digested by the predators. Bivalve larvae have been reported as major components of the diets of several species of scyphomedusae (e.g. Brewer 1989, Larson 1991, Behrends & Schneider 1995) and some juvenile fishes (e.g. Bailey et al. 1975, Coyle & Paul 1992, Sturdevant & Willette 1999); however, whether or not the veligers were digested (open shell, reduced tissue) generally has not been reported. Purcell et al. (1991) showed that 99% of the bivalve veligers were egested alive by the scyphomedusan *Chrysaora quinquecirrha*, even after retention in the medusae for up to 7 h. In the present study, ≤0.5% of the bivalve veligers were digested in the preserved gut contents of medusae: *Aurelia labiata* (10 of 9398 veligers), *Cyanea capillata* (2 of 413 veligers), and *Aequorea aequorea* (0 of 52 veligers). Mollusc veligers appeared to be undigested in northern anchovy and herring larva gut contents (summarized in Checkley 1982). Similarly, bivalve veligers were usually closed in the fish gut contents (Sturdevant unpubl. data). We conclude that the closed shells of captured bivalve veligers may protect them from digestion by these predators. In contrast, *Mnemiopsis leidyi* ctenophores, which use ciliary currents during digestion, did digest the bivalve veligers (Purcell et al. 1991). We do not know how broadly this indigestibility of bivalves applies across various predator taxa, or if gastropod veligers and thecosome pteropods are similarly protected from digestion.

We did not adjust gut-content data for possible differences in digestion rates of the various prey taxa by pelagic coelenterates or fishes. Adjusting for digestion time is not typical in studies using dietary data for jellyfish or for fishes. For *Aurelia labiata* and *Cyanea capillata* medusae, small copepods and cladocerans were digested in about 2 h, and larvaceans in about 1 h (Purcell unpubl. data). Data on digestion times of these prey by the forage fish species in this study are not available, to our knowledge. Sutela & Huusko (2000) found that crustacean prey were more resistant to digestion by fish larvae than soft-bodied prey (rotifers). Therefore, we expect that the trends in our study would be similar for both predator groups. Because selection patterns were strong when comparing crustacean and larvacean prey, and these differences in digestion rates would generally enhance the differences rather than reduce them, we believe our conclusions would be unchanged.

During July 1997 in PWS, *Aurelia labiata* medusae contained 75% small crustaceans and 10% larvaceans. The diet of this species has not been determined before; however, the diet of its congener, *A. aurita*, similarly contains a mixture of plankton organisms.

The diet of *A. aurita* sometimes is dominated by specific prey types that occur in great abundance at a sampling location or season. For example, Möller (1980) reported great numbers of herring larvae in the spring diet of *A. aurita* medusae in Kiel Bight, Germany; their summer diet from the same location, however, contained no fish larvae, but 25% copepods and 75% mollusc larvae (Behrends & Schneider 1995).

Our study and others show that the diet of *Pleurobrachia bachei* ctenophores consistently contains 97 to 98% crustaceans, with the percentages of copepods, cladocerans, and other prey varying with availability (Hirota 1974, Larson 1987).

Unlike the previous 2 species, the diet of *Cyanea capillata* medusae can contain large amounts of soft-bodied prey. Again, the dietary composition depends on the prey available. For example, the diet composition of *C. capillata* diet varied from 3 to 22% copepods, 3 to 75% cladocerans, 3 to 80% larvaceans, 0 to 34% hydromedusae, and 2 to 63% ichthyoplankton on 7 sampling dates in Port Phillip Bay, Australia (Fancett 1988), and varied seasonally as different prey became available in the Niantic estuary, USA (Brewer 1989). In July 1997 in PWS, *C. capillata* consumed an average of 70% larvaceans and only 20% crustacean prey. We also observed *C. capillata* feeding on *Aurelia labiata* and *Aequorea aequorea* medusae in 1999. Predation by *C. capillata* on *Aurelia aurita* medusae and ctenophores is believed to be an important source of food for this species (Båmstedt et al. 1997).

