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The Early Life History of Walleye Pollock *(Theragra chalcogramma)* in the Eastern Bering Sea: a Summary and Reference List

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The early life history of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea: a summary and reference list

by

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Introduction

This report surveys the current state of knowledge of the early life history of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea. It is essentially a brief description of the topics for which some information is available, together with the list of references from which this summary was compiled.

The papers have been grouped into seven main subject areas: 1) developmental stages and identification, 2) growth, 3) feeding, 4) behavior, 5) vertical distribution, 6) geographical distribution, and 7) modeling. Some papers present material which falls in several categories and are cited more than once.

This report is meant to be a guide to the literature, or at least a starting point for a survey. For this reason every reference which contains relevant information is listed--including unpublished reports, progress reports, and other so-called grey literature. Papers dealing exclusively with adult walleye pollock or the walleye pollock fishery are not included.

Much of the research on walleye pollock has been done by Japanese researchers and published in Japanese without translation. These works are of limited value to those who don't read Japanese, although some have English summaries and some have English captions to figures and tables. All are included in the list of references. However, not all the references listed are cited in the text. Some have simply been culled from the references cited by others in the list. Whenever a reference has not been seen, that is noted in the list.

Developmental stages and identification

Pollock larvae are difficult to separate from Pacific cod and Pacific tomcod larvae, which often co-occur. To aid in identification, Gorbunova (1954) collected eggs, larvae, and juveniles and described them in detail. A developmental series was also obtained by artificial fertilization and incubation of pollock eggs. The development of pollock was compared to that of other co-occurring gadids, Pacific tomcod, Pacific cod, and saffron cod.

Yusa (1954) described in detail the development of artificially fertilized pollock eggs. Of course, the times of events given in this paper depend on the water temperature, in this case 6-7^{o}C, which is warmer than the spawning grounds in the eastern Bering Sea.

Takeuchi (1972) described the development of the alimentary canal of larvae 6-43 mm standard length (SL).

Haryu (1981) defined the developmental stages of pollock larvae. He assigned larvae to the juvenile stage when they reached the full number of fin rays. This occured at a length of about 22 mm SL. Haryu's terminolgy is adopted throughout this report.

The most recent, comprehensive, and useful guide to the identification of pollock larvae is that of Matarese et al. (1981). They described how pollock larvae can be distinguished from Pacific cod, *Gadus macrocephalus*, larvae on the basis of pigment patterns (Figure 1, Table 1).

In summary, pollock eggs and larvae have been described in enough detail so they can be identified in field samples. Eggs can be classified by developmental stage, although not all authors use the same terminology. Therefore, the current state of knowledge in this area appears to be adequate for field investigations.

Growth and metabolism

Although the various developmental stages have been described for both eggs and larvae, developmental times are not well-known either in the laboratory or natural environment.

Hamai et al. (1971) incubated artificially fertilized eggs at three temperatures. At the lowest temperature studied (2^{o}C), nearly a month was required after fertilization for 50% of the eggs to hatch. Since most of the larvae died before, or shortly after, yolk absorption, it appears that feeding was not successful and the growth rates obtained for larvae in this experiment are not reliable. Hamai et al. (1974) attempted to culture larvae with a variety of diets, but the growth rates that were determined are so low that little can be concluded. Although neither of these studies provide useful information about larval growth rates, they do provide estimates of rates of egg development and yolk sac absorption. They also show that antibiotics are useful in reducing mortality in laboratory experiments with larval pollock.

Several authors have inferred larval and juvenile growth rates in the natural environment from length-frequency distributions taken over time. Cooney, English, and Nishiyama (1978) and Cooney et al. (1978) found growth rates of 0.1-0.7 mm/day for larval and juvenile pollock.

Ohigashi and Ito (1955), Hayashi et al. (1968), and Hayashi (1976) presented length-frequency distributions for samples taken over time in Japanese coastal waters. These could be used to obtain growth rates for juvenile walleye pollock. However, only Hayashi (1976) discussed growth rates, and he apparently estimated growth by determining the average length of one-year-olds during the winter. For several years in the coastal waters of southwestern Hokkaido, the average length of one-year-olds varied inversely with their year class abundance.

