Abstract. - The feeding habits of late-larval and early-juvenile walleve pollock Theragra chalcogramma from a coastal nursery habitat in the western Gulf of Alaska were examined in relation to fish size (10.0-29.9 mm SL) and site of collection. Pseudocalanus sp. was the dominant prey. Copepod nauplii and Pseudocalanus copepodids decreased in importance in the diet as fish size increased, concomitant with an increase in importance of adult Pseudocalanus sp. and Calanus spp. Other prey showed no clear relation to fish size. A comparison of diet between collection stations revealed considerable variability. Along two transects perpendicular to the Alaska Peninsula, betweenstation diet overlap was observed to be high for one transect, and low for the other. Along a transect parallel to the Alaska Peninsula, some adiacent stations vielded high diet overlap, and other yielded low overlap, while the most distant stations produced high diet overlap. Patchiness of food resources likely contributed subtantially to these patterns. One possible consequence of the ingestion of different prey in different locales is that differential growth rates could result.

Feeding Ecology of Late-Larval and Early-Juvenile Walleye Pollock *Theragra chalcogramma* from the Gulf of Alaska in 1987*

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The recent discovery of large spawning aggregations of walleve pollock Theragra chalcogramma in Shelikof Strait from late March to mid-April suggests that this is the principal spawning center for the species in the Gulf of Alaska (Dunn et al. 1984, Kendall et al. 1987). The concentrated mass of eggs produced in Shelikof Strait in early spring and the ensuing dense patch of larvae provide uncommon access to the early life history of the species. The spawning aggregations produce distinct cohort patches $(20 \times 50 \text{ km or larger})$ of eggs at depths greater than 150 m (Incze et al. 1989). After about 14 days, the eggs hatch (Dunn and Matarese 1987, Kim 1989) and larvae ascend to the upper 50 m (Incze et al. 1989). The larval patches can be followed for up to 30 days as they drift with prevailing currents to the southwest (Kendall et al. 1987, Hinckley et al. 1989, Incze et al. 1989). The cohesiveness of the patches likely results from the restricted spawning area within Shelikof Strait (Hinckley et al. 1989) as well as Alaska Coastal Current circulation patterns (Incze et al. 1989).

Ichthyoplankton has been surveyed regularly in and around Shelikof Strait since 1979, and much is known regarding the early life history of walleye pollock in this area (e.g., Kendall et all 1987, Incze et al. 1989, Kim 1989, Yoklavich and Bailey 1989). However, considerably less is known about life history of late-larval and juvenile stages within nursery habitats in the western Gulf of Alaska. A survey in June and July 1987 collected late-larval and early-juvenile pollock from a coastal nursery area over the continental shelf along the Alaska Peninsula (Hinckley et al. 1989). While the center of distribution was between the Shumagin and Semidi Islands, a large number of late larvae and juveniles were collected over a broad area running nearly the length of the Alaska Peninsula. The broad distribution enabled us to examine whether diet varied along the length of the Alaska Peninsula and along a nearshore-offshore transect. Although the feeding habits of the late larvae have been previously reported from several locations, in all cases results have been pooled across collection stations (Kamba 1977, Clarke 1978, Cooney et al. 1980, Lee 1985, Kendall et al. 1987). In the present study, feeding habits of late larvae were analyzed by size and these data are compared to previous reports. Further, diet was analyzed by collection station, and betweenstation differences were examined using a measure of diet overlap.

Materials and methods

Pollock larvae were collected in the Gulf of Alaska during June 1987 by the RV *Miller Freeman*. Collections were made using a 5-m^2 Methot frame trawl (Methot 1986) (2×3 mm oval mesh) that was fished obliquely

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Figure 1 Location of collection stations in the Gulf of Alaska. Stations represent one transect parallel to the Alaska peninsula, and two perpendicular offshore transects, with stations 38 and 48 located near the shelf break.

from 15 m off-bottom (to a maximum of 300 m depth) to the surface (Hinckley et al. 1989). Samples from 10 stations, representing 2 nearshore-offshire transects (stations 38, 40, and 42 and stations 44, 45, and 48) and one transect parallel to the Alaska Peninsula (stations 21, 30, 32, 42, 44, and 58; see Figure 1), that were collected from 20 to 25 June, were the focus of this study. The total number of fish examined was 490.

