Abstract–Diets of young-of-the-year (YOY) walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) were compared between seasons (summer and autumn), years (autumn), and allopatric and sympatric fish aggregations (autumn) in Prince William Sound (PWS), Alaska. Fish were collected principally by mid-water trawl 20 July–12 August 1995, 5–14 October 1995, and 7–13 November 1994. Prey fields were assessed from zooplankton samples in 1995.

During the summer, the principal prey of allopatric pollock and herring was small calanoids and diet overlap was high ($R_0>0.76$). During the autumn, diets were composed of large calanoids, larvaceans, and euphausiids. Diet overlap between sympatric species was greater in November 1994 ($R_0 \leq 0.94$) than in October 1995 ($R_0 \leq 0.69$). The seasonal diet shift to larger prey coincided with larger fish size and with decreased abundance and proportions of the principal zooplankter, small calanoids, and increased abundance and proportions of large calanoids and larvaceans in zooplankton tows. However, feeding decreased in autumn, compared with summer, especially for herring. Sympatric fish had higher rates of nonfeeding than allopatric fish, and subtle differences in prey selection existed between the aggregations, but sampling variation could explain these feeding differences.

The similarity in diets of YOY pollock and herring indicate the potential for competition. These species are important to commercial fisheries and as forage for marine birds and mammals. An understanding of their trophic interactions could help to explain shifts in fish community structure and bird predation. If sympatry increases as prey resources decline, competition in autumn may be particularly important in regulating populations.

Feeding habits, prey fields, and potential competition of young-of-the-year walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska, 1994–1995

Molly V. Sturdevant

Auke Bay Laboratory
Alaska Fisheries Science Center
11305 Glacier Highway
Juneau, Alaska 99801
E-mail address: Molly.Sturdevant@noaa.gov

Audra L. J. Brase

Commercial Fisheries Division
Alaska Department of Fish and Game
P.O. Box 20
Douglas, Alaska 99824

Leland B. Hulbert

Auke Bay Laboratory
Alaska Fisheries Science Center
11305 Glacier Highway
Juneau, Alaska 99801

Walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) are forage fish that inhabit the northeastern Pacific Ocean rim. Both species are important components of marine bird, mammal, and fish diets, both support important commercial fisheries in the Gulf of Alaska (GOA), and historical data show dramatic variability in both their populations (Springer, 1992; Bechtol, 1997; Springer and Speckman, 1997; Anderson and Piatt, 1999). Young-of-the-year (YOY) walleye pollock and YOY Pacific herring are found at the same locations and depths during at least part of the year (Brodeur and Wilson, 1996a; Willette et al., 1997; Stokesbury et al., 2000) and both consume zooplankton as their primary prey[1,2] (Willette et al., 1997; Foy and Norcross, 1999a, 1999b). Because of these similarities and because the frequency and nature of their interactions may change as fish population structure shifts, we investigated the potential for feeding competition between these species.

Several recent studies have found that the species composition of forage fish populations in the GOA and Prince William Sound (PWS) has changed dramatically (Bechtol, 1997; Kuletz et al., 1997; Anderson and Piatt, 1999). Short-term population changes were attributed to the *Exxon Valdez* oil spill in March 1989 (Brown et al., 1996a; Kuletz, 1996; Oakley and Kuletz, 1996; Kuletz et al.,

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[1] Jewett, S., and E. Debevee. 1999. Diet composition, diet overlap and size of 14 species of forage fish collected monthly in Prince William Sound, Alaska, 1994–1996. *In* Forage fish diet overlap, 1994–1996, p. 10–37. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 97163C), Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Hwy., Juneau, AK 99801-8626.

[2] Boldt, J. L. 1997. Condition and distribution of forage fish in Prince William Sound, Alaska. Unpubl. M.S. thesis, Juneau Center School of Fisheries and Ocean Science, Univ. Alaska Fairbanks, 11120 Glacier Hwy., Juneau, AK 99801, 155 p.
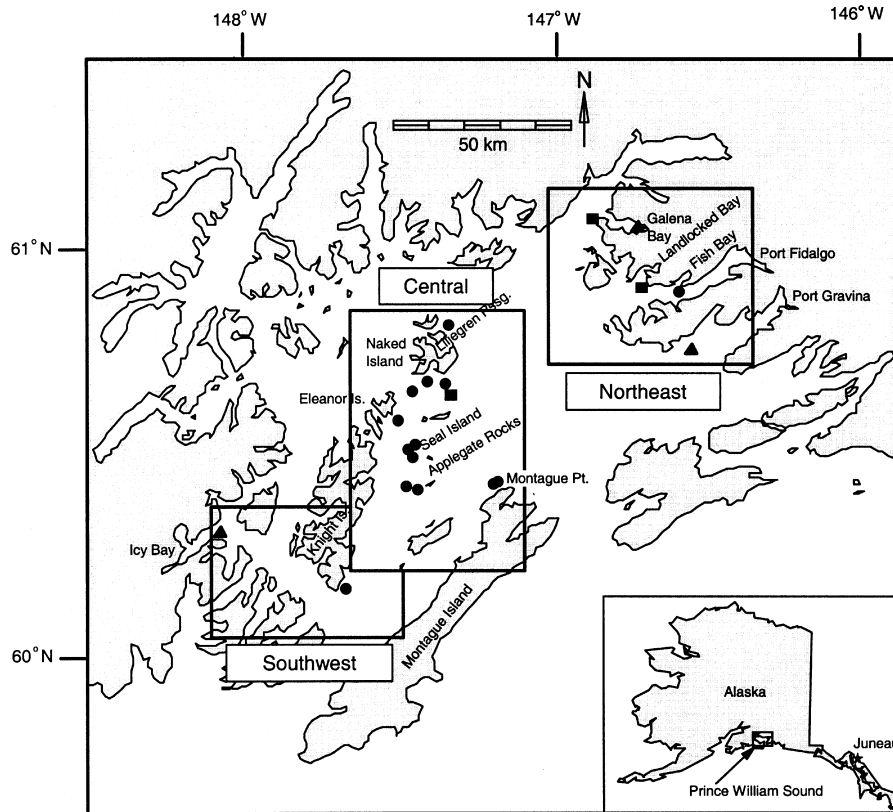
Figure 1

Sampling regions and stations for YOY walleye pollock and Pacific herring diet samples collected in Prince William Sound, Alaska. Circles: July–August 1995; squares: October 1995; triangles: November 1994.

1997), but researchers believe that long-term changes began with a climate regime shift prior to the oil spill (Bailey et al., 1995; Piatt and Anderson, 1996; Anderson and Piatt, 1999). For example, the number of walleye pollock and other demersal fish increased at the same time that the other taxa decreased (Anderson and Piatt, 1999), the PWS spawning population of Pacific herring declined by 75% by 1993 (Brown et al., 1996b), and fish biomass of PWS decreased by 50% (Piatt and Anderson, 1996). Concomitant decreases in populations of marine birds and mammals in PWS may be related to these shifts in the composition and abundance of forage fish prey (Oakley and Kuletz, 1996; Piatt and Anderson, 1996; Iverson et al., 1997). Apparently, fewer high-quality forage fish have been available, and the species composition has changed to one in which the predominant fish taxa are less energetically valuable to marine piscivores (Piatt and Anderson, 1996; Anthony and Roby, 1997; Anderson and Piatt, 1999; Payne et al., 1999). The potential for such shifts to cascade throughout marine food webs (Livingston, 1993; Springer and Speckman, 1997) is an important reason to understand the trophic interactions of forage fish.

This reports stems from the Alaska Predator Ecosystem Experiment (APEX), a multidisciplinary study that attempted to link current knowledge about the forage fish of PWS with their seabird predator populations. We describe differences in the feeding habits of YOY walleye pollock and YOY Pacific herring caught in summer and autumn in PWS and compare feeding attributes of fish caught in allopatric (single species) and sympatric (co-occurring, multispecies) aggregations in autumn to support the hypothesis that the presence of potential competitors may induce changes in feeding habits. We compare fish size, zooplankton prey fields, fish feeding habits, prey selection, food quantity, and diet overlap of these species.

Materials and methods

Field methods

Fish stomach and zooplankton samples were collected during APEX forage fish population surveys in central, northeastern, and southwestern PWS[3,4,5] (Fig. 1). In a pilot study in 1994, we sampled from 7 to 13 November aboard the Alaska Department of Fish and Game RV *Medeia*; in 1995, we sampled from 20 July to 12 August aboard the charter FV *Caravelle,* and from 5 to 14 October aboard the RV *Medeia.* Surveys were conducted offshore along a grid of parallel transects spaced at two-mile

intervals and ending as near shore as possible. Bottom depths averaged approximately 120 m (range: 25–220 m). The grid was surveyed twice in summer and once, partially, each autumn. Hydroacoustic and hydrographic profile data were collected but are presented elsewhere.[3,4,5] Where fish were detected with hydroacoustic equipment, we either interrupted the survey or returned after the transect was completed to fish with a mid-water beam trawl. The net was generally fished 20–35 minutes each trawl.[3,4] The trawl's effective mouth opening was 50 m^2, and net mesh sizes diminished from 5 cm in the wings to 1 cm in the codend. A 0.3-cm mesh liner was sewn into the codend, which terminated in a plankton bucket having 500-µm nytex mesh. In summer, beach-seine and dip-net samples occasionally supplemented the trawl catches. Subsamples of forage species (n=10 to 15 per species) were preserved in 10% buffered formalin-seawater solution on the vessels for later stomach analysis in the laboratory. We classified samples collected between 08:00 and 20:00 as "day" and those between 20:01 and 07:59 as "night."

In 1995, the zooplankton prey spectrum was assessed from dual vertical hauls taken at each station within two hours of fish catches by using conical nets that were 0.5 m in diameter and equipped with 303-µm mesh in summer and 243-µm mesh in autumn. We towed the nets from a standard depth of 20 m or to the depth at which fish were caught (or using a combination of both depths). Depth of hauls were categorized as "shallow" (≤25 m) or "deep" (>25 to <100 m). Samples were collected at both depths at seven stations in summer (from 95-1-53 to 95-1-62 and 95-1-112) and one station in autumn (95-2-7, Table 1).