The diet of *Aequorea aequorea* medusae, which has not been previously reported, contained a high percentage of soft-bodied prey (>40% larvaceans) and low percentages of crustaceans (<20% total). The diet of its congener, *A. victoria*, from Vancouver Island, British Columbia, varied with prey abundance, but also consistently contained high percentages of soft-bodied prey, like fish larvae (2 to 48%), larvaceans (35%), and other gelatinous species (3 to 13%), but generally low percentages of crustacean prey (14 to 49%) (Purcell 1989).

The zooplanktivorous diet and predominance of calanoid copepods in 3 of the forage species' diets that we report generally agree with other workers' observations. Juvenile pollock in the North Pacific feed on small calanoids and larval euphausiids in summer, shifting to larger prey, such as large calanoids and larger euphausiids, with growth (e.g. Kamba 1977, Krieger 1985, Grover 1991, Kendall & Nakatani 1992, Brodeur 1998). Larvaceans can be important prey in some geographic areas (Merati & Brodeur 1996), and epibenthic prey may increase as zooplankton stocks diminish and fishes become demersal in fall and winter (Rogers et al. 1979, Simenstad et al. 1979, Krieger 1985, Nakatani 1988).

For Pacific sandlance and congeners, multiple stages of small and large calanoids prevail in the diets, with diverse other taxa (e.g. barnacle larvae, larvaceans, euphausiids, gammarid amphipods) important at times such as late autumn, when calanoids are not abundant (Sekiguchi et al. 1974, Meyer et al. 1979, Craig 1987, Monteleone & Peterson 1986, Blackburn & Anderson 1997).

Diets of Age-0 Pacific herring consist of predominantly calanoid copepods in spring and summer (Haegele 1997, Foy & Norcross 1999). Prey include both large and small copepods, crustacean larvae (e.g. decapod zoeae and barnacle larvae), invertebrate eggs, chaetognaths, larvaceans, mysids, amphipods and euphausiids (Sherman & Perkins 1971, Harris & Hartt 1977, Simenstad et al. 1979, Coyle & Paul 1992). Change from predation on calanoids by younger herring to macrozooplankton such as euphausiids and hyperiids by older fish has also been reported (Wailes 1936, Lassuy 1989, Last 1989, Haegele 1997). For juvenile herring in PWS, the relative proportions of large and small calanoid prey varied both seasonally and spatially, but proportionally more biomass tended to come from large calanoids and a combination of malacostraca, hyperiids and euphausiids by late summer (Foy & Norcross 1999, Sturdevant & Willette 1999).

The mono-specific diet (larvaceans) of juvenile pink salmon in our study is somewhat unusual, but was also observed by Healey (1991). Larvaceans are common in juvenile pink salmon diets, but small crustaceans typically contribute most prey biomass (e.g. Manzer 1969, Bailey et al. 1975, Cooney et al. 1981, Sturdevant et al. 1996, Sturdevant & Willette 1999). Throughout the spring, pink salmon prey on both pelagic and epibenthic taxa, including small and large calanoids, cyclopoids and harpacticoids, with lesser amounts of other small taxa such as cumaceans, cladocerans, barnacle and bivalve larvae, and pteropods; by late summer, more of their prey tend to come from larger specimens of these taxa, larger crustacean taxa (especially hyperiid amphipods and euphausiids), or fishes (Karpenko & Piskunova 1985, Perry et al. 1996, Haegele 1997, Moulton 1997, Landingham et al. 1998).

Prey selection by pelagic coelenterates and fishes

Most species of medusae and ctenophores have broad diets in which crustacean prey predominate, but prey selection typically occurs. Because these predators do not actively attack prey, prey selection depends on various characteristics of the predators and prey (reviewed in Purcell 1997). Prey selection analyses theoretically do not vary with relative prey abundances (Pearre 1982); hence they are more consistent than

dietary analysis and enable general patterns of feeding to emerge. The selection analyses here confirm the patterns seen among diets of pelagic coelenterate and fish predators.