Ohigashi and Ito (1955) discuss variations in condition factor with growth and present length-weight relationships for juvenile pollock.

Walline (1980, 1981b) used the method of enumerating daily growth increments to determine the growth rates and birthdates of field-caught larval and juvenile walleye pollock. He found a linear relationship between growth rate and length for larvae between 4 mm and 30 mm SL. In 1979 larval growth rates averaged 0.39 mm/day. Small differences were found in larvae from different geographic areas. Only two years, 1978 and 1979, were sampled, so relationships of growth rates with year-class abundance could not be determined.

Feeding

Gorbunova (1954) reported some information about the feeding habits of larval pollock from the western Bering Sea. Takeuchi (1972) examined the guts of larvae from coastal waters off the Kamchatka Peninsula, and Kamba (1977) investigated the feeding habits of larval pollock from Uchuira Bay, Hokkaido, Japan. Clarke (1978) examined larval pollock from the southeastern Bering Sea, as did Cooney et al. (1978a). All of the studies reported the importance of small copepods and nauplii as food items for the youngest larvae (Figure 2), although in some cases these larvae were observed to have phytoplankton cells in the gut. An increasing diversity of plankton prey was consumed as the larvae grew.

Walleye pollock are distributed from the Bering Sea south along the west coast of North America to Puget Sound. Studies by Barraclough (1967), Parker and Kask (1974), Simenstad et al. (1977), Smith et al. (1978), and Rogers et al. (1979) show that throughout its range outside the Bering Sea juvenile walleye pollock feed on a variety of planktonic crustacea, especially calanoid copepods and euphausiids. In addition, they frequently feed on caridean shrimp.

The prevalence of calanoid copepods and euphausiids in the diet of juvenile walleye pollock is observed also in the Bering Sea (Takahashi and Yamaguchi 1972; Smith et al. 1978; Bailey and Dunn 1979; English 1979). Euphausiids occur frequently in the diet (Figure 3), and seem to be especially important in terms of prey biomass. Fish (primarily pollock) do not become important dietary components until fish approach maturity (Mito 1974).

Behavior

Reports concerning the behavior of young walleye pollock are extremely scarce. Cooney and Van Hyning (1974) observed small walleye pollock (20 mm SL) congregating beneath a large jellyfish in Prince William Sound. Gorbunova (1954) noted that larvae begin to move actively after absorbtion of the yolk sac, but her conclusions were reached on the basis of fin ray development and not observation of living larvae. Nothing is published concerning physical orientation, methods of capturing food, schooling behavior, or predator avoidance mechanisms, all of which would be included under this heading.

Vertical distribution

Walleye pollock is one of the few species present in the Bering Sea for which there is some information available on the vertical distribution of larvae and juveniles. Both Kanoh (1954) and Gorbunova (1954) described pollock eggs as buoyant when spawned, but sinking in later developmental stages. The maximum number of eggs are usually found subsurface (Gorbunova 1954; Nishiyama and Hirano 1979), although a few authors found most at the surface (Takeuchi 1972; Kamba 1974).

Serobaba (1974) encountered larval walleye pollock to depths of 1000 m, although maximum numbers usually occur in the upper 40 m (Kamba 1974; Nishiyama 1979). Kamba sampled over 24 hr and found that although there was always a subsurface maximum in numbers between 10-30 m, larvae in the upper part of this distribution rose at night. He did not discuss the problem of net avoidance that was indicated by the larger catches taken at night.

Cooney, English, and Nishiyama (1978) showed that at night walleye pollock larvae apparently migrate both upward and downward from the mid-day, subsurface maximum.

Walline (1981b) showed a subsurface maximum in larval numbers which was more pronounced during the day than at night. He concluded that if any vertical migration occurred, it was only over a limited depth range of about 10 m (Figure 4).

Almost nothing is known of the vertical distribution of juvenile walleye pollock. They are caught in both bottom and mid-water trawls (Cooney, English, and Nishiyama 1978), and believed to be distributed generally higher in the water column than adults (Serobaba 1974).

