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Reprinted from the Alaska Fishery Research Bulletin Vol. 8 No. 2, Winter 2001

The Alaska Fisheries Research Bulletin can be found on the World Wide Web at URL: http://www.state.ak.us/adfg/geninfo/pubs/afrb/afrbhome.htm

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ABSTRACT: The abundance and composition of mesozooplankton in the top 20 m of the water column were compared between NORPAC nets having 105-, 243- and 303-µm meshes to evaluate net retention and gear suitability for sampling prey fields of age-0 and age-1 forage fish. Single, consecutive vertical hauls were made with each net in daylight at 3 stations in northeastern Prince William Sound, Alaska, on August 5-6, 1995. Individual samples were examined microscopically, and data were pooled by mesh size for analysis. Total zooplankton abundance differed by an order of magnitude between 105- and 303-µm mesh nets (41,000 and 1,400 organisms m⁻³). Small calanoid copepods comprised ≤86% of the composition in all the net mesh sizes. Net retention in the smallest meshes was significantly higher for the small species and stages of calanoids and for several other small taxa (bivalve larvae, invertebrate eggs, barnacle larvae) compared to the largest mesh; conversely, retention for chaetognaths was significantly higher in the largest mesh. The 105-um mesh net best represented abundances and composition of mesozooplankton consumed by forage fish in summer, predominantly small calanoids, because the others undersampled taxa present in the diets of Pacific herring Clupea pallasi, pink salmon Oncorhynchus gorbuscha, walleye pollock Theragra chalcogramma, Pacific tomcod Microgadus proximus, capelin Mallotus villosus, and Pacific sand lance Ammodytes hexapterus. Although sampling gear bias has long been recognized as critical to estimates of zooplankton production and community structure, this study demonstrates the importance of selecting the appropriate sampling net mesh to characterize prey selection and consumption by planktivorous fish.

INTRODUCTION

Zooplankton abundance and composition are important aspects of marine trophic studies. These measures are commonly used in studies of production (e.g., McLaren et al. 1989; Napp et al. 1996), abundance (e.g., Bollens, Frost, Schwaninger et al. 1992), carrying capacity (e.g., Simenstad and Salo 1982; Cooney 1993), and prey selection (e.g., Parsons and LeBrasseur 1970; Checkley 1982; Suzuki et al. 1994). Selection indices are used to estimate prey preference by comparing the proportional number of prey consumed by a predator to the proportional abundance of the prey in the environment (Krebs 1989). Adequate representation of both the diet and the prey resources is essential to an accurate description of prey selection (e.g., Feller and Kaczynski 1975; Frank 1988; Siefert 1994).

Choice of gear for sampling zooplankton in pelagic nearshore and oceanic habitats is also of concern in trophic studies. The mesh size and type of net used are typically chosen based on the predator's expected prey preference given its life history stage (e.g., Hauser 1982), size and depth distribution (Celewycz and Cordell 1988; Paul and Paul 1996), as well as on net filtration efficiency (Smith et al. 1968), the relationship of net size to prey avoidance (McGowan and Fraundorf 1966), and other factors (UNESCO 1968; Jacobs and Grant 1978; Omori and Ikeda 1984). Microzooplankton prey fields targeted by larval fish are often sampled with a water bottle or pump and a fine mesh sieve (Haldorson et al. 1989; Paul and Paul 1996) or are sampled directly with fine mesh nets (e.g., 73–216 µm, Bollens, Frost, Thoreson, and Watts 1992). Mesozooplankton typically eaten by juvenile fish is sampled with nets having mesh openings between 105 µm and 335 µm (e.g., Bailey et al. 1975; Cooney et al. 1994; Celewycz and Wertheimer 1996; Napp et al. 1996). Macrozooplankton typically eaten by larger fish

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is captured with nets having larger mouths and mesh openings between 300 and 1,000 μm (e.g., Karpenko and Piskunova 1985; Bollens et al. 1993; Landingham et al. 1998). Zooplankton nets may be towed horizontally, vertically, or (double-) obliquely in the water column ranging from near surface to slightly off the bottom (e.g., Feller and Kaczynski 1975; Celewycz and Cordell 1988; Napp et al. 1996) depending on the study objectives and habitat sampled.

Although no single gear type or sampling methodology is appropriate for characterizing the prey community of all ages and species of fish or in all seasons and habitats, since the early 1980s a standard methodology termed "Plankton Watch" has been widely used in Alaska. Plankton Watch was developed by biologists involved in Alaskan salmon hatchery programs and salmon ecology studies who were interested in food abundance and other factors that affect marine survival of juvenile pink Oncorhynchus gorbuscha and chum O. keta salmon. Plankton Watch standardized the materials and methods used to monitor prey fields of young salmon to a 0.5-m diameter, conical ring net (NORPAC net) with 243-335 µm mesh towed vertically from 20-m depth (Hauser 1982; Sturdevant and Landingham 1993; Cooney et al. 1994; Moulton 1997). This simple method targets the near-surface water column where juvenile salmon feed, but has been adapted for studies of other species (e.g., Coyle and Paul 1992; Foy and Norcross 1999a, 1999b; Sturdevant et al. 2001). Zooplankton abundance and biomass estimates based on many different nets and for different fractions of the prey field have been reported, but few studies have directly compared the abundance and species composition collected with different meshes (Wing 1988a, 1988b; Siefert 1994).