Samples were preserved in 5% formalin at sea, and transferred to 70% ethanol prior to their examination. Specimen shrinkage most likely occurred as a result of fixation.

After the standard length (SL) of each larva was measured, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified: invertebrate eggs, copepod nauplii, barnacle nauplii, euphausiid larvae, pteropods, other non-copepod prey, and copepods including Pseudocalanus sp. adults (CVI), Pseudocalanus copepodids (CI-CV), Acartia longiremis, Acartia sp., Calanus marshallae, Calanus sp., Centropages abdominalis, Eucalanus bungii, Metridia sp., Oithona sp., Oncaea sp., unidentified calanoid copepodids <1.5 mm, and unidentified calanoid copepodids >1.5 mm. Copepod eggs comprised over 99% of the "invertebrate eggs" category and Oithona similis comprised over 99% of the "Oithona sp." category. While the taxonomy of the genus Pseudocalanus has recently been clarified (Frost 1989), no attempt at specific identifications of Pseudocalanus was made in the present study. For all copepods except Pseudocalanus sp., copepodid (CI-CV) through adult stages were considered together. Copepodids were inconsequential in all species except *Calanus* sp.

Diet was analyzed in terms of numerical percentage composition (%N), volumetric percentage composition (%VOL), and percent frequency of occurrence (%FO). Prey volumes were estimated using prey dimensions (Grover and Olla 1987). Over 8000 prey items were measured for prey volume calculations. The three analyses (%N, %VOL, and %FO) were combined to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI = (%N + %VOL) × %FO) (Pinkas et al. 1971). Data were pooled across stations for analysis by size class. The four size classes were defined as 10.0–14.9, 15.0–19.9, 20.0–24.9, and 25.0–29.9 mm SL. For station-by-station analyses, data were pooled across size classes.

Diet overlap was calculated using an index of proportional similarity (Wallace 1981, Linton et al. 1981, Kohn and Riggs 1982) defined as

$$PS = 1 - 0.5 \left(\sum_{i=1}^{n} |P_{xi} - P_{yi}| \right)$$

where PS is the index of proportional similarity or overlap, P_{xi} is the proportion of prey category *i* in the diet at location *x*, P_{yi} is the proportion of prey category *i* in the diet at location *y*, and *n* is the number of prey categories. Mean percent volume was used as a measure of diet for these calculations (Wallace 1981). Although this index has been traditionally used to examine diet overlap between species at one location, I have used it to examine diet overlap between locations for

Mean lengt collected a standard d	Table 1 ths of late-larval and early t 10 stations in the Gulf eviations), and date and	y-juvenile walley of Alaska in 19 time of collect	7e pollock 987 (with ion.
		Collec	tion
Station	Standard length		Time
no.	(mm)	Date	(h)
21	16.1 (2.11)	20 June	2156
30	18.2 (2.27)	22 June	0144
32	17.4 (1.74)	22 June	0704
38	19.3 (3.27)	22 June	2205
40	18.6 (2.06)	23 June	0114
42	18.4 (2.44)	23 June	0558
44	17.1 (2.47)	24 June	1756
45	19.9 (2.40)	24 June	1956
48	20.2 (2.55)	25 June	0117
58	19.0 (3.36)	25 June	2314

a single species. This index was chosen because it does not require resource-availability data (Wallace 1981), it is independent of sample size (Kohn and Riggs 1982), and it estimates overlap accurately for real overlaps between 7 and 85%, whereas three other indices performed poorly (Linton et al. 1981). *PS* values greater than 60% are generally considered to demonstrate significant overlap (Mathur 1977, Wallace and Ramsey 1983). In order to minimize size-related bias in the measurement of diet overlap, proportional similarity indices were calculated for only the 15.0–19.9 mm SL size class.

Results

Standard length tended to increase with date of collection (Table 1, correlation coefficient r = 0.678, P < 0.05). The dominant size class for all stations was 15.0–19.9 mm SL, accounting for 62% of the larvae, with a minimum of 21 larvae of this size collected at each station. The mean lengths of larvae from five stations located along a transect parallel to the Alaska Peninsula were significantly different (P < 0.001) (ANOVA, Zar 1974), while of the two transects perpendicular to the Alaska Peninsula, larval lengths were significantly different (P < 0.001) along only one of these transects (stations 44, 45, and 48).