Laboratory methods

After a minimum of six weeks in formalin solution, fish samples were transferred to a solution of 50% isopropanol for at least 10 days before stomach analysis was performed. Ten specimens of each species were measured (mm fork length, FL; mg wet weight), and size was used to develop age-class categories for diet samples (Smith, 1981; Paul et al., 1998a). Walleye pollock (20 to 120 mm FL) and

Pacific herring (60 to 120 mm FL) were classified as YOY (age-class 0). Stomachs were excised, weighed, and their contents were removed. The weight of prey contents was recorded as the difference between full and empty stomach weights. Fish were considered to have been feeding if their stomachs contained more than a trace of food. Relative stomach fullness was recorded as integers representing empty stomachs (1), stomach containing trace contents (2), stomachs that were 25%, 50%, 75%, or 100% full (3–6), or stomachs that were distended (7). State of digestion was recorded as partially digested contents (1), mostly digested contents (2), and empty stomachs (3).

Stomach contents and zooplankton samples were identified with a binocular microscope to the highest taxonomic resolution possible and enumerated. The prey category of calanoid copepods was also segregated into "large" (≥2.5 mm total length, TL) and "small" individuals (≥2.5 mm TL). We pooled the common pelagic cyclopoid copepod *Oithona similis* with small calanoids. We subsampled all zooplankton samples and stomach samples when practical, using a Folsom splitter to achieve a minimum count of 200 of the predominant taxon. Counts were expanded and total prey weights were determined by multiplying the expanded number observed by the mean weight per taxon. Weights per taxon were obtained from data on file (specimens from zooplankton samples or fish stomachs) collected from spring through autumn of various years in southeastern Alaska or PWS (Coyle et al., 1990; Stark[6]; senior author, unpubl. data).

Analytical methods

Forage fish were considered to occur in allopatric aggregations if only one species and one age class were caught in a net haul. They were considered to be sympatric if at least two species or age classes (≥10 fish each) were caught together. For this study, we restricted analyses to YOY pollock and herring that were allopatric or that co-occurred only with each other to limit the complexity of trophic interactions; we excluded pollock and herring that were caught in other types of aggregations, such as with other species or older conspecifics. We examined the size of forage fish and their feeding attributes. Size included FL and wet weight. Feeding attributes included measures of the quantity of food consumed, measures of feeding frequency, and measures of prey composition. Food quantity was expressed as means of the total number and weight of prey (ln-transformed), stomach fullness index (rounded to nearest 25%), and prey percent body weight (%BW; ratio of wet stomach-content weight to fish body weight). Feeding frequency was measured as the percentages of feeding fish and the percentages of fish with partially or mostly digested stomach contents. Prey composition was expressed as the percent number and percent biomass of prey categories. Zooplankton density per cubic meter and numerical percent composition was calculated for species,

[3] Haldorson, L.   1995.   Fish net sampling.   *In* Forage fish study in Prince William Sound, Alaska, p. 55–83.   *Exxon Valdez* Oil Spill Restoration Project 94163A Annual Report, Juneau Center School of Fisheries and Ocean Science, Univ. Alaska Fairbanks, 11120 Glacier Hwy., Juneau, AK 99801.

[4] Haldorson, L. J., T. C. Shirley, and K. O. Coyle.   1996.   Biomass and distribution of forage species in Prince William Sound.   *In* APEX project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska (D. C. Duffy, compiler), Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 95163 A–Q), Alaska Natural Heritage Program, Department of Biology, Univ. Alaska Anchorage, 707 A Street, Anchorage, AK 99501.

[5] Haldorson, L. T. Shirley, K. Coyle, and R. Thorne.   1997.   Forage species studies in Prince William Sound.   *In* Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska (D. C. Duffy, compiler).   Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 96163 A–Q), Alaska Natural Heritage Program, Department of Biology, Univ. Alaska Anchorage, 707 A Street, Anchorage, AK 99501.

[6] Stark, C.   1995.   Personal commun.   Institute of Marine Science, Univ. Alaska Fairbanks, P. O. Box 757220, Fairbanks, AK 99775-7220.

Table 1

Mean zooplankton density and percent density (standard errors, SE, in parentheses) from pooled vertical hauls in summer (n=37 hauls, 303-μm mesh) and autumn (n=8 hauls, 243-μm mesh), and from shallow (≤ 25 m) and deep (50–100 m) hauls in Prince William Sound, 1995.

| | Mean density (number of zooplankton/m³) | | | | | |
| | Summer | | | Autumn | | |
Prey category	Overall	Shallow	Deep	Overall	Shallow	Deep
Barnacle larvae	<1	<1	<1	<1	<1	<1
Calanoids, large	29 (4)	37 (7)	28 (6)	204 (60)	104 (3)	176 (3)
Calanoids, small	1018 (133)	1175 (181)	550 (87)	828 (130)	685 (48)	426 (40)
Chaetognaths	4 (<1)	3 (1)	4 (1)	3 (<1)	1 (<1)	5 (<1)
Cladocera	33 (9)	25 (9)	6 (1)	0	0	0
Cyphonautes larvae	0	0	0	205 (50)	297 (7)	333 (8)
Decapod larvae	1 (<1)	2 (<1)	<1	0	<1	0
Euphausiid larvae	3 (1)	3 (1)	2 (<1)	2 (<1)	1 (<1)	2 (1)
Gastropods	60 (10)	99 (23)	36 (5)	96 (19)	141 (4)	84 (5)
Hyperiid amphipods	2 (<1)	2 (<1)	2 (<1)	1 (<1)	1 (<1)	1 (<1)
Larvaceans	14 (4)	6 (2)	8 (3)	45 (11)	50 (12)	22 (7)
Other	17 (2)	17 (3)	8 (1)	14 (2)	18 (6)	9 (1)
Total[1]	1184 (138)	1371 (191)	645 (91)	1414 (185)	1299 (64)	1064 (56)

| | Percent composition | | | | | |
| | Summer | | | Autumn | | |
Prey category	Overall	Shallow	Deep	Overall	Shallow	Deep
Barnacle larvae	0	0	0	0	0	0
Calanoids, large	3	3	5	13	8	17
Calanoids, small	84	84	84	58	53	40
Chaetognaths	<1	<1	<1	<1	<1	<1
Cladocera	5	2	1	0	0	0
Cyphonautes larvae	0	0	0	16	23	14
Decapod larvae	0	0	0	0	0	0
Euphausiid larvae	<1	<1	<1	<1	<1	<1
Gastropods	6	7	6	7	11	8
Hyperiid amphipods	<1	<1	<1	<1	<1	<1
Larvaceans	<1	<1	<1	2	4	2
Other	2	1	1	1	1	1

[1] Numbers do not add to column totals because of rounding.

principal prey taxa, and total organisms in each vertical tow by using the expanded organism count divided by the water volume of the tow; mean values of replicate tows were used to represent each station.

Feeding selectivity of allopatric and sympatric aggregations of pollock and herring was calculated for summer and early autumn, 1995, when zooplankton were collected at the fish sampling stations. Occasionally, in summer, zooplankton samples from adjacent stations were substituted for those fishing stations without prey samples (Table 1). At stations where zooplankton was collected at two depths, the selection values presented were based on zooplankton from the depth where fish diet samples were collected. We used Strauss' linear selection index, L_0 (Strauss, 1979), a measure varying from −1 to +1, where negative values indicate no preference for the prey taxon and positive values indicate preference for the prey taxon:

$$L_0 = r_i - p_i,$$

where r_i = percentage of ith prey resource in the diet; and
  p_i = percentage of ith prey resource in the environment.

Prey resources for selection were defined as the species, stages, and sizes of prey pooled into principal taxa.

Feeding overlap between species and within species between fish in allopatric and sympatric aggregations was described by using Horn's overlap index (Horn, 1966; Smith and Zaret, 1982; Krebs, 1989). This index minimizes bias due to changing numbers of resource categories and resource evenness. Overlap was computed at two levels: prey resources were defined at the lowest level (species, stage, and size) and at a pooled level (principal taxa). Horn's overlap index values, R_0, were expressed from 0 (no overlap) to 1 (total overlap) for predator species j and k:

$$R_0 = \frac{\sum (p_{ij} + p_{ik}) \times \ln(p_{ij} + p_{ik}) - \sum p_{ij} \times \ln p_{ij} - \sum p_{ik} \times \ln p_{ik}}{2 \times \ln 2}$$

where p_{ij} = proportion of ith resource in total prey resources utilized by jth species; and
p_{ik} = proportion of ith resource in total prey resources utilized by kth species.

We considered R_0 values >0.60 to indicate similar use of resources and R_0 >0.75 to indicate very similar use of resources.

In this report, we examined both intraspecific and interspecific differences in YOY pollock and herring and qualitatively compared data between seasons, between years (in autumn), between allopatric and sympatric aggregation types, and between sympatric species. We also compared day-night feeding frequencies and prey condition to assess principal time of day of feeding. We compared zooplankton densities and percent densities of principal taxa between seasons and between depths (shallow and deep) sampled each season. Because our data were limited and the sampling design unbalanced, we present means and standard errors without statistical tests.

Results

Zooplankton prey fields

Total zooplankton densities for all samples pooled were similar in summer and autumn of 1995, averaging approximately 1200 and 1400 organisms/m³ (n=37 and 8, mesh=303 μm and 243 μm, respectively; Table 1, Fig. 2). Approximately 3/4 of samples from each season were collected in daylight, between 10:00 and 20:00.

Zooplankton taxa were less diverse in summer than in autumn, but small calanoids predominated in both seasons. Seasonal differences in the density and percentage contribution of a few taxa were apparent. Small calanoids made up a greater percentage of the total in summer compared with autumn (84% vs. 58%), but their density was similar in each season. Large calanoid density and percent density were both lower in summer than in autumn. Only a few other taxa contributed ≥5% to the total numbers of zooplankters in either season. In summer, these included cladocera and gastropods (primarily the pteropod *Limacina helicina*); in autumn, they included large calanoids, bryozoan cyphonautes larvae, and gastropods (Table 1, Fig. 2).