The objective of this study was to compare the abundance and species composition of the mesozooplankton in the upper 20 m of the water column of Prince William Sound (PWS) in summer as retained by 3 NORPAC nets with different mesh openings and to evaluate their representation of the prev composition of forage fish. The study was conducted in conjunction with the Alaska Predator Ecosystem Experiment (APEX), a multiyear, multidisciplinary project designed to examine the trophic interactions of seabirds, forage fish, and their prey (Haldorson et al. 1996, 1997; Duffy 1998). Forage fish include several species of small, planktivorous, schooling fishes (Springer and Speckman 1997), such as juvenile Pacific sand lance Ammodytes hexapterus, walleye pollock Theragra chalcogramma, capelin Mallotus villosus, Pacific herring Clupea pallasi, pink salmon O. gorbuscha, and Pacific tomcod Microgadus

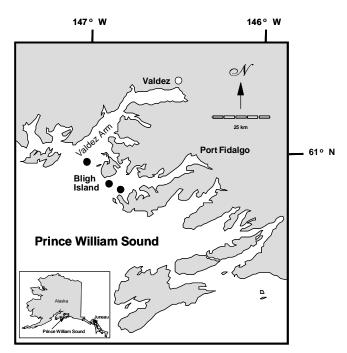


Figure 1. Northeastern region of Prince William Sound, Alaska, where sampling for zooplankton (stations indicated with closed circles) was conducted in July–August, 1995.

proximus. Detailed results of forage fish diet and prey selection investigations are presented elsewhere (Sturdevant and Hulbert 1999; Sturdevant et al. 1999; Sturdevant et al. 2001). Here, I briefly discuss the diet compositions of those 6 species of forage fish collected in PWS over the time period that zooplankton net-mesh trials were conducted to illustrate the importance of zooplankton net selectivity in relation to fish feeding studies.

METHODS

Mesh trials were conducted at 3 stations in northeastern PWS using conical, NORPAC nets identical in their mouth sizes (0.5-m diameter) but with 3 different meshes, 105-µm, 243-µm, and 303-µm openings. Stations were located in northeastern PWS at the mouth of Port Fidalgo (station 81), at the mouth of Valdez Arm (station 85), and south of Bligh Island (station 84; Figure 1). Single, consecutive 20-m vertical tows were made with each net at each station on August 5–6, 1995, during daylight, between 0945 and 1820 Alaska time. Samples were preserved individually in 5% formalin-seawater solution.

In the laboratory zooplankton samples were individually subsampled using a Folsom splitter to achieve

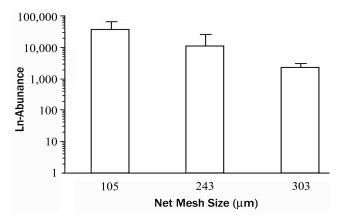


Figure 2. Abundance of zooplankton (logarithmically-transformed, mean and standard deviation) by mesh size from pooled stations in northeastern Prince William Sound, Alaska, July–August, 1995.

a count of 200-500 of the predominant taxon. Organisms in each sample were identified to species and size class, where possible, and enumerated using a binocular microscope. Calanoid copepods were staged as adult male or female, C5 copepodite, ≤C4 copepodite, or nauplius. Calanoid species with adult total lengths (TL) ≤2.5 mm were grouped as small calanoids, while those >2.5 mm TL were grouped as large calanoids. The cyclopoids Oithona spp. were included in the small calanoid category. General categories were devised for taxa such as unidentified small copepodites. Other identified taxa were pooled into broad taxonomic categories, generally by order. Organism counts were expanded (X) by the zooplankton sample fraction examined. Zooplankton abundance per cubic meter (D) was calculated for species, principal taxa, and total organisms in each vertical tow:

$$D = \frac{X}{V} = \frac{X}{\pi \times r^2 \times h} ,$$

where V is the cylindrical volume sampled by the 0.5-m diameter net towed from depth h.

Zooplankton samples from identical mesh sizes and different stations were considered to be replicates. At each station, a consistent pattern of zooplankton abundance and composition by mesh size was observed, allowing the data to be pooled for analyses. ANOVA was used to test for differences in total zooplankton abundance [ln(x+1) transformed] among mesh sizes and in abundances and proportional abundances (rank or square root transformed) of principal taxa among

mesh sizes. When significant differences were indicated ($\alpha = 0.05$), post hoc Student–Newman–Keuls (SNK) comparisons were performed to determine differences between mesh pairs.

RESULTS

Differences in logarithmically transformed total abundances of zooplankton were significant (ANOVA, P = 0.001) and existed between all pairs of mesh sizes (SNK, P < 0.05; Figure 2). The greatest difference in mean total abundance of zooplankters, an order of magnitude, was observed between the smallest- and largest-mesh nets, approximately 41,000 organisms·m⁻³ from the 105-µm net compared to 1,400 organisms·m⁻³ from the 303-µm net (Table 1). The estimate from the 243-µm mesh was intermediate in value, 12,000 organisms·m⁻³, nearly 9 times greater than from the 303-µm mesh net and more than 3 times lower than from the 105-µm mesh net.

Zooplankton taxonomic composition from all meshes was dominated by small calanoids (Figure 3), but their abundances decreased with increasing mesh size, from approximately 36,000 to 10,000 to 1,000 organisms·m⁻³ (Table 1). Net retention of small calanoids differed significantly between all mesh pairs (ANOVA, P = 0.001, SNK P < 0.05). Retention of the second most abundant group, "other" (mostly invertebrate eggs and bivalve larvae), and of barnacle larvae and chaetognaths also differed significantly (ANOVA, P = 0.025, P = 0.001, and P = 0.029, respectively). Differences among meshes varied by taxon. The group "other" decreased significantly with increasing mesh size from approximately 2,800 organisms·m⁻³ in the 105um mesh to 28 organisms·m⁻³ in the 303-μm mesh (Table 1; SNK, P < 0.05). Significantly fewer barnacle larvae were retained by the 243- and 303-µm nets than by the 105- μ m net (SNK, P < 0.05), but significantly more chaetognaths were retained by the 303-um mesh net than by either of the smaller mesh nets (SNK, P < 0.05). Abundance estimates did not differ among mesh sizes for any other principal taxon (large calanoids, larvaceans, cladocerans, or gastropods; ANOVA, P > 0.10). Minor taxa were not tested because of patchy occurrence in samples.