Diet of wa	lleye p	Table 2 eye pollock from the Gulf of Alaska in 1987, by size class, expressed as %N, %VOL, %FO, and %IRI.														
	10.0-14.9 mm SL (N=50)			1	15.0–19.9 mm SL (N=302)			20.0–24.9 mm SL (N=127)			25.0–29.9 mm SL (N=7)					
	%N	%VOL	%FO	%IRI	%N	%VOL	%FO	%IRI	%N	%VOL	%FO	%IRI	%N	%VOL	%FO	%IR
Invertebrate eggs	15.8	0.8	66.0	7.3	25.8	0.9	62.6	12.4	27.1	0.6	67.7	13.3	15.9	0.3	42.9	4.7
Copepod nauplii	25.3	2.8	86.0	16.1	9.3	0.7	63.2	4.7	1.5	0.1	40.9	0.5	0.5	< 0.1	14.3	<0.1
Barnacle nauplii					0.1	< 0.1	4.3	< 0.1	0.1	< 0.1	4.7	< 0.1				
Euphausiids	1.1	6.4	24.0	1.2	0.8	3.0	20.5	0.6	0.7	1.9	20.5	0.4	0.7	1.3	28.6	0.4
Pteropods	0.6	0.3	8.0	<0.1	1.6	0.5	16.9	0.3	0.4	0.1	6.3	<0.1				
Other					0.2	0.1	5.3	< 0.1	< 0.1	<0.1	3.1	<0.1				
Pseudocalanus sp.	8.8	30.7	82.0	21.6	14.6	35.5	79.5	29.5	26.6	43.1	87.4	43.3	37.2	40.7	100.0	52.9
Pseudocalanus																
copepodids	6.7	9.1	76.0	8.0	7.5	7.2	66.6	7.3	7.8	5.0	69.3	6.3	8.6	3.7	57.1	4.8
Acartia																
longiremis	6.4	13.8	64.0	8.6	9.2	14.0	66.2	11.4	6.9	7.0	69.3	6.8	2.1	1.4	42.9	1.0
Acartia sp.	1.0	1.5	22.0	0.4	0.9	1.0	18.2	0.2	0.6	0.4	11.0	0.1				
Calanus																
marshallae	<0.1	0.9	2.0	<0.1	0.3	3.5	10.3	0.3	0.9	7.2	27.6	1.6	3.2	18.3	57.1	8.4
Calanus sp.					0.1	2.5	5.0	0.1	0.4	4.6	11.8	0.4	0.7	5.7	14.3	0.0
Centropages																
abdominalis	0.2	1.3	6.0	< 0.1	0.2	0.9	8.9	0.1	0.3	0.8	14.2	0.1				
Eucalanus bungii					0.2	6.5	5.0	0.2	0.6	11.3	15.0	1.2	0.9	12.3	14.3	1.3
<i>Metridia</i> sp.	< 0.1	0.9	2.0	<0.1	< 0.1	0.4	1.3	< 0.1								
Unident.																
copepodids																
<1.5 mm	14.4	20.3	96.0	22.1	15.5	15.3	95.7	21.8	17.6	11.6	95.3	19.8	19.4	8.6	85.7	16.
Uniaent. copepodids																
>1.5 mm	< 0.1	0.6	2.0	< 0.1	0.4	2.9	12.3	0.3	0.8	4.3	24.4	0.9	1.6	6.1	42.9	2
Oithma sp.	18.5	10.2	76.0	14.5	12.9	4.9	80.8	10.7	7.6	1.9	76 4	5.2	9.2	1.6	100.0	7
Oncaea sp.	1.0	04	18.0	0.1	0.3	0 1	73	< 0.1	01	<01	21	<01		1.0	10010	



Figure 2 The diet of larval pollock in the Gulf of Alaska in June 1987, by size class, in terms of %*N*, %*VOL*, and %*IRI*.

Diet as a function of size

Small unidentified calanoid copepodids (i.e., <1.5 mm) were the primary prey (*IRI*) for larvae 10.0–14.9 mm SL, followed by *Pseudocalanus* sp. (Table 2, Fig. 2). Copepod nauplii, which ranked as a major food item for only this size class, was third in importance, followed by *Oithona* sp. and *Acartia longiremis*.