Calanoid species composition in the zooplankton also varied seasonally. Small calanoids in summer were predominantly *Pseudocalanus* spp. (75%) and *Acartia longiremis* (5%); in autumn, *Pseudocalanus* spp. was 40%, *Oithona similis*, 15%, and *A. longiremis*, 6% of total zooplankton. Large calanoids in summer were principally *Neocalanus* and *Calanus* spp. (3% of total zooplankton) and in autumn, they were *Metridia pacifica* (10%) and *Calanus* spp. (1%). Among other taxa present in both seasons, density and percent density of gastropods were similar between seasons, but larvaceans were less available in summer than in autumn. Cladocera were present only in summer and cyphonautes only in autumn. Hyperiid amphipods, euphausiid larvae, chaetognaths, and barnacle and decapod larvae were rare in both seasons (Table 1).
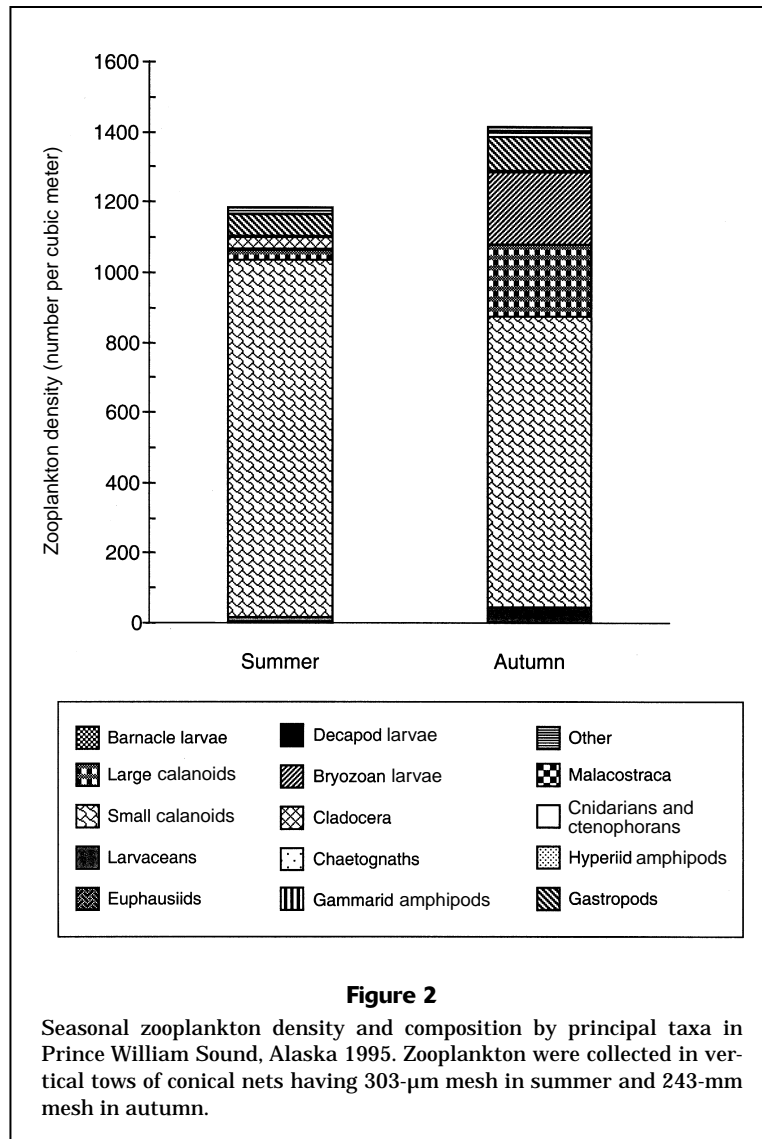
Zooplankton density per cubic meter varied with depth of sampling at all stations for both seasons. In summer (n=7 stations), zooplankton density was more than twice as high in shallow hauls as in deep hauls, whereas in autumn (n=1 station), it was greater in the shallow tows than in the deep tows (Table 1). Depth-related differences in the abundance of principal taxa, but not in their percentage composition, were also observed. Overall, in summer, small calanoids were twice as abundant in the more shallow tows, but they comprised similar percentages at each depth. In autumn, both density and percentage of small calanoids were greater in shallow tows than in deeper tows. Large calanoid density and percentage did not differ between depths in summer, but in autumn they were lower in shallow tows compared with deep tows. Gastropod abundance in both seasons, and cladoceran abundance in summer, were greater in shallow tows than in deep tows, but percentages did not differ with depth. Larvacean abundance and percentage abundance in either season, and the abundance and percentage abundance of cyphonautes in autumn, did not differ between depths.

The macrozooplankters, larval euphausiids and young hyperiids, were present, but rare in our plankton tows. However, euphausiids were captured in 11% of summer trawls and in 43% of autumn trawls. In summer of 1995,[4] juvenile–adult euphausiids were present in the northeastern and southwestern regions of the sound but were not caught in the central region or at any stations where fish were caught; in autumn (1994[7] and 1995[4]), they were present in trawls from all three regions but were absent from the allopatric trawl in October 1995. We have no consistent data on the presence or absence of hyperiid amphipods.

Fish catches

Catches of YOY walleye pollock and Pacific herring sampled from PWS that met our allopatric-sympatric criteria (see "Materials and methods" section) were not evenly rep-

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Figure 2

Seasonal zooplankton density and composition by principal taxa in Prince William Sound, Alaska 1995. Zooplankton were collected in vertical tows of conical nets having 303-µm mesh in summer and 243-mm mesh in autumn.

resented in both seasons. Only allopatric fish qualified in the summer of 1995, but both allopatric and sympatric fish qualified in the autumns of 1994 and 1995 (Table 2). In summer, 18 of the 62 trawl hauls caught sufficient samples of either species.[4] Allopatric YOY pollock were collected at 12 stations in the central region and allopatric YOY herring were collected at one central and one northeastern station in summer (Fig. 1). In autumn, 11 of the 25 trawl hauls (total 14 in November 1994,[3] 11 in October 1995[4]) caught sufficient samples of either species, and 36% of these caught sympatric fish in the northeastern region. Allopatric species were collected in different years: the allopatric pollock in November 1994 were collected in the southwestern region and the allopatric herring in October 1995 in the central region (Table 2). The remainder of pollock and herring caught did not meet our study criteria for age, number, or composition of fish per haul.

The magnitude and relative species composition of the catch varied considerably, and sampling time and depth differed between seasons. In summer, the number of pollock caught in trawls varied by two orders of magnitude between stations, from 22 to 1689 per haul (Table 2). Herring catches in the alternative gear, dip net or beach seine, were of similar magnitude. In autumn, from 14 to 4156 pollock or herring were caught per trawl haul; the catches were not evenly partitioned between the species in sympatric hauls. Similar numbers of pollock and herring were caught at some sympatric stations, whereas, at others, the number per species caught was an order of magnitude greater. In summer, approximately half the samples were collected in the morning, half in the afternoon, and only one was collected at dusk (~22:00). The pollock were caught most often at 50–80 m trawl depths ($\bar{x}$=60 m) offshore and the herring were caught at the surface and near shore. In autumn, sympatric samples were collected in darkness (approximately 22:00–23:00) at a mean depth of 30 m in bays, whereas allopatric samples were collected during daylight and in deeper water (Table 2).

Table 2

Sampling stations, catch, mean size, and feeding attributes for allopatric and sympatric YOY walleye pollock and Pacific herring (*n*=10 each) from locations in PWS in summer 1995 and autumns 1994–1995. Zooplankton samples were collected at most fishing stations only in 1995; asterisks indicate stations where an adjacent zooplankton haul was substituted. Standard error of the means (SE) is shown in parentheses. Abbreviations: T = trawl, D = dip net, B = beach seine, NE = northeast, C = central, SW = southwest.