The percentage composition of zooplankton taxa also varied among the 3 mesh sizes. Small calanoids comprised 86% and 90% of zooplankters in the 243-and 105- μ m mesh nets, dropping to 73% in the 303- μ m mesh net (Figure 3); however, the percentage of small calanoids was not significantly lower in the largest mesh net (ANOVA, square root transformation, P = 0.054).

Table 1. Abundances of zooplankton taxa (mean number·m⁻³, standard deviation) estimated from 3 mesh sizes at 3 stations in Prince William Sound in summer 1995. The total per major taxon is shown in its header row.

	105 μ	105 μm mesh 243 μm		n mesh	303 μn	303 µm mesh	
Taxon	Mean	SD	Mean	SD	Mean	SD	
Barnacle larvae	195.6	130.4	0.0	0.0	0.1	0.1	
Nauplius	130.4	65.2	0.0	0.0	0.0	0.0	
Cyprid	65.2	112.9	0.0	0.0	0.1	0.1	
Large calanoid copepods	43.5	37.7	16.3	16.3	21.0	15.4	
Calanus marshallae C5	21.8	37.8	16.3	16.3	4.6	3.3	
C. marshallae female	0.0	0.0	0.0	0.0	0.1	0.1	
Subtotal	21.8	37.8	16.3	16.3	4.7	3.2	
C. pacificus adult	0.0	0.0	0.0	0.0	2.7	4.7	
C. pacificus general	0.0	0.0	0.0	0.0	2.7	4.7	
Subtotal	0.0	0.0	0.0	0.0	5.4	9.4	
Neocalanus/Calanus unidentified	0.0	0.0	0.0	0.0	1.4	2.0	
Calanus/Neocalanus C1-C4	0.0	0.0	0.0	0.0	0.0	0.0	
Neocalanus spp. C5	21.7	37.6	0.0	0.0	10.9	18.8	
Subtotal	0.0	0.0	0.0	0.0	5.4	9.4	
Small calanoid copepods	36,441.2	3,292.6	9,934.4	7,406.1	1,028.2	107.1	
Acartia sp.	695.4	526.9	135.8	147.9	17.7	27.1	
Acartia clausi male	21.7	37.6	0.0	0.0	0.0	0.0	
Subtotal	717.1	509.1	135.8	147.9	17.7	27.1	
Acartia longiremis adult	0.0	0.0	97.8	169.4	31.2	54.1	
A. longiremis copepodite	108.6	135.7	54.3	94.1	2.7	4.7	
A. longiremis female	65.2	65.2	54.3	94.1	36.7	12.2	
A. longiremis male	195.6	195.6	54.3	94.1	4.1	7.1	
Subtotal	369.4	271.4	260.8	451.6	74.7	53.2	
Centropages abdominalis female	65.2	112.9	0.0	0.0	1.4	2.4	
C. abdominalis male	0.0	0.9	0.0	0.0	1.4	2.4	
Subtotal	65.2	112.9	0.0	0.0	2.7	4.7	
Pseudocalanus sp. C1-C4, general	8,453.0	2,193.7	5,703.8	4,718.9	198.3	35.6	
Pseudocalanus sp. female	1,803.6	815.1	2,914.5	2,357.8	721.2	137.4	
Pseudocalanus sp. gravid female	43.5	75.3	32.6	32.6	4.1	4.1	
Pseudocalanus sp. male	0.0	0.0	304.2	526.9	0.0	0.0	
Subtotal	10,300.0	1,848.5	8,955.1	6,946.1	923.5	100.6	
Nauplius, unidentified	9,756.8	3,217.7	13.6	17.0	0.1	0.1	
Copepodite, unidentified	4,541.6	4,154.0	97.8	169.4	0.0	0.0	
Subtotal	14,298.3	1,133.5	111.4	158.1	0.1	0.1	
Oithona similis, general	8,453.0	3,080.8	134.5	130.6	1.4	2.4	
O. similis copepodite	0.0	0.0	10.9	18.8	0.0	0.0	
O. similis female	1,151.7	1,039.6	76.1	131.7	2.7	4.7	
O. similis male	1,086.5	1,661.2	249.9	432.8	5.4	9.4	
Subtotal	10,691.1	3,676.7	471.4	445.0	9.5	10.3	
Chaetognaths	0.1	0.1	0.3	0.6	2.2	1.6	
Unidentified	0.0	0.0	0.0	0.0	2.0	1.9	
Sagitta elegans	0.1	0.1	0.3	0.6	0.3	0.4	

Table 1. (continued)