For larvae 15.0–19.9 mm SL, the same two prey items dominated the diet, but *Pseudocalanus* sp. was the most important item and small (unidentified) calanoid copepodids were second (Table 2, Fig. 2). Invertebrate eggs, *A. longiremis*, and *Oithona* sp. ranked third through fifth.

For fish 20.0–24.9 mm SL, *Pseudocalanus* sp. contributed twofold more to the diet than any other item (Table 2, Fig. 2). Small calanoid copepodids, invertebrate eggs, and *A. longiremis* were second, third, and fourth most important prey, followed by *Pseudocalanus* copepodids.

Pseudocalanus sp. continued to be the dominant prey for the largest size class that was examined, 25.0-29.9 mm SL, comprising over 52% of the diet, with small calanoid copepodids ranking second in importance (Table 2, Fig. 2). These were followed by Calanus marshallae, a species whose only major contribution to the diet was in this size class, Oithona sp., and Pseudocalanus copepodids.

Considering adult and copepodid forms together, *Pseudocalanus* sp. was the principal prey for all sizes of larvae and early juveniles (Table 2, Fig. 2). The contribution of *Pseudocalanus* sp. adults and all *Calanus* spp. increased directly in relation to fish size. On the

	Station number									
	21	30	32	38	40	42	44	45	48	58
Invertebrate eggs	6.5	0.3	16.7	12.4	1.4	28.3	13.3	26.1	6.9	0.2
Copepod nauplii	9.9	5.5	9.1	0.6	0.6	1.2	1.3	0.6	0.7	10.2
Barnacle nauplii		< 0.1	0.1			< 0.1	0.1			<0.3
Euphausiids	5.2	0.4	0.7	1.2	0.5	0.2	0.7	< 0.1	< 0.1	<0.1
Pteropods			10.7		0.9	< 0.1	< 0.1	< 0.1		
Other	< 0.1		0.4	< 0.1	< 0.1		< 0.1			<0.1
Pseudocalanus sp.	23.3	4.5	7.4	32.8	5.2	31.4	39.2	50.0	49.1	41.2
Pseudocalanus copepodids	11.3	0.1	2.8	13.2	0.3	5.3	11.1	7.1	4.6	6.0
Acartia longiremis	1.7	22.2	7.9	5.6	53.7	4.5	5.8	1.0	6.1	11.2
Acartia sp.	0.1	0.2	5.1	< 0.1		3.6	< 0.1			<0.3
Calanus marshallae		0.5		7.0	0.2	< 0.1	0.7	0.1	0.4	0.6
Calanus sp.	< 0.1		0.1		< 0.1			0.2	6.6	
Centropages abdominalis	< 0.1	0.1	0.3	< 0.1	0.1	0.2	< 0.1		0.4	<0.1
Eucalanus bungii				3.1	13.5					
Metridia sp.	< 0.1	< 0.1					< 0.1	< 0.1		
Unident. copepodids <1.5 mm	16.1	37.8	15.7	16.7	17.2	22.7	23.3	13.2	21.7	20.1
Unident. copepodids >1.5 mm	< 0.1	21.1		0.8	0.7	< 0.1	< 0.1	< 0.1	0.4	0.1
Oithona sp.	25.7	7.2	22.7	6.5	5.6	2.4	4.4	1.6	3.1	10.4
Oncaea sp.	0.1	_	0.3	< 0.1		0.1	< 0.1	< 0.1		<0.

other hand, the contribution of *Pseudocalanus* copepodids and copepod nauplii decreased with increasing fish size. Other major prey categories (i.e., small calanoid copepodids, invertebrate eggs, *A. longiremis*, and *Oithona* sp.) showed no clear relation to fish size.

Diet as related to site of collection

Pseudocalanus sp. was the most important prey at 6 of the 10 stations, accounting for over 30% (IRI) of the diet at each of these locations (Table 3, Fig. 3). Small calanoid copepodids were of secondary importance, ranging from 13.2 to 23.3%, while invertebrate eggs, copepod nauplii, *Pseudocalanus* copepodids, and *A. longiremis* and *Oithona* sp. each contributed more than 10% to the diet at one or more of these stations.