The prey electivities presented here show similar trends to those calculated previously for congenors of *Aurelia labiata* and *Aequorea aequorea*, and for *Pleurobrachia bachei* and *Cyanea capillata*. Only Sullivan et al. (1994) reported electivity indices for *Aurelia aurita*, which showed significant positive selection for hydromedusae on 100% of 9 dates and for calanoid copepods and barnacle nauplii on 14% of 7 dates, and significant negative selection for copepods on 28% of 7 dates and copepod nauplii on 100% of 4 dates. For *A. labiata* in PWS, we found significant positive selection for small copepods (65% of stations) and cladocerans (100%) and significant negative selection for larvaceans (75%) and other prey (primarily bivalve larvae).

In California waters, prey selection by *Pleurobrachia bachei* was positive for small copepods (*Acartia tonsa* and *Labidocera trispinosa*) and cladocerans (*Evadne* spp.), but was negative for the cladoceran *Penilia avirostris* and chaetognaths (Hirota 1974). We obtained opposite results, with negative selection for small copepods and positive selection for cladocerans; however, we did not distinguish between the 2 species of cladocerans present (*Evadne* sp. and *Podon leukarti*) in our analysis.

Cyanea capillata in PWS showed prey selection similar to that in Port Phillip Bay, Australia, where selection was positive for amphipods, decapods, crab zoea, *Podon* spp. and larvaceans, and negative for *Evadne* spp. and for all copepod taxa. In PWS, *C. capillata* showed strong selection against copepods (significant in 100% of collections), and strong selection for larvaceans (100%) and cladocerans (*Evadne* sp. and *Podon leukarti* combined).

We report the same patterns of prey selection here for *Aequorea aequorea* as were reported by Purcell (1989) for *Aequorea victoria*, which showed negative selection for copepods and other crustaceans, and positive selection for soft-bodied organisms, such as larvaceans. Other gelatinous species and ichthyoplankton prey that were highly preferred by *A. victoria* were not abundant in the plankton samples taken in July in PWS, and were not found in the gut contents of *A. aequorea* then.

The patterns of prey selection that we observed for the fish species generally agree with previous reports. Juvenile pollock were selective planktivores at several young stages examined in various areas. In Japanese waters in April, late larvae selected *Pseudocalanus minutus* rather than *Oithona* spp. from among small calanoids, and in May the large calanoid *Eucalanus*

bungii and euphausiid juveniles were selected (Kamba 1977). In the Gulf of Alaska in September, juvenile pollock selected decapod larvae, euphausiids and fish larvae; they strongly avoided copepods relative to their abundance in plankton, taking only the late stages of the large species *Calanus marshallae* and *Metridia* spp. (Brodeur 1998). Prey size generally increased, but minimum prey sizes did not change with increasing fish size (Brodeur 1998). Although we used data from a 303 µm mesh net for the proportions of zooplankton taxa available to pollock in 1995 instead of 243 µm mesh samples used for all other predator species, Sturdevant & Willette (1999) showed that the percentage composition of principal zooplankton taxa did not differ between 243 and 303 µm mesh sizes; thus, we required no adjustment in calculations of prey selection.

The prey selection of the Pacific sandlance *Ammodytes hexapterus* had not been examined before these studies in PWS (Sturdevant & Willette 1999, this study). However, prey selection has been reported for its congeners. In Age-0 *Ammodytes personatus*, smaller individuals selected cladoceran over calanoid species, and targeted *Evadne* spp. over the more abundant *Podon* spp.; larger individuals selected calanoids, and targeted species of *Acartia* and *Calanus* over the more abundant *Paracalanus* and *Oithona* (Sekiguchi et al. 1974). At the same time, however, the predominant prey of this sandlance tracked seasonal changes in the densities of *Acartia* and *Paracalanus* species from March to June (Sekiguchi 1977). The northern sandlance *Ammodytes dubius* preferred the larger zooplankters in plankton tows, large calanoids *Calanus marshallae*, euphausiids and polychaete larvae, but was limited in its ability to prey on the larger euphausiid individuals (Scott 1973).