Geographical distribution

Despite the large number of ichthyoplankton surveys made in the eastern Bering Sea, most focusing on pollock, there are still large gaps in our knowledge. The general distribution of eggs and larvae is known, as pointed out and described by Waldron (1981) who summarized the results of 43 ichthyoplankton surveys in the eastern Bering Sea. He shows that larvae are most abundant between Unimak Pass and the Pribilof Islands along the continental slope in spring and are more widely distributed in summer (Figure 5). Eggs have a similarly broad distribution, so large that none of the individual surveys encompassed the entire distribution. In addition, as shown by Waldron (1981: fig. 15) the center of abundance can change substantially from year to year. For these reasons egg surveys have not proven useful in estimating spawning populations of adult walleye pollock in the Bering Sea. Studies not included in Waldron's survey have obtained equally inconclusive results (Kobayashi 1963; Maeda 1972; Cooney et al. 1978; Haryu 1981; Walline 1981a). (It should be noted that references for surveys listed in Waldron [1981] are not listed in this report). Additional partial surveys of this nature will probably add little to our understanding. Surveys with complete geographical and temporal coverage of the distribution of pollock eggs or larvae are unlikely because of the large area and expense involved.

Even less is known of the geographic distribution of juvenile pollock in the eastern Bering Sea. Although 0-group pollock are too small to be caught by the trawls used in routine surveys of demersal fish, 1-yr-olds are retained in sufficient numbers to draw the conclusion that juveniles are found over the entire shelf, including areas farther inshore than those where adults are concentrated (Pereyra et al. 1976). Smith (1981) stated that from June to mid-August 0-group pollock have been observed over a large portion of the northwestern outer shelf, and are especially concentrated just west of the Pribilof Islands. This observation was confirmed by inspection of the gut contents of demersal fish. Large numbers of 0-group pollock appeared as food items for these demersal fish only in this area.

Modeling

Walsh and McRoy (1978) have adapted a model for the time-dependent distribution of air pollutants to predict the effect of small differences in timing or location of walleye pollock spawning on larval survival and distribution. The model requires a knowledge of the flow field to predict the horizontal movement of larvae and eggs, as well as a description of the distribution of factors affecting the survival of larvae. Since data were lacking in both of these areas, it is not too surprising that initial experiments failed to accurately model known distributions of larvae. However, a large effect of small differences in the location and timing of spawning was demonstrated. Walsh and McRoy (1979) tracked drogues to improve descriptions of the flow field used in the model and state that data on feeding habits and egg development will be included in a refinement of the model.

A numerical simulation model of the population dynamics of walleye pollock has been developed by Knechtel and Bledsoe (1981). Processes modeled include diet selection, consumption rates, assimilation, respiration, starvation, cannibalism, reproduction, and fishing mortality. Since eggs and up to 20 year classes are individually modeled, the effect of variations in these processes on the population size, length, weight, and growth of larval and juvenile pollock can be predicted. However, data on these processes are necessary to fit and validate the model, and unfortunately, such data are scarce. In later publications Knechtel and Bledsoe intend to report on model fitting, validation, and results of model experiments.

A total ecosystem simulation model of the eastern Bering Sea has been developed at the NWAFC (Laevastu and Larkins 1981). The model starts from the upper end of the food pyramid, and therefore avoids problems associated with incomplete knowledge of the magnitude of primary production and difficulties of determining trophic levels. Because the model is biomass-based, it is less sensitive to errors in estimated size of juvenile age-classes than are number-based models. The biomass distributions for juvenile age-classes of pollock and other fishes are computed indirectly in the model. Laevastu and Larkins point out the need for further field studies of the year-class strengths of prefishery juveniles. The model emphasizes the importance of predation mortality in the control of year-class strength.

Conclusions

For most topics our knowledge of the early life history of walleye pollock is fragmentary. We can identify eggs and larvae in field samples. We have a few estimates of growth rates in the sea, but need many more. No reliable estimates of pollock growth rates under laboratory conditions have been published. Nothing has been published concerning the rates of feeding, respiration, or swimming speeds. No account of successful rearing of larvae to the juvenile stage has been published.