Sampling period, target catch, cruise number, and gear	Region and location	Number caught	FL (mm)	% feeders	Fullness (%)	Content %BW	Total number of prey	Total weight of prey (mg)
Summer 1995								
Allopatric Pacific herring								
95-1-27D*	NE, Fish Bay, Port Fidalgo	271	76 (2.0)	100	100	3.8 (0.4)	5968.7 (604.3)	540.71 (62.8)
95-1-110B*	C, Southeast Eleanor Is.	—[1]	30 (0.3)	60	25	0.0 (0.0)	52.6 (28.6)	1.55 (0.7)
Allopatric walleye pollock								
95-1-3T	C, Applegate Rocks	74	59 (1.5)	60	25	0.7 (0.2)	171.0 (113.0)	14.25 (7.5)
95-1-5T	C, Seal Island	31	54 (1.2)	60	50	1.2 (0.3)	37.1 (14.1)	27.27 (12.0)
95-1-19T*	C, Lilhengren Passage	139	58 (1.7)	80	50	1.8 (0.5)	12.4 (3.6)	12.11 (5.0)
95-1-53-1T	C, Montague Point	—[1]	56 (1.1)	100	75	1.1 (0.1)	154.1 (27.5)	13.35 (2.4)
95-1-53-2T	C, Montague Point	694	62 (1.3)	100	75	1.2 (0.2)	261.5 (38.9)	34.84 (5.7)
95-1-54T	C, East Knight Island	1056	54 (1.6)	60	25	1.3 (0.3)	53.5 (30.2)	4.68 (2.2)
95-1-56T	C, Seal Island	1689	58 (1.8)	50	25	0.7 (0.2)	21.8 (10.5)	4.86 (2.1)
95-1-57T	C, Seal Island	386	58 (2.6)	80	50	1.4 (0.5)	45.0 (19.6)	38.59 (26.0)
95-1-58T	C, Knight-Seal Island	843	56 (2.1)	100	100	2.2 (0.4)	242.0 (84.8)	33.70 (9.6)
95-1-62-2T	C, East Eleanor Island	293	53 (1.1)	90	50	1.4 (0.2)	17.2 (4.3)	15.99 (7.8)
95-1-108T*	C, Southeast Knight Is.	22	66 (1.4)	100	100	2.7 (0.4)	2489.5 (351.1)	193.24 (24.6)
95-1-112T	C, South Naked Island	504	65 (2.8)	90	50	0.9 (0.1)	20.6 (4.5)	14.79 (5.0)
October 1995								
Allopatric Pacific herring								
95-2-5T	C, East Naked Island	89	92 (1.4)	100	50	1.4 (0.1)	385.9 (89.5)	103.36 (19.5)
Sympatric Pacific herring								
95-2-6T	NE, Galena Bay	425	84 (4.3)	90	75	1.2 (0.2)	927.1 (303.6)	58.63 (11.4)
95-2-7T	NE, Landlocked Bay	592	95 (3.3)	90	50	0.5 (0.1)	271.1 (103.7)	84.50 (62.3)
Sympatric walleye pollock								
95-2-6T	NE, Galena Bay	4156	93 (2.8)	100	100	1.2 (0.2)	78.3 (14.2)	61.26 (14.4)
95-2-7T	NE, Landlocked Bay	535	90 (2.4)	90	50	0.5 (0.1)	46.8 (15.0)	16.79 (3.9)
November 1994								
Allopatric walleye pollock								
94-2-5T	SW, Icy Bay	61	111 (1.6)	100	100	1.8 (0.4)	722.6 (156.2)	71.62 (11.4)
Sympatric Pacific herring								
94-2-6T	NE, Galena Bay	26	93 (4.1)	20	10	0.1 (0.0)	13.8 (9.0)	0.78 (0.5)
94-2-7T	NE, Port Gravina	398	97 (4.2)	70	25	0.5 (0.2)	31.8 (14.7)	25.64 (12.7)
Sympatric walleye pollock								
94-2-6T	NE, Galena Bay	145	100 (3.1)	70	50	0.5 (0.5)	18.5 (5.1)	18.29 (9.2)
94-2-7T	NE, Port Gravina	14	111 (1.7)	60	25	0.4 (0.1)	6.4 (1.9)	14.56 (7.5)

[1] Data missing.

Table 3

Seasonal fish size and feeding attributes of allopatric and sympatric YOY walleye pollock and Pacific herring from Prince William Sound, 1994–1995. Values are mean and standard error, SE, for fish pooled from stations shown in Table 1.

Species and sampling period	*n*	FL	Wet weight (g)	% non-feeders	Fullness (%)	Content % BW	Total number of prey	Total weight of prey (mg)
Walleye pollock								
Summer (allopatric)	120	58.0 (1.0)	1.1 (0.1)	19	50 (5)	1.4 (0.1)	294 (68)	34.0 (5.6)
Oct. 1995 (sympatric)	20	91.5 (2.4)	5.0 (0.3)	5	75 (10)	0.8 (0.3)	63 (11)	39.0 (8.9)
Nov. 1994	30	107.2 (2.0)	8.1 (0.3)	23	50 (10)	0.9 (0.2)	249 (80)	34.8 (7.2)
Allopatric	10	111.0 (1.6)	9.1 (0.4)	0	100 (5)	1.8 (0.4)	723 (156)	71.6 (11.4)
Sympatric	20	105.4 (2.1)	7.6 (0.5)	35	25 (10)	0.4 (0.1)	13 (3)	16.4 (5.8)
Pacific herring								
Summer (allopatric)	20	52.7 (2.4)	1.5 (0.3)	20	75 (10)	1.9 (0.5)	3011 (739)	271.1 (69.0)
Oct. 1995	30	90.2 (2.0)	6.6 (0.3)	7	50 (5)	1.0 (0.1)	528 (119)	82.2 (21.6)
Allopatric	10	91.6 (1.4)	6.8 (0.4)	0	50 (10)	1.4 (0.1)	386 (90)	103.4 (19.5)
Sympatric	20	89.5 (3.0)	6.5 (0.6)	10	75 (10)	0.9 (0.1)	599 (173)	71.6 (31.0)
Nov. 1994 (sympatric)	20	94.6 (2.4)	6.9 (0.3)	55	10 (10)	0.3 (0.1)	23 (9)	13.2 (6.8)

Size of YOY pollock and herring

Intraspecific patterns of size across seasons differed for YOY pollock and herring. Mean FLs for both species were approximately 60% longer in autumn than in summer. Herring size was similar in autumn of both years, but pollock were 14 mm longer in FL and 50% heavier in November 1994 than in October 1995 (Tables 2 and 3). Interspecific comparisons of size showed that YOY pollock were generally longer, but not heavier, than YOY herring in the same season.

Feeding habits of YOY pollock and herring

Prey composition of YOY pollock was similar to that of YOY herring in both summer and autumn (Figs. 3 and 4), but prey compositions differed between seasons. Small prey predominated in summer and larger prey in autumn, especially in terms of biomass composition.
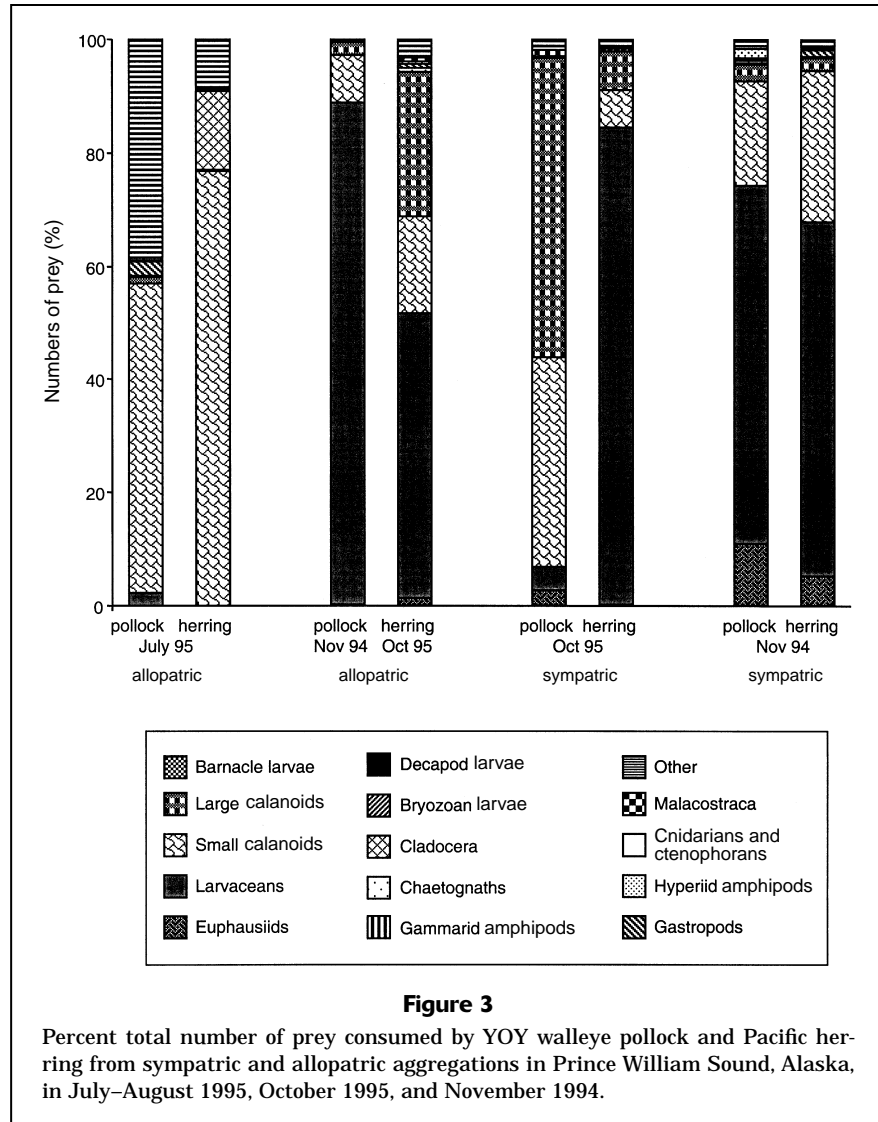
In summer, small calanoid copepods (*Pseudocalanus* spp., *Centropages abdominalis,* and *Acartia longiremis*) dominated the diets, both numerically and in terms of prey biomass (Figs. 3 and 4). For pollock, small calanoids constituted 55% by number and 57% by weight of diet. By number, most of the remainder of summer pollock diet comprised minute invertebrate eggs (39%); by weight, the remainder was large calanoids (principally *Calanus pacificus*, *C. marshallae,* and *Metridia pacifica*), fish, hyperiid amphipods, and euphausiids (both larvae and older stages, including *Thysannoessa* sp.). Pollock also commonly consumed small amounts of other prey, such as larvaceans, gastropods, and chaetognaths. For herring, small calanoids represented proportionally more of the diet than for pollock in summer. Small calanoids made up 77% by number and 88% by weight of herring diet; they were the sole taxon consumed by the YOY herring at Eleanor Is-

land station 110 (Table 2). Most of the rest of herring diet comprised other small prey (cladocerans, bivalve larvae, and minute invertebrate eggs), whereas decapod larvae, gastropods, hyperiids, and euphausiid larvae made minor contributions.

In autumn of both years, pollock and herring again fed on the same prey categories. Compared with summer, small calanoids composed smaller percentages of the diet (only up to 37% of prey number and 9% of prey biomass). Larvaceans and large calanoid copepods numerically dominated their diets (57–91%; Fig. 3), whereas euphausiids and large calanoids generally dominated in terms of biomass percentages (49–89%; Fig. 4). Hyperiids occasionally contributed substantial dietary biomass. Fish in all of the autumn aggregations ate a variety of sizes of juvenile–adult euphausiids (*T. raschii, T. spinifera,* and unidentifiable species), and amphipods (*Themisto pacifica*, *Primno macropa,* and *Hyperia* sp.), but not the larval stages observed in summer diets. The large calanoids consumed included the same species present in summer diets, as well as *M. okhotensis* and *Neocalanus* spp.; the small calanoids included *Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis*. Some differences in autumn diet composition existed between years. Invertebrate eggs (the majority of "other") were present less frequently in autumn diets than in summer diets. In general, the October 1995 diets included proportionally more biomass from large calanoids, whereas the November 1994 diets included proportionally more biomass from euphausiids and proportionally more numbers from larvaceans.