At two of the remaining four stations Oithona sp. was the primary prey (22.7-25.7%). Small calanoid copepodids were most important at another staion (37.8%), and A. longiremis was dominant at the remaining one, comprising more than 53% of the diet. Additionally, invertebrate (mostly copepod) eggs, copepod nauplii, pteropods, Pseudocalanus sp., Pseudocalanus copepodids, A. longiremis, Eucalanus bungii, and small and large unidentified calanoid copepodids (i.e., >1.5 mm), were well represented in the diet at one or more of the stations that were not dominated by Pseudocalanus sp.

Diet overlap between stations

Values of the index of proportional similarity (PS) varied widely, franging from 0.252 to 0.833 (Table 4). Of 11 pairs of adjacent stations, 45% showed no significant diet overlap, while of 34 pairs of non-adjacent stations 50% showed no significant overlap. Two stations, 30 and 40, were quite dissimilar from all other stations, and station 32 showed significant overlap only in relation to stations 21 and 58.

When examining diet overlap for the six stations that comprise the transect parallel to the Alaska Peninsula, a high degree of variation was seen in PS values (Table 5). At the southwestern end of the transect the lowest PS value was obtained for stations in closest proximity (21 and 30), while at the northeastern end of the transect the greatest PS value was obtained for stations in closest proximity (58 and 44). At the same time, diet at the two most distanct stations (21 and 58) showed great similarity.

Along one of the two transects perpendicular to the Alaska Peninsula (stations 44, 45, and 48), PS values indicated considerable overlap (Table 6). In contrast, a different pattern was obtained along the other perpendicular transect (stations 38, 40, and 42) where PS values were wide-ranging. For each of the two transects the greatest diet overlap was between the near-shore and offshore extremes of the transect (i.e., stations 44 and 48, and stations 38 and 42).





The diet of larval pollock in the Gulf of Alaska in June 1987, by collection station in terms of %N, %VOL, and %IRI.

Table 4

Index of proportional similarity (PS) for walleye pollock 15.0–19.9 mm SL, at all stations, calculated using mean volume data. PS values for adjacent stations are underlined.

Sta. no.	21	30	32	38	40	42	44	45	48	58
21	*			_	-					
30	<u>0.384</u>	*								
32	0.605	<u>0.504</u>	*							
38	0.652	0.475	0.507	*						
40	0.303	0.577	0.433	<u>0.519</u>	*					
42	0.695	0.458	<u>0.591</u>	0.682	<u>0.328</u>	*				
44	0.770	0.474	0.524	0.742	0.353	<u>0.833</u>	*			
45	0.658	0.287	0.399	0.628	0.252	<u>0.689</u>	<u>0.755</u>	*		
48	0.676	0.415	0.490	<u>0.676</u>	0.368	0.760	0.805	0.728	*	
58	0.782	0.547	0.626	0.810	0.441	0.754	<u>0.831</u>	0.645	0.706	*

Table !	5
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Index of proportional similarity (PS) for walleye pollock 15.0–19.9 mm SL, along transect parallel to the Alaska Peninsula, calculated using mean volume data. *PS* values for adjacent stations are underlined.

Sta. no.	21	30	32	42	44	58
21	*					
30	0.384	*				
32	0.605	0.504	*			
42	0.695	0.458	0.591	*		
44	0.770	0.474	0.524	0.833	*	
58	0.782	0.547	0.626	0.754	0.831	*

Index of pollock, perpendi lated usi adjacent	Tabl proportional sim 15.0–19.9 mm S cular to the Al ng mean volum stations are ur	e 6 nilarity (<i>PS</i>) for L, along two tr aska Peninsula e data. <i>PS</i> val nderlined.	walleye ansects , calcu- lues for
Sta.			
no.	38	40	42
38	*		
40	<u>0.519</u>	*	
42	0.682	0.328	*
	44	45	48
44	*		
45	0.755	*	
48	0.805	0.728	*