The diet of larval and juvenile pollock has been established in general outline but daily rations, the effect of different foods on growth and survival, diet selection as a function of prey abundance, and feeding behavior (diel periodicity) have not been determined. The winter diet of 0-group and 1-yr-old fish has not been determined.

The vertical distribution of eggs and larval pollock is fairly well known. The vertical distribution of juveniles (and adults for that matter) is not well known, so it follows that the probable diel vertical migration of juvenile walleye pollock has not been documented yet either.

The geographic distribution of the young stages of walleye pollock in the eastern Bering Sea is still unclear because surveys have not had complete areal or temporeal coverage. Because even larval pollock can avoid plankton nets, and 0-group juvenile pollock escape or are extruded from demersal fish trawls, the distribution of young juveniles is particularly poorly known. The distribution of juveniles in winter is unknown.

Several models of aspects of the early life history of walleye pollock in the eastern Bering Sea have been developed. Their further refinement and usefulness awaits the collection of a more complete data set for model fitting and validation.

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Tables

Table 1. Characters useful in separating larvae of *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* at specific size ranges (from Matarese et al. 1981).

Figures

Figure 1. Larvae of *Theragra chalcogramma* and *Gadus macrocephalus*: A. *T. chalcogramma*, 6.2 mm SL; B. *T. chalcogramma*, 9.8 mm SL; C. *G. macrocephalus*, 5.6 mm SL; D. *G. macrocephalus*, 6.5 mm SL (from Matarese et al. 1981).

Figure 2. Percent composition by number of six food categories, taken by thirteen size groups of larval walleye pollock (from Clarke 1978).

Figure 3. For 5 size categories, the percent of juvenile pollock stomachs containing each food item. The main food items are coded as follows: 1) copepods, 2) euphausiids, 3) cyprid larvae, 4) cyprid nauplii, 5) larvaceans, 6) amphipods, 7) cladocerans, 8) chaetognaths, 9) other, and 10) completely empty stomachs (from English 1979).

Figure 4. Vertical distribution at different times of day for walleye pollock at: A. a station in the Outer Shelf Domain of the eastern Bering Sea; B. a station in the Inner Shelf Domain of the eastern Bering Sea (from Walline 1981b). Width of bar is proportional to abundance in numbers per 100 m^3.

Figure 5. Number of stations at which larvae of *Theragra chalcogramma* have been caught: A. surface tows, March-May; B. oblique or vertical tows, March-May; C. surface tows, June-August; D. oblique or vertical tows, June-August (from Waldron 1981).

Table 1. Characters useful in separating larvae of *Microgadus proximus*, *Theragra chalcogramma*, and *Gadus macrocephalus* at specific size ranges (from Matarese et al. 1981).

Character	Size range (mm)	*Microgadus proximus*	*Theragra chalcogramma*	*Gadus macrocephalus*
Anterior pigment bar	5-6			
Percentage of SL		41-53	47-55	40-57
Located at myomeres		14-23	21-26	16-26
Posterior pigment bar	5-6			
Percentage of SL		61-74	69-79	59-81
Located at myomeres		28-39	36-43	26-42
Number of melanophores in each stripe of:				
Anterior bar	3-4			
Dorsal		2	5	7
Ventral		4	5	8
Posterior bar	3-4			
Dorsal		7	5	11
Ventral		7	7	10
Degree of stripe continuity:				
Anterior bar:				
Dorsal	5-13	Separate	Separate	Continuous
Ventral		Continuous	Separate	Continuous
Posterior bar:				
Dorsal	13-16	Separate	Continuous	Continuous
Ventral		Continuous	Separate	Continuous
Head melanophores	4-8	—	—	More on dorsal surface and snout
Melanophores on ventral surface of gut	>13	1-2 rows of spots	No spots or a few reduced spots	1-2 rows of spots
Lateral pigment on gut surface	<13	—	Much less	—
Mediolateral pigment in postanal region	5-8	—	—	More
Ventral caudal pigment	<10	Row of spots	Isolated spots	Isolated spots
Number of rays on superior hypural element	>13	5	4	4