-	105 μm mesh		243 μ	243 µm mesh		303 μm mesh	
Taxon	Mean	SD	Mean	SD	Mean	SD	
Cladocerans	282.5	99.6	388.4	419.7	73.3	29.4	
Evadne sp.	130.4	172.5	249.9	326.5	34.0	20.1	
Podon sp.	152.1	99.6	138.5	104.0	39.4	10.3	
Bryozoa							
Cyphonautes larva	21.7	37.6	0.0	0.0	0.0	0.0	
Decapod zoeae	0.0	0.0	16.6	28.7	6.6	6.6	
Crab, Brachyura	0.0	0.0	0.0	0.0	0.3	0.4	
Crab, Brachyrhyncha	0.0	0.0	1.4	2.4	2.7	4.7	
Crab, general unknown	0.0	0.0	12.2	21.2	0.0	0.0	
Crab, Lithodidae	0.0	0.0	0.0	0.9	2.7	2.4	
Crab, Oregoninae	0.0	0.0	0.9	1.6	0.8	1.5	
Crab, Paguridae	0.0	0.0	0.7	1.2	0.0	0.0	
Shrimp, general	0.0	0.0	1.4	2.4	0.1	0.1	
Euphausiids	0.0	0.0	0.0	0.0	4.4	3.6	
Nauplius larvae	0.0	0.0	0.0	0.0	2.7	4.7	
Calyptopis larvae	0.0	0.0	0.0	0.0	0.0	0.0	
Furcilia larvae	0.0	0.0	0.0	0.0	1.5	2.2	
Juvenile, general	0.0	0.0	0.0	0.0	0.2	0.3	
Gammarid amphipods							
Unidentified, 2–7 mm	0.1	0.1	0.0	0.0	0.0	0.0	
Gastropods	456.3	195.6	812.2	1,106.6	129.0	65.9	
Snail 1, black juvenile	65.2	112.9	315.1	545.7	20.4	31.8	
Snail 2, general juvenile	0.0	0.0	32.6	56.5	0.0	0.0	
Limacina helicina >1 mm	0.0	0.0	10.9	18.8	19.0	32.9	
L. helicina < 1 mm	391.1	112.9	453.6	568.1	89.6	45.9	
Hyperiid amphipods	0.1	0.1	0.0	0.0	0.2	0.3	
Unidentified, < 2 mm	0.0	0.0	0.0	0.0	0.0	0.0	
Unidentified, 2–7 mm	0.0	0.0	0.0	0.0	0.2	0.3	
Themisto sp. 2–7 mm	0.0	0.0	0.0	0.0	0.2	0.3	
Cnidaria	0.3	0.3	0.9	0.5	0.9	0.9	
Medusa, >2 mm	0.3	0.3	0.9	0.5	0.8	0.8	
Siphonophore "larva"	0.0	0.0	0.0	0.0	0.1	0.1	
Larvacea							
Oikopleura sp.	738.8	804.6	668.2	779.7	118.2	46.3	
Other	2,759.7	2,747.5	396.6	562.8	27.2	26.2	
Bivalve, larvae	108.6	99.6	260.8	396.5	1.4	2.4	
Unident. invert. egg, < 0.2 mm	2,629.3	2,776.8	70.6	80.4	0.0	0.0	
Unident. invert. egg, > 0.2 mm	21.7	37.6	43.5	49.8	24.4	25.4	
Isopod, general	0.0	0.0	0.0	0.0	1.4	2.4	
Unidentified	0.0	0.0	10.9	18.8	0.0	0.0	
Unidentified nauplius	0.0	0.0	10.9	18.8	0.0	0.0	
Total	40,939.9	6,764.4	12,233.9	10,172.1	1,412.6	201.5	

Large calanoids comprised ≤1.5% of total zooplankton abundance, with no significant differences among mesh sizes (ANOVA, square root transformation, P = 0.077). The mean percentage compositions of cladocerans, gastropods, and larvaceans (maximum 9% abundance) differed with mesh size (ANOVA; P = 0.026, P = 0.021, and P = 0.019, respectively); all were significantly greater (SNK, P < 0.05) by a few percentage points in the 303-µm mesh net than in the 105-µm mesh net. The percentage of the "other" group was also low, and did not differ significantly among meshes (ANOVA, P = 0.273). The coefficient of variation (CV) for percentage of small calanoids was much lower than for other taxa. The CV ranged from 7–10% for the percentage of small calanoids by mesh size, 19-100% for other principal taxa, and up to 175% for the minor taxa.

Although small calanoids were the dominant organism caught by all mesh sizes, the species and life stages differed with mesh size (Figure 4; Table 1). The smallest of the small calanoids were not well represented in the 243-µm and 303-µm mesh nets. *Pseudocalanus* spp. predominated (>90%) in these larger mesh samples, particularly mature females; the

proportion of smaller species and younger life history stages of small calanoids that were retained increased with decreasing mesh size. In the smallest mesh samples, Pseudocalanus spp., Oithona similis, and unidentified calanoid nauplii each comprised about onethird of the organisms present (10,000·m⁻³); unidentified small copepodites were also abundant, contributing about 4,500 organisms·m⁻³ to the 105-µm samples. Unidentified small copepodites and nauplii were less abundant in the 243-um samples and were absent from the 303-µm samples (Table 1). Differences in retention by pairs of meshes were also specific to calanoid taxa. The abundances of *Pseudocalanus*, *Oithona*, Acartia, and unidentified nauplii were all significantly greater in the 105-µm net than in the 303-µm net (ANOVA; P = 0.003, P = 0.001, P = 0.018, and P =0.001, respectively; SNK, P < 0.05); only Pseudocalanus and Oithona abundances were significantly greater in the 243-um net compared to the 303-um net (SNK, P <0.05). For the 105-µm mesh net compared to the 243-um, only *Oithona* and nauplii abundances were significantly greater in the smallest mesh (SNK, P <0.05). Finally, for all mesh pairs, only the abundances

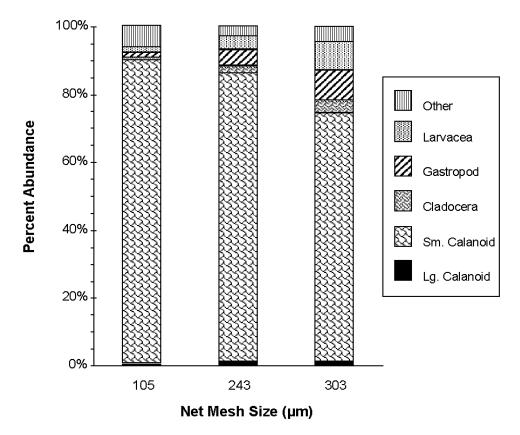


Figure 3. Numerical percentage composition of zooplankton by mesh size from pooled stations in northeastern Prince William Sound, Alaska, July-August, 1995. Taxa representing less than 2% of the total are not shown.

of the smallest taxa (unidentified small copepodites and nauplii combined, and *Oithona*) differed significantly (ANOVA, P = 0.001; SNK, P < 0.05).

DISCUSSION

Zooplankton nets of 3 different mesh sizes had significantly different retention of mesozooplankters in northeastern PWS in summer. Of the 3 meshes tested, the 105-µm mesh best represented daytime surface abundance of mesozooplankton important in summer forage fish diets. The 303-µm mesh undersampled important plankters, retaining only the largest of the small calanoids, adult female *Pseudocalanus* spp. The intermediate mesh net retained some of all taxa encountered, but it undersampled *Acartia*, *Oithona*, and small copepodites (including *Pseudocalanus* spp.) compared to the 105-µm net. Although relatively few samples were collected for this study, the results are consistent with trends suggested by the plankton literature.