Herring feed selectively with respect to both particle size and type; selection varies with particle visibility, prey escape ability and larval feeding experience (Checkley 1982, Munk 1992, Tsuda et al. 1998), as well as the prey taxa available by region. For example, Pacific herring up to 33 mm long selected *Acartia longiremis* females and rarely consumed the larger calanoids *Pseudocalanus newmani*, *Neocalanus plumchrus* or *Eucalanus bungii* (Tsuda et al. 1998). Baltic herring smaller than 49 mm in length selected cladocerans rather than calanoids, but larger juveniles selected the calanoid *Acartia* sp. over *Pseudocalanus* sp. (Arrhenius 1996). In contrast, Atlantic herring larvae in western Scotland waters did not select *Acartia* sp., and preferred copepodites of *Oithona* sp. over those of *Pseudocalanus* sp. as fish size increased (Checkley 1982). In the North Sea, small larvae selected *Acartia tonsa* while larger larvae selected *Calanus finmarchicus* (Munk 1992). However, young herring preferred copepods of constant relative size

(Checkley 1982, Munk 1992) and, like pollock, consumed prey in a narrower size range than they were capable of. Non-selective filter-feeding on very small, highly abundant prey like invertebrate eggs, which we pooled in 'other,' has been shown for both pollock (e.g. Grover 1991) and sandlance (Scott 1973).

When available, large calanoids such as species of *Metridia* and *Calanus / Neocalanus* were selected even by recently emerged pink salmon fry (Cooney et al. 1981). In summer, larger juvenile pink salmon selected for macroplankton (Willette et al. 1997); they avoided small copepods and selected crab zoeae, large calanoids, euphausiids, hyperiids, and larvaceans (Karpenko & Piskunova 1985, Healey 1991, Landingham et al. 1998). However, a size-related shift to larger prey is not always evident for juvenile pink salmon (Healey 1991).

Dietary overlap among pelagic coelenterates and fishes

The dietary overlap among different pelagic coelenterate species has not been examined previously. Prior emphasis has been on distinguishing dietary patterns among broad taxonomic categories (e.g. Purcell & Mills 1988, Purcell 1997). We demonstrate here that in addition to showing differences in selectivity, with some species utilizing mainly crustacean prey and other species utilizing high proportions of soft-bodied prey, diets of the co-occurring species overlapped by an average of 41% when compared mainly within the same year. Comparisons between years for jellyfish collected from the same stations in 1997 and 1998 showed 42 and 48% dietary overlap within species for *Aurelia labiata* and *Cyanea capillata*, respectively, due to the high proportions of bivalve veligers in the diets in 1998.

The dietary overlaps among these fish species have rarely been examined, although several reports on food webs of the Pacific Northwest include descriptions of their food habits. In Puget Sound/Strait of Juan de Fuca, Simenstad et al. (1979) classified all 4 species as pelagic planktivores, but Pacific sandlance, Pacific herring and pink salmon belonged to the same neritic assemblage, while juvenile walleye pollock was assigned to a shallow sublittoral assemblage. This suggests that the greatest potential for dietary overlap occurs among the species pairs not including pollock, although the authors felt that sandlance feeding was more specialized than herring feeding (Simenstad et al. 1979). Similarities among the species were also shown by studies in the nearshore zone of Kodiak Island (Harris & Hartt 1977, Rogers et al. 1979). In both spring and summer, pollock, sandlance and juvenile

pink salmon up to 150 mm in length fed on zooplankton, principally calanoids, and on epibenthic crustaceans, while herring ate mainly calanoids (Harris & Hartt 1977). In a Strait of Georgia study (Haegele 1997), planktivorous juvenile salmon generally did not target copepods, unlike herring; however, Tsuda et al.'s (1998) laboratory study showed that young chum salmon, which often have diets very similar to those of pink salmon (e.g. Bailey et al. 1975, Willette et al. 1997, Landingham et al. 1998), preferred larger calanoids than did herring. McGurk et al. (1992) inferred competition between sandlance and herring larvae feeding on the same types of prey with similar lengths but different widths. A comparison of forage species diets in summer 1994 in PWS (Willette et al. 1997) used cluster analysis to show greater similarity between juvenile herring and pollock diets than between either of these species and sandlance diet, and pink salmon diet was not similar to any of them. The behavioral mechanisms for prey-partitioning among these co-occurring fishes have not been investigated.