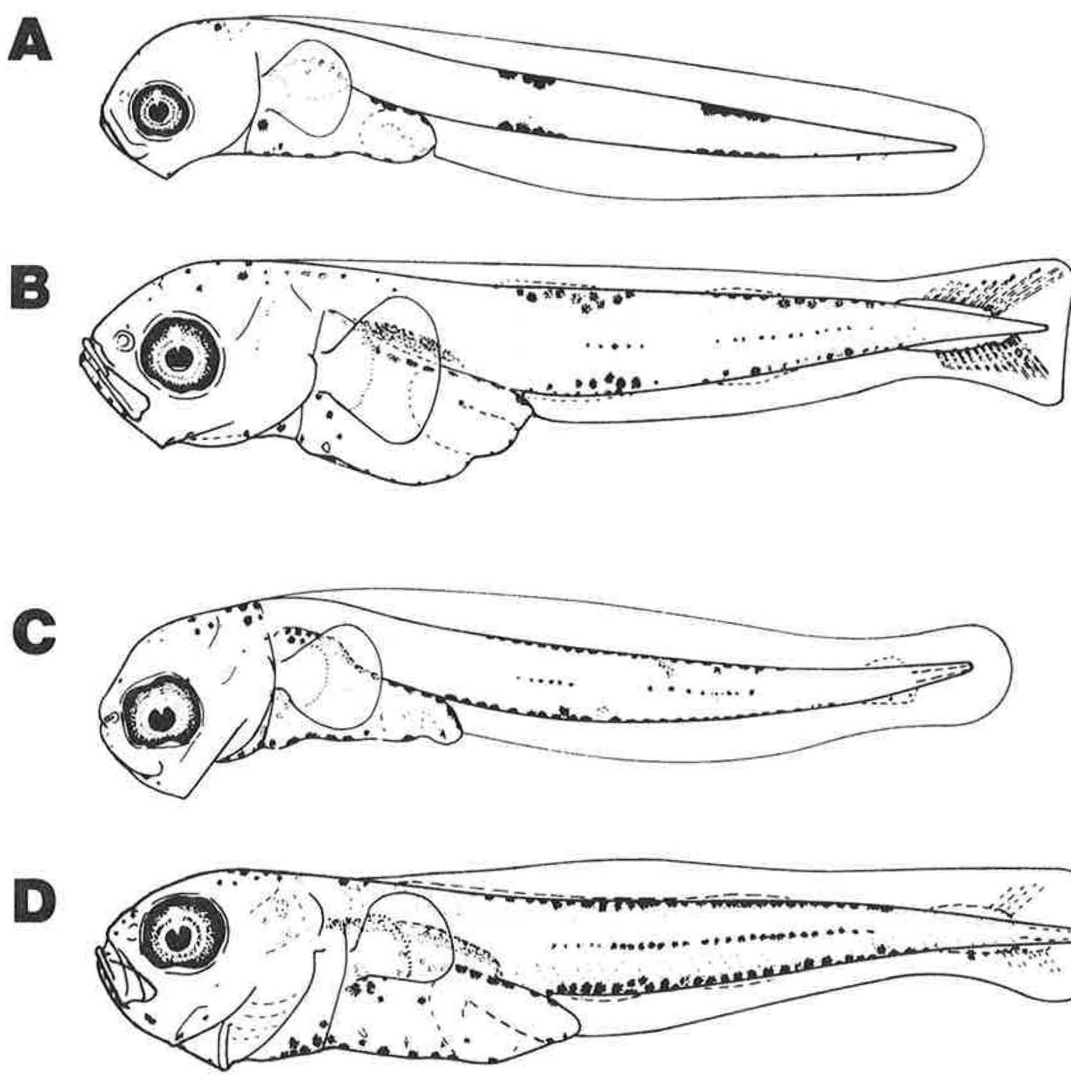

Figure 1. Larvae of *Theragra chalcogramma* and *Gadus macrocephalus*: A. *T. chalcogramma*, 6.2 mm SL; B. *T. chalcogramma*, 9.8 mm SL; C. *G. macrocephalus*, 5.6 mm SL; D. *G. macrocephalus*, 6.5 mm SL (from Matarese et al. 1981).