I tabulated abundance estimates from Alaskan studies that used nets with mesh sizes similar to mine to show the general decline in abundance with mesh size (Table 2). Data were collected in different years and locations, but trends in abundance were consistent with my results and indicate net selectivity for zooplankton size fractions. This is not surprising given the size range of small taxa. The TLs (and widths) of adult small calanoids differ by more than a factor of 2, with *Oithona* the smallest common genus and *Pseudocalanus* the largest. Female *O. similis* are 1.0 mm in TL, *Acartia longiremis* and *A. clausi* are 1.3 and 1.4 mm, *Centropages abdominalis* males and females are 1.5–2.1 mm, and *Pseudocalanus* spp. are up to 2.0 mm. The copepodites (C1–C5 stages) of these genera range from 0.5–1.4 mm in TL (Gardner and Szabo 1982) but can be difficult to identify.

I found only 2 studies published from Alaska that compared the abundance and size selectivity of different mesh nets (Siefert 1994; Incze et al. 1997), both in Shelikof Strait. Siefert (1994) showed that adult female *Pseudocalanus* spp. retention varied not only between 2 mesh sizes (150 and 333 μm), but the retention ratio of the meshes varied seasonally; variation in size and species composition of *Pseudocalanus* spp. from May to October accounted for these differences.

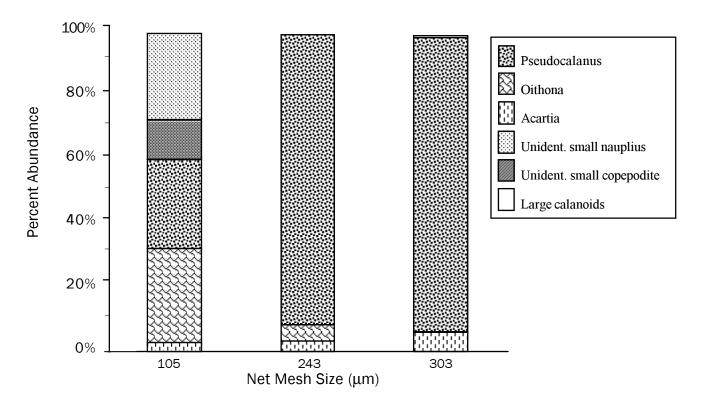


Figure 4. Taxonomic composition of calanoid copepods in zooplankton samples from pooled stations using 3 mesh sizes in northeastern in Prince William Sound, Alaska, July–August, 1995. Taxa representing less than 2% of the total are not shown. Large calanoids were principally *Neocalamus* sp. and *Calamus* sp.

Incze et al. (1997) found that copepods were 79–89% of the total zooplankters retained by 333-µm mesh but determined that only 55–67% of the copepod species and stages were quantitatively retained (Siefert 1994; Incze et al. 1997); those poorly retained included *Pseudocalanus* spp., *Acartia* spp., *Oithona* spp., and copepodite *Metridia pacifica*. The abundance of calanoids estimated from the 150-µm mesh was approximately 3 times the abundance from the 333-µm mesh, principally due to retention of *Pseudocalanus* spp. by the smaller mesh (Incze et al. 1997).

Quantitative sampling of calanoids has long been recognized to require different mesh sizes, from studies in other areas using, for example, silk mesh conical nets (Saville 1958), a high-speed multipurpose sampler (Nichols and Thompson 1991), and WP-2 vertical tows (Tremblay and Roff 1983a; McLaren et al. 1989). Numerous studies examined the filtration efficiency and performance of zooplankton nets (e.g., Jacobs and Grant 1978; Omori and Ikeda 1984). For example, the 333-um mesh was the minimum size that maintained over 85% filtration efficiency in one study (Smith et al. 1968), but in another, its filtration efficiency was lower, 77–84% (Frank 1988). Filtration efficiency of highspeed samplers declined with mesh size, from >90% for nets of $90-270-\mu m$ mesh to 55% for $35-\mu m$ mesh. Plankton mesh 75% of the target animals' widths generally caught approximately 95% of them (Nichols and Thompson 1991). For calanoids, 250-um mesh nets undersampled small species such as O. similis and Microcalanus pusillus (Tremblay and Roff 1983b), or *Pseudocalanus* spp. and nauplii-C2 of *Calanus* spp. (McLaren et al. 1989), and failed both in sampling zooplankton presence and in revealing temporal trends (Frank 1988). The 250-µm mesh net was thought to retain larger species, including all copepodites and adults of Calanus spp. (McLaren et al. 1989). Many studies requiring data on zooplankton abundance and size rely on multiple nets and do not directly compare the abundance of taxa between meshes (e.g., Springer et al. 1989; Coyle and Paul 1990). Particularly for production studies, use of multiple mesh sizes is recommended to represent all taxa and stages (Anderson and Warren 1991). Nets that retain small taxa may still not sample efficiently because of backflushing. Backflushing is less likely to occur when less water volume is filtered (as in shallow vertical tows), but it does sometimes occur during peak phytoplankton blooms or when superabundant small taxa or gelatinous slub clog the net (personal observations).

Trophic studies must also consider the appropriateness of nets used to represent prey of young fish. Several recent studies have shown that small calanoids are important in the diets of forage fish in PWS (Foy and Norcross 1999a; Sturdevant and Hulbert 1999; Sturdevant et al. 1999; Purcell and Sturdevant 2001;

Table 2. Estimates of total abundance from selected zooplankton studies in Alaska using nets with various mesh sizes.