The degree of dietary overlap varies between pairs of zooplanktivorous fish species. Overlap can change seasonally or when prey becomes limited, and can depend on relative predator sizes, densities, or spatial proximity (e.g. Sekiguchi 1977, Cooney et al. 1981, Perry et al. 1996, Haegele 1997, Foy & Norcross 1999, Sturdevant & Willette 1999). For example, dietary overlap among juvenile pollock, sandlance, herring and pink salmon (aged 0 to 2 yr) in PWS ranged from 32 to 81% between May and November 1994 (Sturdevant & Willette 1999). The months of greatest dietary overlap differed among the species pairs. Herring diet overlap with pollock exceeded 50% in June and November, with pink salmon in July, and with sandlance in May and September; pink salmon overlap with pollock never exceeded 50%, while pink salmon overlap with sandlance exceeded 50% only in June; pollock overlap with sandlance exceeded 50% in July. Thus, June and July were the only months with high dietary overlap between more than 1 pair of species. Sturdevant & Willette 1999 demonstrated variation in diet overlap according to the degree of spatial overlap between species; dietary overlap between sandlance and herring declined in summer from >70% among allopatric fish to <50% among sympatric fishes. This decline in similarity and changes in prey composition indicated prey-partitioning. Willette et al. (1997), however, showed an increase in similarity between diets of herring and pollock in late summer 1994 from 27% for allopatric fishes to 71% for sympatric fishes, while in 1995 diet overlap of both summer allopatric and autumn sympatric pollock and herring were high (Sturdevant & Willette 1999). We found species' diets to be similar among years when comparisons were

possible. The diets of sandlance collected in 1995 and 1996 overlapped by only 36% due to greater utilization of invertebrate eggs in 1995 (Sturdevant et al. 1996, Sturdevant & Willette 1999). The diets of herring in 1995 and 1996 overlapped by 76%.

The diets of pelagic coelenterates and zooplanktivorous fishes overlapped substantially in PWS. The greatest dietary overlaps occurred among species that ate mostly crustacean prey and among species that ate mostly larvaceans. The degrees of dietary overlap probably vary both spatially and temporally, because diet composition and food quantity differ with the prey taxa available and the amount of food present, respectively (e.g. Perry et al. 1996). Although the gut contents of pelagic coelenterates and fishes could not be collected in the same years, the zooplankton populations showed great similarity (mean 85%) among all regions and years, allowing us to make dietary comparisons. Even though the dietary overlaps among pelagic coelenterate species (mean 41%) and fish species (mean 42%) were calculated mostly within a season, dietary overlaps among pelagic coelenterates and fishes collected from different years showed an even higher average (50%). Greater dietary overlaps among pelagic coelenterates and fishes might be expected if all data were collected from the same years and locations. For example, dietary overlap of pollock and sandlance in 1995 was 78% compared with 50% when data from 1995 and 1996 were compared, and the dietary overlap of pollock and herring in 1995 was 71%, compared with 47% in 1995 versus 1996.

The potential for competition for zooplankton prey among pelagic coelenterates and fishes is very difficult to assess. Whether competition would occur depends on the extent of the spatial, depth and temporal co-occurrence of the various predators considered here, as well as their abundances and consumption rates of zooplankton and the density and production rates of the zooplankton. Determination of those parameters was beyond the scope of the present paper, but will be addressed in a future paper. In addition to the gelatinous species considered here, numerous small zooplanktivorous hydromedusae and chaetognaths also occur in PWS (R. T. Cooney et al. unpubl. data), and would increase the potential for competition for prey among pelagic coelenterates and fishes. Previous publications on the carrying capacity of PWS have not considered seasonal dietary changes or multi-species interactions (Cooney 1993).