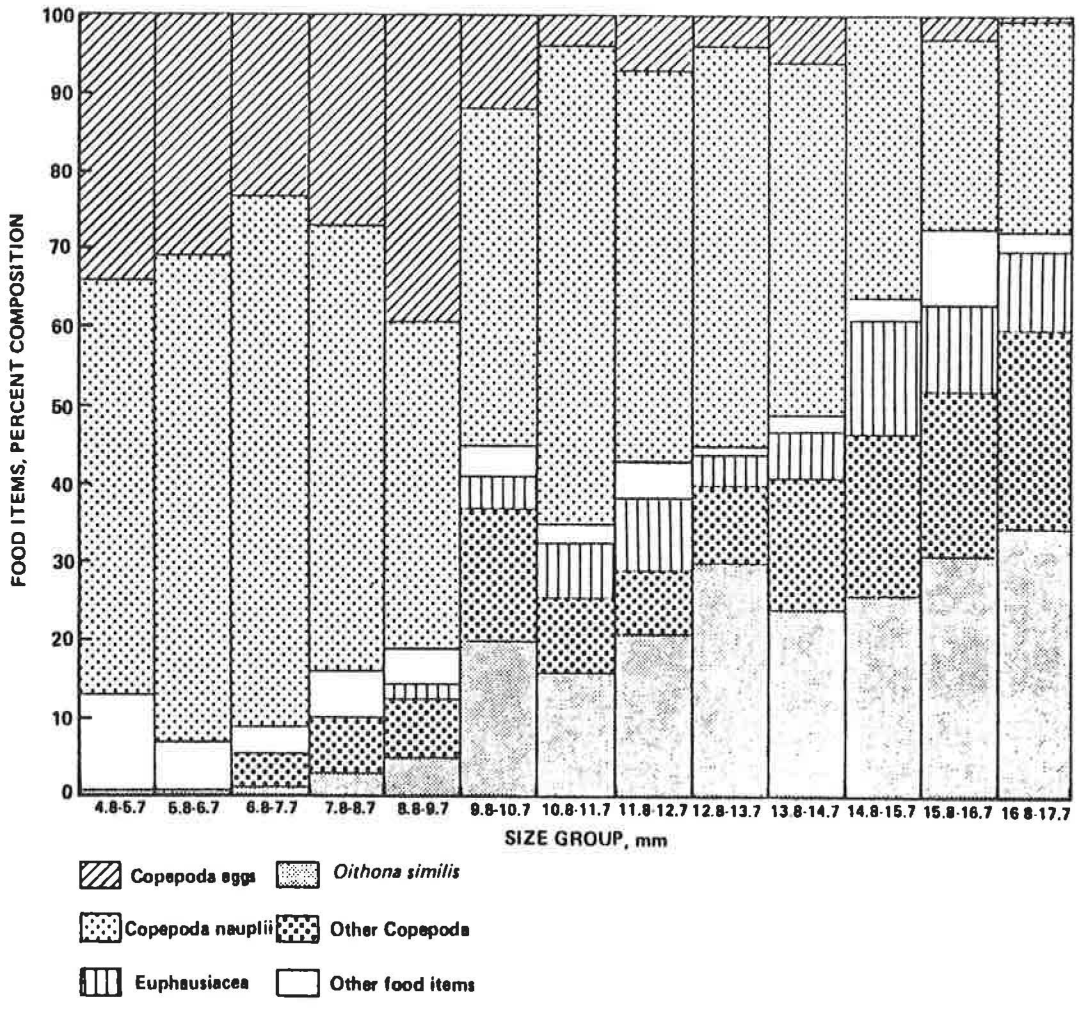

Figure 2. Percent composition by number of six food categories, taken by thirteen size groups of larval walleye pollock (from Clarke 1978).