Mesh Opening (µm	Net Type	Tow Depth (m)	Abundance (no.·m ⁻³)	Date	Authors
25	bottle	10-40	16-84,000	May-Jul 1990	McGurk et al. 1992
105	NORPAC	25	23,200	Aug-Sep 1994	Willette, Sturdevant, Jewett, and Debevec (unpublished data)
158	Clarke-Bumpus	0.5^{a}	40-154,000	Jun 1965–1966	Bailey et al. 1975
165	CalVet	50	4,000-17,000	May-Jun 1987-1989	Coyle and Paul 1990
165	bongo	50	8,102	Jul 1986	Wing 1988a, 1988b
216	NORPAC	20ª	46,000	Jun 1977	Cooney et al. 1981
243	NORPAC	20	11-19,000	May-Jun 1991	Sturdevant and Landingham 1993
243	NORPAC	20	2-7,000	Jun 1989-1990	Celewycz and Wertheimer 1996
243	NORPAC	1ъ	16,306	Jul 1986	Wing 1988a, 1988b
250	NORPAC	20	5,347	Jul 1993	Moulton 1997
333	bongo	250	475°	Jul 1985	Incze et al. 1997
335	NORPAC	20	1,000-3,500	May-Jun 1989	Cooney (unpublished data)
505	bongo	50	1,085	Jul 1986	Wing 1988a, 1988b

^aPresumed depth.

^bHorizontal surface tow.

^cAbundance converted from 95,000·m⁻² based on depth of 200 m.

Sturdevant et al. 2001). For example, small calanoids ranged from 41–94% of prey numbers in the diets of young of the year and age-1 Pacific herring, walleye pollock, capelin, sand lance, and young of the year Pacific tomcod, but they were not prominent in young of the year pink salmon or age-1 Pacific tomcod diets. Fish consumed many of the same taxa sampled by the nets used in this study. The most prevalent prev taxon in fish stomachs was unidentified small copepodites, the rarest was calanoid nauplii, and the most common genera were Pseudocalanus and Oithona. Forage species selected large calanoids when available, but large calanoids were uncommon prey in summer (Sturdevant and Hulbert 1999; Sturdevant et al. 2001) and important prey in spring (Foy and Norcross 1999b; Sturdevant et al. 1999). Thus, different nets may be required for trophic studies conducted in different seasons. The seasonality, diel vertical migration (Cooney 1987; Bollens et al. 1993) and life history of prey (Cooney et al. 1981; Coyle et al. 1990; Anderson and Warren 1991; Incze et al. 1997; Foy and Norcross 1999b), as well as sampling conditions, must be considered in choosing sampling gear for trophic studies.

Estimations of prey species preference can also vary depending on how zooplankton is sampled because of the differences in species proportions caught by different meshes. This study shows that coarse-mesh nets underrepresent the small calanoid taxa most abundant in zooplankton (Figure 3), which are also those most consumed by young of the year and age-1 fish in summer (e.g., Sturdevant et al. 2001). For example, comparing the percentage composition of calanoid taxa in

fish diets to their percentage composition in net samples would indicate avoidance of Pseudocalanus and small taxa based on the 243-um and 303-um mesh nets, but would indicate selection for these taxa based on the 105-μm net. The calanoid nauplii that passed through mesh ≥ 243 µm were avoided by most juvenile fish, but the equally small invertebrate eggs and veligers often made up substantial percentages of prey numbers in juvenile walleye pollock and Pacific herring diets (Sturdevant and Hulbert 1999), known filter feeders (Gibson and Ezzi 1990; Grover 1991). Successful feeding depends on both prev size and abundance (Parsons) and LeBrasseur 1970; Gibson and Ezzi 1990; McGurk et al. 1992, 1993). Only the 105-um mesh measured abundances high enough to support the daily ration of certain juvenile fish (Parsons and LeBrasseur 1970).

Although the zooplankton abundances and the species and sizes of calanoids retained by each mesh in this study were significantly different, the proportions of pooled large or small calanoid groups retained were similar. Each mesh would thus produce similar estimates of prey selection from these pooled taxonomic categories. At the species level, however, they would produce very different characterizations of selection from the prey environment. Such differences are important in bioenergetic, secondary production, or carrying capacity studies. The abundance and composition of small zooplankton prey of many young of the year fish species may not be adequately represented by nets with ≥ 243 -µm mesh. A study comparing abundances from different meshes at different times of year would provide additional useful information.

LITERATURE CITED

- Anderson, J. T., and S. G. Warren. 1991. Comparison of catch rates among small and large bongo samplers for *Calanus finmarchicus* copepodite stages. Canadian Journal of Fisheries and Aquatic Sciences 48:303–308.
- Bailey, J. E., B. L. Wing, and C. R. Mattson. 1975. Zooplankton abundance and feeding habits of fry of pink salmon, Oncorhynchus gorbuscha, and chum salmon, Oncorhynchus keta, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fishery Bulletin 73(4):846–861.
- Bollens, S. M., B. W. Frost, H. R. Schwaninger, C. S. Davis, K. J. Way, and M. C. Landsteiner. 1992. Seasonal plankton cycles in a temperate fjord and comments on the match-mismatch hypothesis. Journal of Plankton Research 14(9):1179–1305.
- Bollens, S. M., B. W. Frost, D. S. Thoreson, and S. D. Watts. 1992. Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis. Hydrobiologia 234:33–39.

- Bollens, S. M., K. Osgood, B. W. Frost, and S. D. Watts. 1993. Vertical distributions and susceptibilities to vertebrate predation of the marine copepods *Metridia lucens* and *Calanus pacificus*. Limnology and Oceanography 38(8):1827–1837.
- Celewycz, A., and J. Cordell. 1988. Occurrence of potential prey items of juvenile pink salmon in nearshore waters of Auke Bay, Alaska, in 1987, as sampled with three gear types. Pages 473–499 *in* Vol. II. APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem) Annual Report SFOS APP87-100. School of Fisheries and Ocean Sciences, University of Alaska Fairbanks.
- Celewycz, A. G., and A. C. Wertheimer. 1996. Prey availability to juvenile salmon after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:564–577.
- Checkley, D. M. Jr. 1982. Selective feeding by Atlantic herring (*Chipea harengus*) larvae on zooplankton in natural assemblages. Marine Ecology Progress Series 9:245–253.