Populations of the pelagic coelenterate species considered here develop in June to July and persist only until October, which limits the potential for competition with fishes to that time period. During the period that pelagic coelenterates and fish co-occur in PWS, a number of mechanisms act to limit competitive inter-

actions. For example, at the time of this study, the majority of pink salmon had exited from PWS to the Gulf of Alaska (Cooney 1993), a migration possibly triggered by declining abundance and diversity of optimally sized prey (Simenstad & Salo 1982, Healey 1991). Pink salmon diets were least similar to those of other fish species′, and overlapped substantially with half of the pelagic coelenterate species. Their exodus from PWS followed several months of moderate diet overlap (Sturdevant & Willette 1999) between predominant fish species, and limited predation on common prey at that time to the year-round residents such as the other 3 forage species. Thus, the number of potential competitors decreases as food stocks decline. The more passively feeding pelagic coelenterates are less likely to use the same mechanisms as the fish species to avoid competition, such as switching to epibenthic prey, as for herring, pollock and sandlance (e.g. Krieger 1985, Craig 1987, Foy & Norcross 1999), partitioning food by depth, as for herring (e.g. Coyle & Paul 1992), or feeding at different times of day (Sturdevant & Willette 1999).

Co-occurrence of jellyfish and fishes in PWS

We present preliminary qualitative evidence to illustrate that the fishes and the large jellyfish species do overlap in space and time in PWS. Untargeted sets of an anchovy seine 250 m long by 34 m deep with a 25 mm stretch mesh were made during 1 to 22 July 1999 at the same stations in PWS as in 1997 and 1998. Both jellyfish and fishes were sorted by species and counted only in 1998 and 1999, but fish data are unavailable to us for 1998. *Aurelia labiata*, *Cyanea capillata*, and *Aequorea aequorea* occurred with juvenile walleye pollock and with juvenile pink salmon in 98 to 100% of the seine sets in which the jellyfish were collected, respectively (Table 6). The percentages of jellyfish collected with herring (35 to 39%) and sandlance (14 to 15%) were much lower. These fish species spend the majority of their lives in shoals, and aggregate more or less tightly, depending on whether or not they are feeding (Hobson 1986, Robinson & Pitcher 1989). They were not targeted in this sampling, and were probably not collected in purse seine hauls because of their orientation along beaches and because sandlance readily escaped through the seine mesh. *A. labiata*

Table 6. Co-occurrence of jellyfish and forage fish species in 45 seine sets taken in July 1999 in Prince William Sound. Percentages in the top series (% of jellyfish sets with fish species) are the numbers of sets with each fish species divided by the numbers in the last column. Percentages in the bottom series (% of fish sets with jellyfish species) were calculated from the numbers of sets with each jellyfish species divided by numbers in the last row. Specific names of fishes are given in Table 3 legend

	Walleye pollock	Pacific sandlance	Pacific herring	Pink salmon	No. of sets with jellyfish species
Aurelia labiata	100%	96%	35%	100%	20
Cyanea capillata	100%	14%	37%	98%	43
Aequorea aequorea	100%	15%	39%	98%	41
Aurelia labiata	46%	50%	41%	45%	–
Cyanea capillata	100%	100%	94%	100%	–
Aequorea aequorea	95%	100%	94%	95%	–
No. of sets with fish species	43	6	17	42	–

occurred in 41 to 50% of the seine sets in which the 4 fish species were collected, but *C. capillata* and *A. aequorea* occurred in 94 to 100% of the sets (Table 6). No seine set contained only jellyfish or only fishes. Similarly, in July 1996, *A. labiata* and herring were more abundant and pollock less abundant than in 1999, and 20 to 25% of seine sets that targeted on fish schools also contained jellyfish (Purcell et al. 2000). Additionally, juvenile walleye pollock were observed by underwater video to be associated with aggregations of *A. labiata* in 1996 and with individual *C. capillata* in 1999 (Purcell et al. 2000). Clearly, the jellyfish and fish species included in this study overlap spatially and temporally and utilize the same foods in PWS.

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