Discussion

The portion of the present study dealing with the relationship between diet and fish size complements the study by Kendall et al. (1987) conducted in the Gulf of Alaska during May 1983. As the samples in 1983 were collected earlier in the year using different gear (a 505- μ m mesh bongo net) than in 1987, the size range of larvae was substantially different in the two studies. However, a comparison of the diet of larvae 10.0–19.0 mm can be made between the two years. From this it was clear that copepod eggs and nauplii were of some consequence in the diet in both years. A between-year comparison of the relative importance of Pseudocalanus sp. adults and copepodids cannot be made because the 1983 dietary analysis considered adult and immature stages together as copepodids (CI-CVI). In both years Pseudocalanus sp. was the dominant copepod, followed by Acartia sp. and Oithona sp. As Pseudocalanus sp. carries its eggs (Corkett and McLaren 1978), the majority of copepod eggs in the diet were probably incidentally ingested attached to adult females. However, berried females were not observed in pollock stomachs. While the delicate structure of Pseudocalanus egg sacs may preclude larval fish from ingesting females with eggs intact (A.J. Paul, Univ Alaska, Seward, pers. commun., Nov. 1988), it is also possible that some of the eggs that were ingested could have been from other genera such as Acartia or Calanus that broadcast their eggs into the sea (C.B. Miller, Oregon State Univ., Corvallis, pers. commun., June 1989). The source of copepod eggs cannot be resolved without observing female copepods with eggs in the diet or identifying eggs to species. Neither condition was met in the present study.

The dietary importance of copepod nauplii decreased and Pseudocalanus minutus increased with increasing larval size for larvae 9-20 mm SL in Uchiura Bay, Hokkaido (Kamba 1977), as was the case in the present study. However, while A. longiremis, Oithona sp., and various copepodids were important in the Gulf of Alaska, they were not in Uchiura Bay. Since copepod eggs were excluded from the dietary analyses by Kamba, it is not possible to compare their relative importance in Uchiura Bay with the Gulf of Alaska. In the Bering Sea, Clarke (1978) reported that copepod nauplii and Oithona similis were the primary prey for pollock 9-18 mm SL, and Cooney et al. (1980) reported that copepodids (CI-CVI) and copepod nauplii were dominant. Oithona similis was the dominant copepod species. followed by Pseudocalanus sp. and A. longiremis. In both Bering Sea accounts, copepod eggs accounted for approximately 5% of the diet of this size class, less than in the Gulf of Alaska.

While the diet of 20.0–29.9 mm SL fish in the Gulf of Alaska appeared to be more diverse than in Uchiura Bay (Kamba 1977), in both areas *Pseudocalanus* sp. was the dominant prey, and *Calanus* sp. was well represented in the diet. In the Bering Sea *Pseudocalanus* sp. copepodids were the dominant prey and copepod eggs were also very important in the diet of early juveniles, although a broader size class, 20.1–60.0 mm SL, was utilized (Cooney et al. 1980). In a more recent study, also in the Bering Sea, cyclopoid copepods proved to be the primary prey for fish 20.0–29.9 mm TL, with *Pseudocalanus* sp. adults second in importance (Lee 1985). In the Gulf of Alaska, *Oithona* sp. (the dominant cyclopoid) was of highly localized importance.

The manner in which diet of larval and juvenile pollock varied between different locales and between years in the same locale illustrates how diet may vary in response to available food resources, which vary in response to oceanographic conditions (e.g., Grover and Olla 1987). As plankton data for the present study were unavailable, the extent to which diet resulted from prev selectivity cannot be determined. However, assuming that diet was at least reflective of available food resources, the wide range in PS values would indicate that food resources were not homogeneous. Diet varied widely from station to station, with nearly as many nonadjacent as adjacent station pairs showing significant dietary overlap. This type of variation would suggest areas of planktonic patchiness, perhaps reflecting underlying hydrographic heterogeneities. Low PS values may indicate small prey patches, while high values that were seen across several stations may be indicative of large prey patches.

Regardless of whether prey were energetically equivalent at each station, the incidence of feeding was

100%. It is unclear whether differential growth rates may have resulted from the ingestion of different prey since growth rates were not measured in the present study. However, it remains a possibility since Yoklavich and Bailey (1989) reported differential growth rates for late larval and early juveniles at three locations in the Gulf of Alaska in 1987. These fish, which ranged from 12.8 to 40.8 mm SL, were collected in the same survey of late-stage larval pollock (Hinckley et al. 1989) as the present study, from 18 June to 15 July 1987. While specific collection stations differed between the two studies, Yoklavich and Bailey found that growth rates increased from southwest to northeast

Acknowledgments

along the Alaskan Peninsula.

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