Diet overlap between YOY pollock and herring was high, particularly when prey species were grouped into principal taxa (Table 4). In summer, diets were very similar ($R_0 \geq 0.76$) between allopatric species in terms of numbers and weights of prey species or principal prey taxa. In autumn, interspecific diet overlap was also observed

Figure 3

Percent total number of prey consumed by YOY walleye pollock and Pacific herring from sympatric and allopatric aggregations in Prince William Sound, Alaska, in July–August 1995, October 1995, and November 1994.
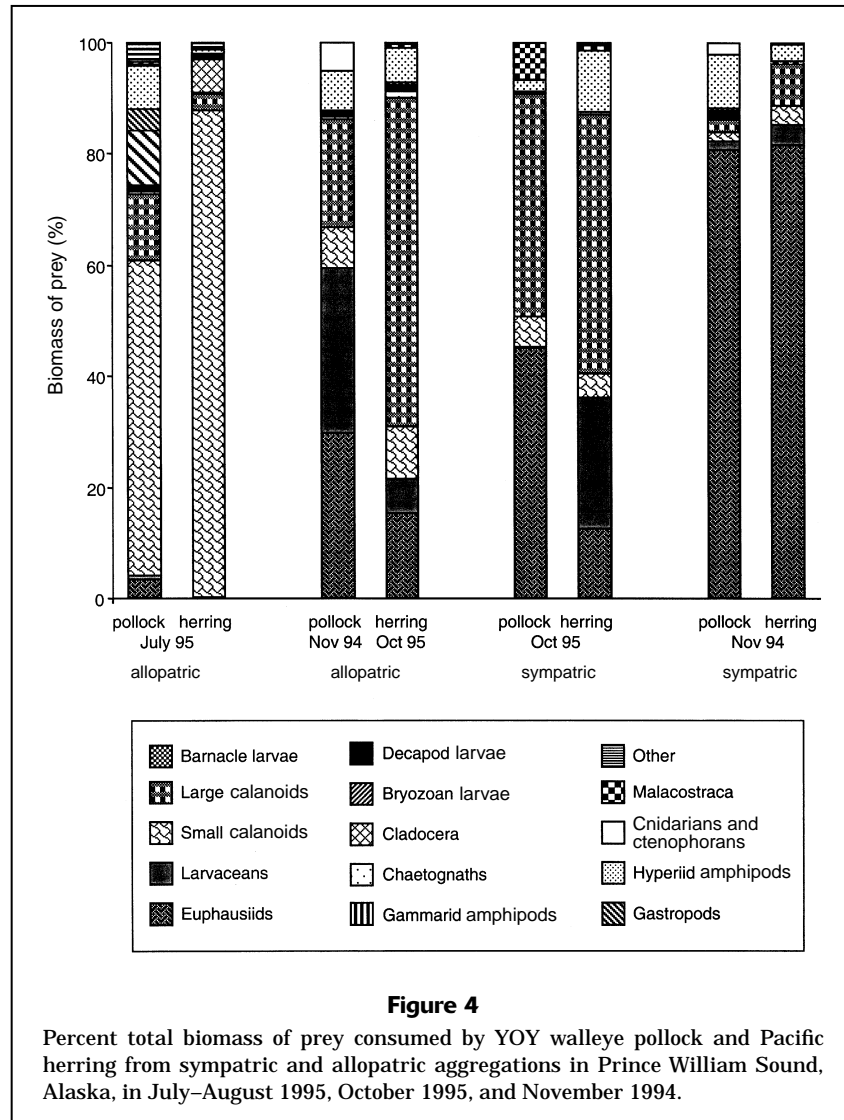
in terms of prey numbers and weights. Numeric overlap for the November 1994 sympatric species was observed at both stations, and the mean was approximately twice that for the October 1995 sympatric species (R_0=0.97 versus 0.43). Biomass overlap between sympatric fish occurred at three out of four autumn stations when based on principal prey taxa, but only at one station (in November) when based on prey species. Overall, diets of sympatric pollock and herring overlapped more in terms of biomass in November (R_0=0.95) than in October (R_0=0.69). We did not have autumn samples from the same year to compare allopatric diet overlap between species.

Prey selection

We noted selection from zooplankton prey resources by pollock in summer and by pollock and herring in autumn, 1995 (Fig. 5). Selection patterns were almost identical whether calculated from shallow or deep zooplankton

abundances; values were always in the same direction (selection or avoidance), and their magnitude was within 10 points. Neither species selected small calanoids, the most abundant zooplankton taxon in both seasons. In summer, even though small calanoids made up >50% of YOY pollock and herring diets (Figs. 3 and 4), this taxon was avoided by pollock and was consumed in close proportion to its availability by herring (Fig. 5). Summer pollock moderately selected for large calanoids, gastropods, and larvaceans, but summer herring did not strongly select for any prey category.

Changes in zooplankton composition from summer to autumn were reflected in fish diets and prey selection. The percent density of small calanoids in the zooplankton declined by nearly 30% from summer to autumn, the percentage consumed by fish was likewise much reduced, and selection values were more strongly negative. In contrast, both large calanoids and larvaceans were more abundant in zooplankton samples in autumn than in summer and,

Figure 4

Percent total biomass of prey consumed by YOY walleye pollock and Pacific herring from sympatric and allopatric aggregations in Prince William Sound, Alaska, in July–August 1995, October 1995, and November 1994.
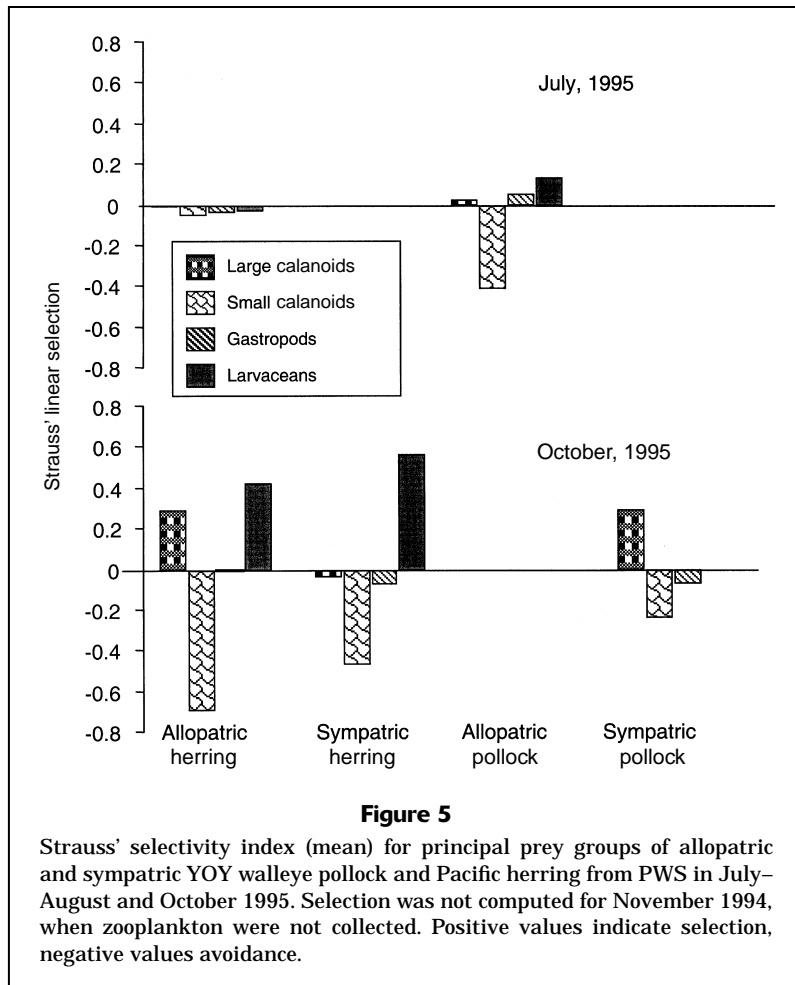
along with euphausiids and hyperiids, formed larger dietary components at that time. In autumn (October 1995), pollock strongly selected for large calanoid copepods and herring strongly selected for larvaceans (Figs. 3–5). Additional differences were noted in terms of prey frequency. In summer, pollock consumed hyperiids more frequently than they consumed euphausiids, and in autumn, both pollock and herring consumed euphausiids more frequently than hyperiids.