- Cooney, R. T. 1987. Zooplankton. Pages 285–303 in D. W. Hood and S. T. Zimmerman, editors. The Gulf of Alaska: physical environment and biological resources. U.S. Government Printing Office, Springfield, Virginia.
- Cooney, R. T. 1993. A theoretical evaluation of the carrying capacity of Prince William Sound, Alaska, for juvenile Pacific salmon. Fisheries Research 18:77–87.
- Cooney, R. T., D. Urquhart, and D. Barnard. 1981. The behavior, feeding biology and growth of hatchery-released pink and chum salmon fry in Prince William Sound, Alaska. University of Alaska Sea Grant College Program Report 81-5, Fairbanks.
- Cooney, R. T., K. Engle, J. Milton, T. Carter, M. Sommerville, T. Henderson, R. Pellissier, and J. Vansant. 1994. Characterizing the growth environment for juvenile pink and chum salmon in Prince William Sound, Alaska. Pages 17–30 *in* Proceedings of the 16th Northeast Pacific pink and chum salmon workshop, February 24–26, 1993, Juneau, Alaska. University of Alaska Sea Grant College Program Report AK-SG-94-02, Fairbanks.
- Coyle, K. O., and A. J. Paul. 1990. Abundance and biomass of meroplankton during the spring bloom in an Alaskan bay. Ophelia 32(3):199–210.
- Coyle, K. O., and A. J. Paul. 1992. Interannual differences in prey taken by capelin, herring, and red salmon relative to zooplankton abundance during the spring bloom in a southeast Alaskan embayment. Fisheries Oceanography 1(3):294–305.
- Coyle, K. O., A. J. Paul, and D. A. Ziemann. 1990. Copepod populations during the spring bloom in an Alaskan subarctic embayment. Journal of Plankton Research 12(4):759–797.
- Duffy, D. C. 1998. APEX Project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 97163 A-Q), Alaska Natural Heritage Program and Department of Biology, University of Alaska Anchorage.
- Feller, R. J., and V. W. Kaczynski. 1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. Journal of the Fisheries Research Board of Canada 32:1419–1429.
- Foy, R. J., and B. L. Norcross. 1999a. Spatial and temporal variability in the diet of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. Canadian Journal of Zoology 77:1–10.
- Foy, R. J., and B. L. Norcross. 1999b. Feeding behavior of herring (*Clupea pallasi*) associated with zooplankton availability in Prince William Sound, Alaska. Pages 129– 135 in Ecosystem approaches for fisheries management. University of Alaska Sea Grant College Program Report AK-SG-99-01, Fairbanks.
- Frank, K. T. 1988. Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? Canadian Journal of Fisheries and Aquatic Sciences 45:48–59.
- Gardner, G. A., and I. Szabo. 1982. British Columbia pelagic marine copepoda: an identification manual and annotated bibliography. Canadian Special Publication of Fisheries and Aquatic Sciences 62.

- Gibson, R. N., and I. A. Ezzi. 1990. Relative importance of prey size and concentration in determining the feeding behaviour of the herring *Chupea harengus*. Marine Biology 107:357–362.
- Grover, J. J. 1991. Trophic relationship of age-0 and age-1 walleye pollock *Theragra chalcogramma* collected together in the eastern Bering Sea. Fishery Bulletin 89:719– 722
- Haldorson, L., A. J. Paul, D. Sterritt, and J. Watts. 1989. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer 191:220–225.
- Haldorson, L., T. Shirley, K. Coyle, and R. Thorne. 1997.
 Forage species studies in Prince William Sound. Project 96163A Annual Report. Appendix A in D. C. Duffy, compiler. APEX Project: Alaska Predator Ecosystem Experiment in Prince William Sound and the Gulf of Alaska. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 96163 A-Q), Alaska Natural Heritage Program and Department of Biology, University of Alaska Anchorage.
- Haldorson, L. J., T. C. Shirley, and K. O. Coyle. 1996. Biomass and distribution of forage species in Prince William Sound. Appendix A in D. C. Duffy, compiler. APEX Project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 95163 A-Q), Alaska Natural Heritage Program and Department of Biology, University of Alaska Anchorage.
- Hauser, W. J. 1982. Manual for estuarine environmental and zooplankton studies. Alaska Department of Fish and Game, Division of Fisheries Rehabilitation Enhancement and Development, Anchorage.
- Incze, L. S., D. W. Siefert, and J. M. Napp. 1997. Mesozooplankton of Shelikof Strait, Alaska: abundance and community composition. Continental Shelf Research 17(3):287–305.
- Jacobs, F., and G. C. Grant. 1978. Guidelines for zooplankton sampling in quantitative baseline and monitoring programs. Environmental Research Laboratory, EPA-600/3-78-026, Corvallis, Oregon.
- Karpenko, V. I., and L. V. Piskunova. 1985. Importance of macroplankton in the diet of young salmons of genus *Oncorhynchus* (Salmonidae) and their trophic relationships in the southwestern Bering Sea. Journal of Ichthyology 24:98–106.
- Krebs, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York.
- Landingham, J. H., M. V. Sturdevant, and R. D. Brodeur. 1998. Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia. Fishery Bulletin 96:285–302.
- McGowan, J. A., and V. J. Fraundorf. 1966. The relationship between size of net used and estimates of zooplankton diversity. Limnology and Oceanography 11:456–469.
- McGurk, M. D., A. J. Paul, K. O. Coyle, D. A. Ziemann, and L. J. Haldorson. 1993. Relationships between prey concentration and growth, condition, and mortality of Pacific

herring, *Clupea pallasi*, larvae in an Alaskan subarctic embayment. Canadian Journal of Fisheries and Aquatic Sciences 50:163–180.