Seasonal feeding

Several measures of feeding in autumn indicated that YOY pollock continued to feed moderately, whereas the pattern for YOY herring showed more of a decline from summer (Tables 1 and 3). Very similar high percentages of pollock and herring had fed in summer and in October 1995 (≥80%), but in November 1994, the percentage of nonfeeding herring was greater than the percentage of

feeding herring, and was more than twice the percentage of nonfeeding pollock (Table 3). For pollock, the November 1994 feeding measures were only lower than the high summer measures, whereas for herring, feeding measures in autumn of 1994 were lower than in either summer or autumn of 1995. Although pollock stomachs were at least half full in each season, herring stomach fullness declined from 75% full in summer to half full in October 1995, to only trace amounts of food in November 1994. Similarly, prey content %BW declined less between seasons for pollock than for herring. Total prey numbers and weights were generally lower for pollock than for herring in a season, but numbers of prey were highly variable and biomass of prey was relatively stable for pollock, whereas these measures showed declining trends for herring (Fig. 6, Table 3).
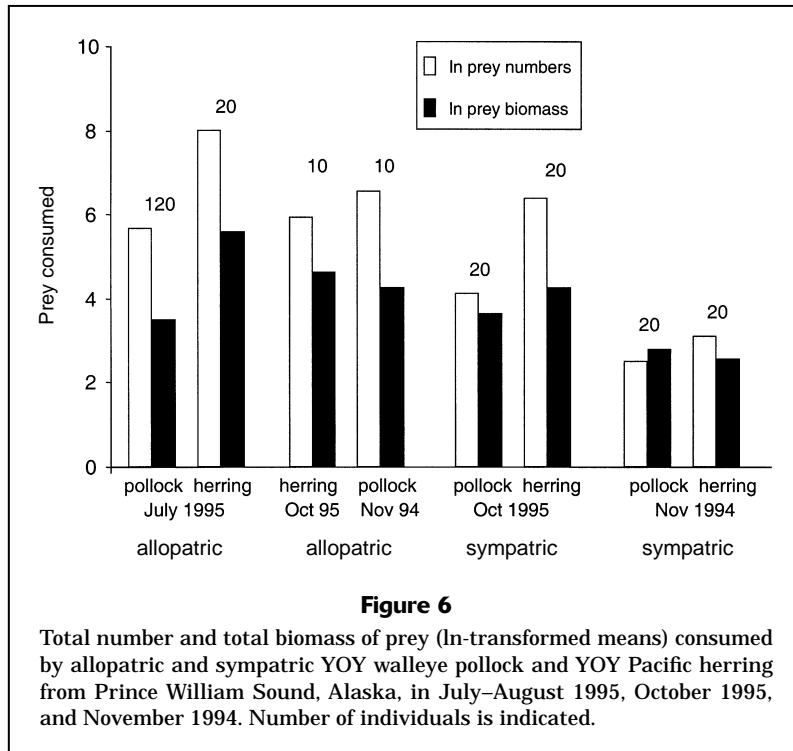
Digestion data and feeding-frequency data for individual fish were pooled across seasons to compare day and night feeding patterns. The condition of stomach contents

Figure 5

Strauss' selectivity index (mean) for principal prey groups of allopatric and sympatric YOY walleye pollock and Pacific herring from PWS in July–August and October 1995. Selection was not computed for November 1994, when zooplankton were not collected. Positive values indicate selection, negative values avoidance.

Table 4

Horn's overlap index values for total numbers and biomass of prey consumed by YOY walleye pollock and Pacific herring caught separately in summer and together in autumn in Prince William Sound, 1994–1995. No summer sympatric fish were available and autumn allopatric fish were not caught in the same year. Overlap greater than 0.60 indicates similar diets (see text). C = central; NE = northeast.

Sampling period and target catch		By prey Region	Overlap in number		Overlap in biomass	
			By prey species	By prey category	By prey species	category
Interspecific diet overlap						
July 1995 allopatric fish	1995	C, NE	0.79	0.82	0.76	0.83
October 1995 sympatric fish	1995–96	NE	0.16	0.22	0.44	0.64
	1995–97	NE	0.43	0.48	0.53	0.69
	Average	NE	0.31	0.43	0.55	0.69
Intraspecific diet overlap						
November 1994 sympatric fish	1994–96	NE	0.69	0.94	0.08	0.39
	1994–97	NE	0.86	0.91	0.88	0.91
	Average	NE	0.87	0.97	0.88	0.95
Allopatric-sympatric fish						
October 1995 herring			0.51	0.89	0.56	0.93
November 1994 pollock			0.87	0.91	0.56	0.73

Figure 6

Total number and total biomass of prey (ln-transformed means) consumed by allopatric and sympatric YOY walleye pollock and YOY Pacific herring from Prince William Sound, Alaska, in July–August 1995, October 1995, and November 1994. Number of individuals is indicated.

by time of day was different for the two species. Pollock had greater percentages of mostly digested contents during the day than during the night (before and after 22:00). Conversely, herring had greater percentages of mostly digested contents during the night than during the day. The day-night percentages of feeding and nonfeeding fish were similar for both, however.

Comparisons between allopatric and sympatric fish aggregations

The allopatric-sympatric size pattern was different for pollock and herring. We did not pool sympatric fish from October 1995 and November 1994 for comparison with allopatric groups because of the interannual differences in size and feeding measures. For pollock in November 1994, FLs of allopatric and sympatric fish were similar, but fish were approximately 1.5 g lighter in sympatric aggregations than fish in allopatric aggregations. For herring in October 1995, the sizes of allopatric and sympatric fish were similar (Table 3).

The allopatric-sympatric feeding pattern was somewhat different for pollock than for herring in autumn. Among November 1994 pollock, the allopatric fish consistently had the highest feeding measures and the sympatric fish consistently had the lowest feeding measures (Fig. 6, Table 3). This finding coincided with slightly increased numerical percentages of larvaceans, increased gravimetric percentages of euphausiids, and increased frequencies of euphausiids, amphipods, and large calanoids in the diet of allopatric pollock compared with the diet of sympatric pollock (Figs. 3 and 4). For October 1995 herring, allopatric

fish consumed the greatest prey biomass and %BW, but their prey numbers and fullness index were lower than those of sympatric fish (Fig. 6, Table 3). This finding coincided with decreased numerical percentages of larvaceans, increased numerical and gravimetric percentages of large calanoids and euphausiids, and increased frequencies of occurrence of hyperiids and euphausiids in the diet of allopatric herring compared with diet of sympatric herring (Figs. 3 and 4). Allopatric herring were more selective of large calanoids, but selection for larvaceans was similar for both groups of herring (Fig. 5). For both species, intraspecific diet overlap between allopatric and sympatric fish was extensive at the principal taxon level. In October 1995 intraspecific overlap in terms of prey biomass was 0.93 for herring, and in November 1994, intraspecific overlap in terms of prey number was 0.91 for pollock.

Discussion

Zooplankton prey fields

The prey fields available to planktivorous YOY walleye pollock and Pacific herring were different in summer and autumn 1995. Although we report similar total zooplankton densities for the two seasons, we believe that summer densities of small calanoids were underestimated with the 303-μm net. This conclusion is based on a 1995 companion study that showed that a 243-μm mesh net retained small calanoids better than a 303-μm mesh net.[8] The sea-

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[8] Sturdevant, M. V.   In review.

sonal densities presented in our study were not directly comparable because of the different gear used, and our summer mesozooplankton densities were lower than those reported from other summer collections in PWS[9] (Cooney et al., 1981; Celewycz and Wertheimer, 1996). The food supply available to juvenile fish was likely more abundant in summer than in autumn, because other studies in the northeastern Pacific showed a steady decline in zooplankton biomass from summer to winter (Peterson and Miller, 1977; Cooney, 1986; Incze et al., 1997; Foy and Paul, 1999). Zooplankton taxonomic compositions also differed seasonally, mainly in the larger percentages of alternate prey available in autumn.

We found the surface-water feeding environment to be richer in numbers of prey than the deeper water in both seasons. Lower zooplankton density with depth has been reported by other authors in PWS,[10] Shelikof Strait (Napp et al., 1996), off the Oregon Coast (Marlowe and Miller, 1975), and at Ocean Station "P" (Petersen and Miller, 1977). Large calanoids were an exception in autumn, however, when their densities and percentages were greater in the deeper tows, typical of subarctic locations (e.g. Marlowe and Miller, 1975; Nakatani, 1988; Napp et al., 1996).

High abundances of *Pseudocalanus* spp. and other small calanoids and high biomass of large calanoids are characteristic of neritic locations in subarctic Pacific waters, such as those of PWS in summer (Springer et al., 1989; Coyle et al., 1990; Celewycz and Wertheimer, 1996; Incze et al., 1997). The time of collection for zooplankton is important, however, because the location of peak abundance in the water column varies with their diel vertical migration. Calanoid copepods are usually most abundant at the surface at night, migrating deeper during the day (e.g. Sekiguchi, 1975). Even though most of our samples were collected during the day, it is not surprising that abundances were greater in shallow tows than in deeper tows because *Pseudocalanus* was dominant. Of the species important in our study, *Pseudocalanus newmani* was typically the shallowest in depth distribution, *Calanus pacificus* was intermediate and *Metridia pacifica*, the deepest (e.g. Bollens and Frost, 1989; Frost and Bollens, 1992; Bollens et al., 1993; Bollens et al., 1992b). However, the vertical distribution patterns of these species were influenced by the presence of predators and other factors (e.g. Bollens and Frost, 1989; Bollens et al., 1992b; Frost and Bol-

lens, 1992; Bollens et al., 1993). The seasonal difference in depth distribution of large calanoids could have been due to seasonal vertical migrations (Sekiguchi, 1975; Mackas et al, 1993), differences in sampling time, or a response to the changing light regime in autumn.

Feeding habits

Summer and autumn diets of YOY allopatric and sympatric walleye pollock and Pacific herring in PWS were similar to those reported from other areas and to those of other pollock and herring caught during the study that did not meet our criteria (Sturdevant, unpubl. data; see "Materials and methods" section). In summer, both species consumed the abundant calanoid taxa as well as less abundant small prey. Calanoid copepods were likewise the predominant summer prey of YOY pollock in Japanese waters (Kamba, 1977; Nakatani, 1988), the region of the Kodiak Island-Alaska Peninsula,[11] the Gulf of Alaska and eastern Bering Sea (Grover, 1990, 1991; Brodeur et al., 1997), PWS (Willette et al., 1997; Foy and Norcross, 1999a), and southeastern Alaska.[12] The small calanoid *Acartia clausi* was particularly important in southeastern Alaska diets from August to October,[12] but by late summer in other areas, euphausiids accounted for more prey biomass and calanoids continued to dominate numerically (Merati and Brodeur, 1996). The autumn prey composition of pollock in our study was also similar to that of YOY pollock in the Gulf of Alaska (Merati and Brodeur, 1996; Brodeur et al., 2000), eastern Kamchatka (Sobolevskii and Senchenko, 1996), and southeastern Alaska.[12] In those studies, increased fish size was correlated with decreased predation on small copepods and increased predation on large copepods, larvaceans, and euphausiids. By winter, large copepods virtually disappeared from diets in some areas (Sobolevskii and Senchenko, 1996); chaetognaths and epibenthic prey such as mysids, shrimps, caprellid amphipods, and cumaceans were incorporated in the diet as vertical distributions of the fish changed and pelagic prey became scarce[12] (Merati and Brodeur, 1996; Sobolevskii and Senchenko, 1996; Brodeur et al., 2000). Seasonal changes in prey have also been correlated with change in YOY pollock distribution and the use of different habitats (Nakatani, 1988).

Like pollock, YOY Pacific herring depended on small calanoid prey in PWS and throughout their range. Additional small prey taxa are commonly reported in Pacific herring and other species diets, including invertebrate eggs, barnacle larvae, cladocerans, oikopleurans, and juvenile amphipods and euphausiids[9] (Wailes, 1936; Sherman and Perkins, 1971; Last, 1989; Arrhenius and Hans-

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[8] (*continued*) Summer zooplankton density and composition estimates from 20-m vertical hauls using three net meshes. Alaska Fisheries Research Bull., Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Hwy., Juneau, AK 99801.

[9] Sturdevant, M. V., and L. B. Hulbert. 1999. Diet overlap, prey selection, and potential food competition among allopatric and sympatric forage fish species in Prince William Sound, 1996. *In* Forage fish diet overlap, 1994–1996, p. 72–100. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 97163C), Auke Bay Laboratory, National Marine Fisheries Service, 11305 Glacier Hwy., Juneau, Alaska 99801.

[10] Foy, R. J., and B. L. Norcross. In prep. Nearshore zooplankton community ecology in Prince William Sound, Alaska. J. Plankton Res., Institute of Marine Science, Univ. Alaska Fairbanks, P. O. Box 757220, Fairbanks, AK 99775-7220.

[11] Livingston, P. A. 1985. Summer food habits of young-of-the-year walleye pollock, *Theragra chalcogramma*, in the Kodiak area of the Gulf of Alaska during 1985. Unpubl. manuscr., Alaska Fish. Sci. Center, National Marine Fisheries Center, 7600 Sand Point Way NE, Seattle, WA 98115, 8 p.

[12] Krieger, K. J. 1985. Food habits and distribution of first-year walleye pollock, *Theragra chalcogramma* (Pallas), in Auke Bay, Southeastern Alaska. Unpubl. MS thesis, Univ. Alaska Juneau, 11305 Glacier Hwy., Juneau, AK 99801, 57 p.

son, 1994; Arrhenius, 1996; Haegele, 1997; Willette et al., 1997). In addition to pelagic prey, epibenthic prey such as harpacticoid copepods and gammarid amphipods were important in estuarine habitats of the Fraser River for Pacific herring and coastal Maine for Atlantic herring (Sherman and Perkins, 1971; Blaxter and Hunter, 1982; Levings, 1983, in Lassuy, 1989). Spatial differences were found for diets of Pacific herring from four widespread bays in PWS (Foy and Norcross, 1999a). We found seasonal differences in prey similar to reports by others: euphausiids replaced calanoids in the diets of older juvenile herring compared with younger juvenile herring (Wailes,1936; Lassuy, 1989; Haegele, 1997), and larvaceans (Foy and Norcross, 1999a, 1999b), mysids, and other malacostracans (Foy and Norcross, 1999a; Foy and Paul, 1999) were also more common in autumn. In Auke Bay, Alaska, juvenile herring diets varied with abundance of zooplankton prey taxa in spring and early summer and included large calanoids and euphausiids when they were present (Coyle and Paul, 1992). The marine distribution of the alewife, *Alosa pseudoharengus,* another herring, was correlated with the seasonal distribution, availability, and abundance of its euphausiid prey (Stone and Jessop, 1994).

Prey selection, feeding time, and depth

Segregation by depth is one way to reduce interspecific competition among fish with overlapping distributions (e.g. Jessop, 1990; Arrhenius, 1996). Both pollock and herring perform diel vertical migrations (Smith, 1981; Blaxter and Hunter, 1982), the pattern of which can vary seasonally and ontogenetically (e.g., Kamba, 1977; Lassuy, 1989; Olla et al., 1996; Stokesbury et al., 2000). We observed some interspecific differences in prey selection that may relate to diel vertical distributions of predator and prey, prey preferences, ontogenetic changes in prey size, or different feeding rhythms for both species. Neither species selected small calanoids in summer, and pollock selected taxa that herring did not (large calanoids, pteropods, and larvaceans). The summer herring were located nearshore and at the surface where densities of their main prey were twice as high as deep in the water column and where light for feeding was most intense. In contrast, summer pollock were located in relatively deep water with less light and lower prey densities. Even though small calanoids were the predominant prey of pollock and the predominant zooplankter, they were avoided in relation to their availability. In autumn, both species avoided small calanoids even more strongly than in summer. In autumn, sympatric pollock in shallow water selected large calanoids, mainly *Metrida pacifica*, that were less available than in deeper water, but only the deeper allopatric herring selected them. Young Pacific herring in another study selected *Calanus pacificus* over *Metridia lucens*, perhaps in relation to fine-scale differences in prey depth distributions (Fortier and Leggett, 1983 in Munk et al., 1989; Bollens et al., 1993). Both sympatric herring and allopatric herring strongly selected the larvaceans that were more evenly distributed in the water column. We primarily sampled fish schools that were located acoustically and

assumed that the fish would be located where food was available (e.g. Arrhenius and Hansson, 1999). Comparisons of prey selection between seasons are valid because the calculations are based on prey percentages which did not differ between the 243- and 303-μm mesh sizes used.[8]

The less-digested condition of herring stomach contents by day compared with night suggests that the summer fish and autumn allopatric fish were actively feeding and that the autumn sympatric fish were not. The condition of pollock prey and the fact that the fish were not located where their selected prey were in either season suggest that pollock were not actively feeding at the times we sampled in either season. The change in digested state of their prey with time of day also suggests that YOY pollock may seasonally or ontogenetically switch from feeding principally during the day to feeding at night[12] (Merati and Brodeur, 1996; Brodeur et al., 2000).

Past diel studies have reported different patterns of feeding for pollock and various herring species. For example, peak time of feeding for pollock was at midnight or just before dawn in some studies (Brodeur and Wilson,1996a; Merati and Brodeur, 1996; Willette et al., 1997), but another study showed a change in feeding chronology from sunset in small fish to night in larger fish (Brodeur et al., 2000). Peak time of feeding for Atlantic, Baltic, and Pacific herring occurred in the afternoon or evening, with the lowest feeding rates in early morning (e.g. de Silva, 1973; Blaxter and Hunter, 1982; Mehner and Heerkloss, 1994; Willette et al., 1997; Arrhenius, 1998). Changes in prey composition with time of day and ontogeny have also been noted in some studies (e.g. Nakatani, 1988; Grover, 1991; Munk, 1992; Stone and Jessop, 1994) and not others (Brodeur et al., 2000). If co-occurring fish feed at different times, their diets could be highly similar without direct competition because predation on the same prey resources would be temporally or spatially separated. This could be the case with small calanoid prey, which both species fed on in summer, but only herring were co-located at the depth of prey concentration. Different feeding periodicities could result in indirect competition if prey resources are limited, however.

Sampling time could also affect the appearance in the diet of vertically migrating macrozooplankton, such as juvenile-adult euphausiids and hyperiid amphipods, because the vertical locations of peak abundance of predator and prey may not overlap continually. For example, euphausiids could be consumed at night near the surface or during the day near the bottom[12] (Pearcy et al., 1979; Nakatani, 1988). Juvenile euphausiids were rare summer prey in our study and were present only in those trawls taken below the 60-m mean depth of pollock catches.[2] In autumn, the euphausiid and fish distributions were more likely to overlap during the night sampling time (e.g. Bailey, 1989; Bollens et al., 1992a), and euphausiids were indeed a principal prey in terms of biomass, particularly for pollock. Large calanoids and euphausiids could have been consumed at different feedings, particularly if their vertical distributions overlapped with those of the fish at different times. Predation by pollock and herring on euphausiids in areas where these macrozooplankters were not

collected suggests that the fish fed in a different area or at a different time.

Comparison of allopatric and sympatric aggregations

If competition occurs between sympatric species, one would expect that, given similar prey fields, the quantity or quality of prey consumed would improve when fish are allopatric. If such changes are prolonged, growth or survival differences are probable. We found intraspecific changes in diet composition and food quantity for both species from allopatric to sympatric aggregations, and weak interspecific differences in feeding between sympatric fish. Both species of fish avoided small calanoids whether a competitor was present or not, but the proportional use of energetically advantageous taxa (large calanoid, euphausiid, and hyperiid prey) and the selection for large calanoids were lower in the presence of competitors. Comparisons of sympatric fish showed that pollock ate proportionally more high energy-producing prey (euphausiid biomass, hyperiid frequency, large calanoid numbers) and selected *Metridia* spp. more strongly than herring. Overall, however, high diet overlap between allopatric and sympatric fish of either species in autumn indicated little change in diet composition owing to sympatry. Because both species of sympatric fish ate less total prey than allopatric fish, quantity, rather than quality of prey decreased in the presence of competitors or perhaps as a density-dependent response. Drastic diet shifts were demonstrated in one study involving fish removal; planktivorous species became benthivorous when their competitors were removed from a lake (Persson and Hansson, 1999). In our study, however, although the intraspecific comparisons (allopatric-sympatric) were within month, they differed by depth, time, or region; the interspecific comparisons of allopatric fish were a month apart in different years. Many authors have found differences in zooplankton prey fields on these scales[10] (e.g. Springer et al., 1989; Celewycz and Wertheimer, 1996), making it difficult in our study to separate the effects of sampling differences from those due to competition on diet and feeding.

Seasonal feeding

We observed the highest frequency of empty stomachs for both species in the November 1994 samples; empty stomachs, however, were more frequent for herring than for pollock. Similarly, in other seasonal studies, the proportion of empty stomachs in YOY herring peaked in winter (Foy and Norcross, 1999a; Foy and Paul, 1999), but empty stomachs were never observed among YOY pollock, even though stomachs were least full in December.[12] As zooplankton biomass declined between the winter months of October and February, the feeding response and whole body energy content of herring also declined (Foy and Paul, 1999). The herring relied on stored energy to overwinter (Paul et al., 1998a; Paul and Paul, 1998), but pollock are thought to allocate energy from year-round feeding for somatic growth (Paul et al., 1998b).