- McGurk, M. D., H. D. Warburton, M. Galbraith, and W. C. Kusser. 1992. RNA-DNA ratio of herring and sand lance larvae from Port Moller, Alaska: comparison with prey concentration and temperature. Fisheries Oceanography 1–3:193–207.
- McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff. 1989. Copepod production on the Scotian Shelf based on life history analyses and laboratory rearings. Canadian Journal of Fisheries and Aquatic Sciences 46:560– 583
- Moulton, L. L. 1997. Early marine residence, growth, and feeding by juvenile salmon in northern Cook Inlet, Alaska. Alaska Fishery Research Bulletin 4(2):154–177.
- Napp, J. M., L. S. Incze, P. B. Ortner, D. L. W. Siefert, and L. Britt. 1996. The plankton of Shelikof Strait, Alaska: standing stock, production, mesoscale variability and their relevance to larval fish survival. Fisheries Oceanography 5(Suppl.):19–38.
- Nichols, J. H., and B. Thompson. 1991. Mesh selection of copepodite and nauplius stages of four calanoid copepod species. Journal of Plankton Research 13:661–671.
- Omori, M., and T. Ikeda. 1984. Methods in marine zooplankton ecology. Wiley and Sons, New York.
- Parsons, T. R., and R. J. LeBrasseur. 1970. The availability of food to different trophic levels in the marine food chain. Pages 325–343 in J. H. Steele, editor. Marine food chains. University of California Press, Berkeley.
- Paul, A. J., and J. M. Paul. 1996. Microscale abundance of copepod nauplii prey of larval fishes in a glaciated fiord measured with a 50-ml sampler. Alaska Fishery Research Bulletin 3(1):54–58.
- Purcell, J. E., and M. V. Sturdevant. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Marine Ecology Progress Series 210:67–83.
- Saville, A. 1958. Mesh selection in plankton nets. Journal du Conseil 23(2):192–201.
- Siefert, D. L. W. 1994. The importance of sampler mesh size when estimating total daily egg production by *Pseudocalamus* spp. in Shelikof Strait, Alaska. Journal of Plankton Research 16(11):1489–1498.
- Simenstad, C. A., and E. O. Salo. 1982. Foraging success as a determinant of estuarine and nearshore carrying capacity of juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal, Washington. Pages 21–36 in Proceedings of the North Pacific aquaculture symposium, August 18–21, 1980, Anchorage, Alaska, and August 25–27, 1980, Newport, Oregon. University of Alaska Sea Grant College Program Report 82-2, Fairbanks.
- Smith, P. E., R. C. Counts, and R. I. Clutter. 1968. Changes in filtering efficiency of plankton nets due to clogging under tow. Journal du Conseil Conseil International pour l'Exploration de la Mer 2:232–248.
- Springer, A. M., C. P. McRoy, and K. R. Turco. 1989. The paradox of pelagic food webs in the northern Bering Sea. II. Zooplankton communities. Continental Shelf Research 9(4):359–386.

- Springer, A. M., and S. G. Speckman. 1997. A forage fish is what? Summary of the symposium. Pages 773–805 *in* Forage fishes in marine ecosystems. University of Alaska Sea Grant College Program Report AK-SG-97-01, Fairbanks.
- Sturdevant, M. V., A. L. J. Brase, and L. B. Hulbert. 2001. Feeding habits, prey fields, and potential competition of young-of-the-year walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Chupea pallasi*) in Prince William Sound, Alaska, 1994–1995. Fishery Bulletin 99(3):482–501.
- Sturdevant, M. V., and J. H. Landingham. 1993. Temperature, salinity and zooplankton as indicators of environmental suitability for release of hatchery-reared juvenile salmonids near Juneau, Alaska. U.S. Department of Commerce, National Marine Fisheries Service/Alaska Fisheries Science Center Processed Report 93-10, Juneau, Alaska.
- Sturdevant, M. V., and L. B. Hulbert. 1999. Juvenile forage fish feeding in allopatric and sympatric aggregations: Pacific herring, Pacific sand lance and pink salmon in Prince William Sound, July 1996. Pages 72–100 in Forage fish diet overlap, 1994–1996. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 97163C), Auke Bay Laboratory, National Marine Fisheries Service, Juneau, Alaska.
- Sturdevant, M. V., T. M. Willette, S. Jewett, and E. Debevec. 1999. Diet composition, diet overlap, and size of 14 species of forage fish collected monthly in Prince William Sound, Alaska, 1994–1996. Pages 10–37 in Forage fish diet overlap, 1994–1996. APEX Project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 98163C), Auke Bay Laboratory, National Marine Fisheries Service, Juneau, Alaska.
- Suzuki, T., M. Fukuwaka, I. Shimizu, J. Seki, M. Kaeriyama, and H. Mayama. 1994. Feeding selectivity of juvenile chum salmon in the Japan Sea coast of northern Honshu. Scientific Report of Hokkaido Salmon Hatchery 48:11–16.
- Tremblay, M. J., and J. C. Roff. 1983a. Community gradients in the Scotian Shelf zooplankton. Canadian Journal of Fisheries and Aquatic Sciences 40:598–611.
- Tremblay, M. J., and J. C. Roff. 1983b. Production estimates for Scotian Shelf copepods based on mass specific P/B ratios. Canadian Journal of Fisheries and Aquatic Sciences 40:749–753.
- UNESCO (United Nations Educational, Scientific and Cultural Organization). 1968. Zooplankton sampling. Monographs of oceanographic methodology, 2, Paris.
- Wing, B. L. 1988a. Spring variation of the trophic structure of a subarctic zooplankton population. Pages 257–298 in Vol. I. APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem) Annual Report SFOS APP87-100. School of Fisheries and Ocean Sciences, University of Alaska Fairbanks.
- Wing, B. L. 1988b. Spring variation of the trophic structure of a subarctic zooplankton population. Pages 499–548 in Vol. II. APPRISE (Association of Primary Production and Recruitment in a Subarctic Ecosystem) Annual Report SFOS APP87-100. School of Fisheries and Ocean Sciences, University of Alaska Fairbanks.