We also observed declines in zooplankton coincident with feeding declines in autumn; conversely, a greater food supply of small calanoids supported trends toward more intensive feeding in summer. Feeding on small calanoids in summer could have been density dependent because this taxon was found to be most prominent in the diets when it was more abundant in zooplankton samples. Juvenile Baltic herring exhibited a similar functional response to greater food densities (Arrhenius and Hansson, 1999). However, decreased feeding on small calanoids is more likely related to fish size and energy requirements. Both species (especially pollock in November 1994) were larger in autumn when they ceased consuming small calanoids, and both species avoided them more often. Larger prey are more efficient sources of energy for larger fish, if available. The larger autumn fish were probably better able to prey on late stages of macrozooplankton than the summer fish (Merati and Brodeur, 1996; Haegele, 1997; Kamba, 1977), in synchronism with a seasonal difference in their abundance and availability[13] (Bollens et al., 1992a; Stone and Jessop, 1994; Incze et al., 1997). A shift to larger prey is consistent with a decrease in prey numbers without a change in prey weight because fewer large prey are needed for equivalent weight. The biomass percentages of large prey consumed (large calanoids and euphausiids) and the numeric percentages of small prey consumed (larvaceans) both increased in autumn compared with summer (see also Foy and Norcross, 1999a). Ontogenetic changes and size-selective feeding have been reported by others, as well, for juvenile herring (e.g. Raid, 1985; Munk, 1992; Arrhenius, 1996) and juvenile pollock (Grover, 1991; Brodeur, 1998).

In conjunction with the seasonal diet transition, total prey number and most other measures of quantity were lower in autumn than in summer, particularly for herring. Autumn declines in juvenile pollock feeding rates were also observed in a study in Southeast Alaska in conjunction with a switch from small prey to larger prey.[12] Similarly, feeding declined seasonally for Atlantic herring (de Silva, 1973), Baltic herring (Arrhenius and Hansson, 1999), and Pacific herring (Foy and Norcross, 1999a). In our study, pollock consumed well above maintenance ration (0.30 %BW at 7.5°C; Smith et al., 1986) in all time periods, but, the low prey %BW of herring in autumn 1994 could indicate starvation, given a ration of 1.3–3.6 %BW at 6.2–8.7°C (de Silva and Balbontin, 1974; Arrhenius and Hansson, 1994). Continued feeding and better fish condition late in the year are advantageous for survival through the extreme conditions of winter, and relate to the species different strategies for overwintering.

Declines in feeding with season were also indicated by increased diet overlap between sympatric species in November compared with overlap in October, which suggests a density-dependent convergence of feeding with declining prey resources in late autumn. For sympatric fish in au-

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[13] Mooney, J. R. 1999. Distribution, energetics, and parasites of euphausiids in Prince William Sound, Alaska. Unpubl. MS thesis, Juneau Center School of Fisheries and Ocean Science, Univ. Alaska Fairbanks, 11122 Glacier Hwy., Juneau, AK 99801, 172 p.

tumn, lower diet overlap occurred when pollock were more selective for large calanoids and ate proportionally more euphausiids, and the herring selected larvaceans (October 1995); greater dietary overlap in autumn occurred when the species ate similar percentages of these taxa and small calanoids (November 1994).

Despite larger size in autumn, energy requirements of fish are lower during this period of less abundant food due to environmental changes. In PWS, surface temperatures declined from approximately 12°C in summer, to 10°C in October 1995, and 7–8°C in November 1994.[2] Temperatures below the thermocline were stable at 5–6°C, but thermocline depth varied seasonally, between approximately 40–60 m in summer and 50–90 m in either autumn.[3,4] Additional seasonal changes in the environment have been reported by Stokesbury et al. (1999). From summer to winter in PWS, surface waters inside bays changed from being colder to being warmer than surface waters outside bays. Such environmental temperature changes in both the vertical and horizontal planes may influence the distribution of pollock and herring, their energy budgets (Smith and Paul, 1986), and the seasonal distribution and abundance of their prey.

Fish can conserve energy during times of reduced prey by altering behaviors to maximize prey searching or to decrease metabolic costs. For example, fish can alter school cohesiveness (Brodeur and Wilson, 1996b; Stokesbury et al., 1999), restrict their movement, or shift in residence to deeper water with colder temperatures (Sogard and Olla, 1996; Ciannelli et al., 1998). However, they may do so at the risk of increased predation or decreased light for feeding. Herring are primarily visual feeders, requiring minimum light levels to feed (Blaxter and Hunter, 1982) but may also filter feed in low light (Batty et al., 1986; Stone and Jessop, 1994). They can respond to prey distributions correlated with thermocline depth (Fossum and Johannessen, 1979) and may shift feeding during the day to depths where light is not restrictive even if prey are concentrated elsewhere (Munk et al., 1989). Similarly, the vertical distribution of juvenile pollock is affected by the relative availability of food and by numerous other factors that affect feeding conditions: predator presence, light, turbidity, pressure, temperature, size, and metabolic requirements (Bailey, 1989; Olla et al., 1996; Sogard and Olla, 1996; Ciannelli et al., 1998). Juvenile pollock avoided light more and avoided cold water less with growth, especially under conditions of low zooplankton (Olla et al., 1996). Both juvenile pollock (Smith et al., 1986) and YOY herring (de Silva and Balbontin, 1974; Arrhenius and Hansson, 1994) decreased prey consumption at colder temperatures; pollock also had lower maintenance rations and grew more rapidly under conditions of low food with colder temperatures (Smith et al., 1986). Competition with pollock for food could compromise the winter survival of YOY herring by limiting the accumulation of their energy stores.

Research showing major differences in the nutritional quality of forage species consumed by piscivores has sparked interest in their trophic interactions. Pollock lipid content was low compared with that of herring, but unlike herring, was not correlated with size (Anthony and Roby, 1997; Payne et al., 1999; Anthony et al., 2000). However, only a few studies have examined the energetic consequences of feeding on different prey for juvenile pollock (e.g. Smith et al., 1986; Davis and Olla, 1992; Ciannelli et al., 1998) and herring (e.g. de Silva and Balbontin, 1974; Arrhenius and Hansson, 1999). Because prey differ in nutritional composition, caloric density (Ikeda, 1972; Lee, 1974; Deibel et al., 1992; Davis et al., 1998), size, mobility, and behavior, their relative abundance is not the only factor of importance. For example, larvaceans are a highly visible taxon (Bailey et al., 1975) with caloric value per unit weight similar to that of crustacean zooplankton even though they are gelatinous (Davis et al., 1998), but many more larvaceans must be consumed to accumulate the equivalent calories obtained from the crustaceans. Davis and Olla (1992) showed in a controlled experiment that larval pollock growth, behavior, and lipid concentration were affected by the nutritional quality of prey. In a field study, herring diets had the highest energy density of all in May, when large calanoids were the most important taxon (Foy and Norcross, 1999a); however, they were not examined from late fall—a period for which our study showed that euphausiids were the prominent prey and others have shown they contain higher energy density compared with earlier times of the year.[13] If sympatry induces feeding on prey of lesser nutritional quality for extended periods because of interference competition, fish growth and survival could be affected.

For sympatry to occur, the distribution of juvenile walleye pollock and Pacific herring must overlap in three dimensions: time (seasonal and diel), and both horizontal and vertical space. These species have different life histories (Smith, 1981; Lassuy, 1989) and patterns of movement change ontogenetically, suggesting that spatial overlap is likely to vary. YOY herring generally school near the bottom along shore during the day, then move up to the surface at dusk and disperse (Blaxter and Hunter, 1982; Lassuy, 1989; Haegele, 1997). Early YOY pollock stay principally in surface water above the thermocline, perform a diel vertical migration (DVM), and disperse or move inshore at night; depth distribution increases from summer to autumn[12] and with ontogeny (e.g. Nakatani, 1988; Karp and Walters, 1994; Olla et al., 1996). Stokesbury et al. (1999) found that herring and pollock were generally depth stratified but that both were aggregated in bays in July and October. Rather than having a strong species association, they may simply have an affinity for the same habitats at some points in their life histories (Brodeur and Wilson, 1996a). Data collected monthly in PWS in 1994 (Willette et al., unpubl. data) showed that, after May, >50% of juvenile herring sets also caught juvenile pollock, and after July, >50% of juvenile pollock sets also caught juvenile herring. Willette et al. (1997) noted that diet overlap was more than twice as great for pollock and herring from sympatric sites than for these species from allopatric sites in late summer. These patterns suggest that sympatry and feeding competition increase from spring through summer.

Our study is the first to examine the feeding interactions of juvenile walleye pollock and Pacific herring. Its limited scope, because it was designed for other primary

purposes, necessitates a primarily descriptive approach. Differences that we observed in fish feeding could relate to variable sampling intensity, limited fish sample sizes, gear limitations for certain prey taxa, spatial variation in prey, or differences in fish depths. Nonetheless, the similarity of dietary requirements between YOY pollock and herring could induce competition for limited food when these fish co-occur during periods or in places of low food availability, particularly late autumn and winter. Stokesbury et al. (1999) showed spatial variation in growth of YOY herring among widespread bays in PWS and surmised that density-dependent interspecific competition for food was one variable that affected growth rates; likewise, Paul and Paul (1999) showed interannual and spatial variations in size and energy content of YOY pollock from PWS and speculated that prey production and delivery contributed to the differences. The densities of planktivorous predators may exceed the carrying capacity of bays where walleye pollock and Pacific herring are sympatric, adding interspecific competition to the factors limiting growth. More studies comparing spatial and temporal patterns of distribution, abundance, and feeding are needed to clarify the extent and frequency of interactions between YOY pollock, herring, and other forage species and the impact of changes in prey and climate on these interactions.

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