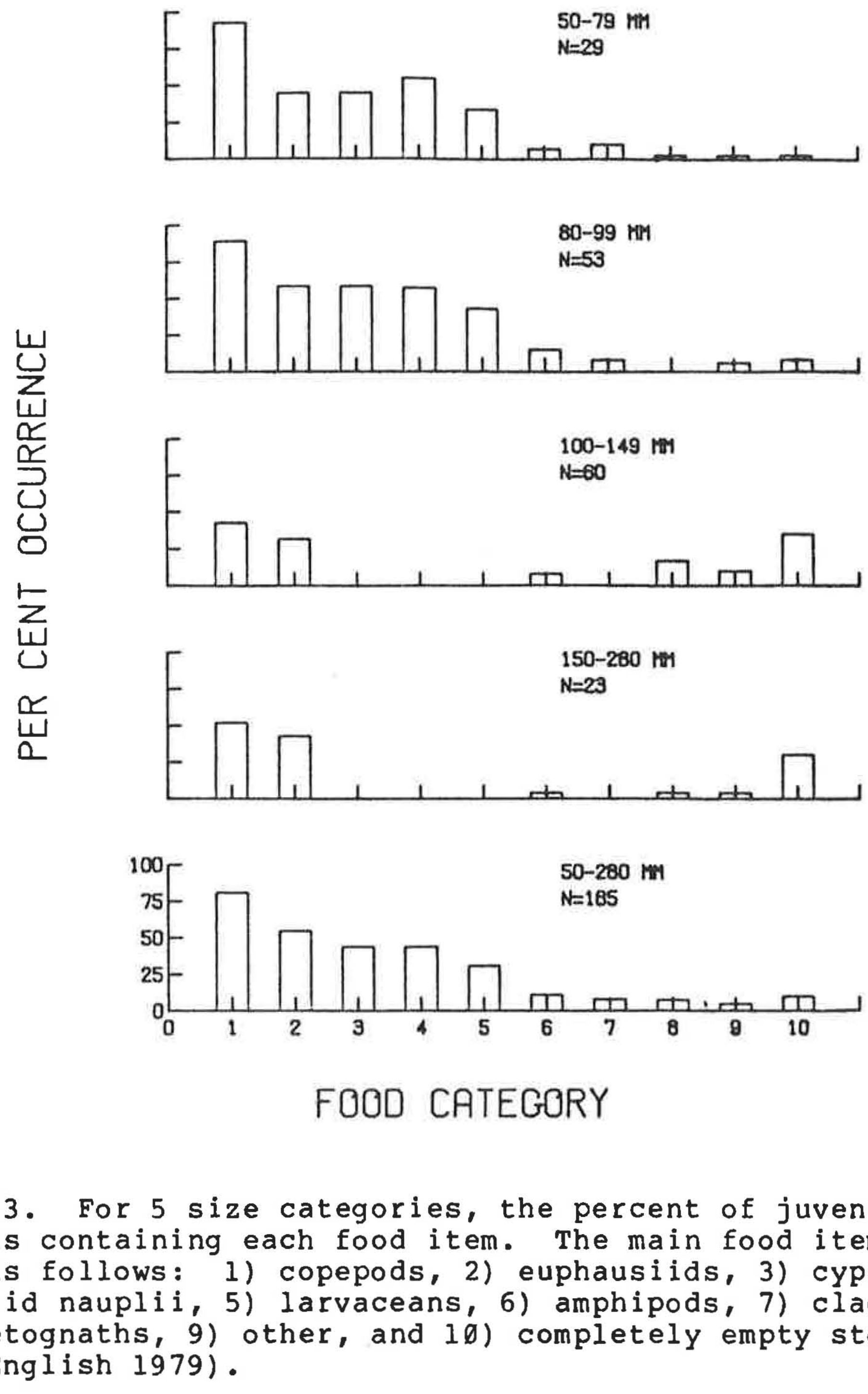

Figure 3. For 5 size categories, the percent of juvenile pollock stomachs containing each food item. The main food items are coded as follows: 1) copepods, 2) euphausiids, 3) cyprid larvae, 4) cyprid nauplii, 5) larvaceans, 6) amphipods, 7) cladocerans, 8) chaetognaths, 9) other, and 10) completely empty stomachs (from English 1979).

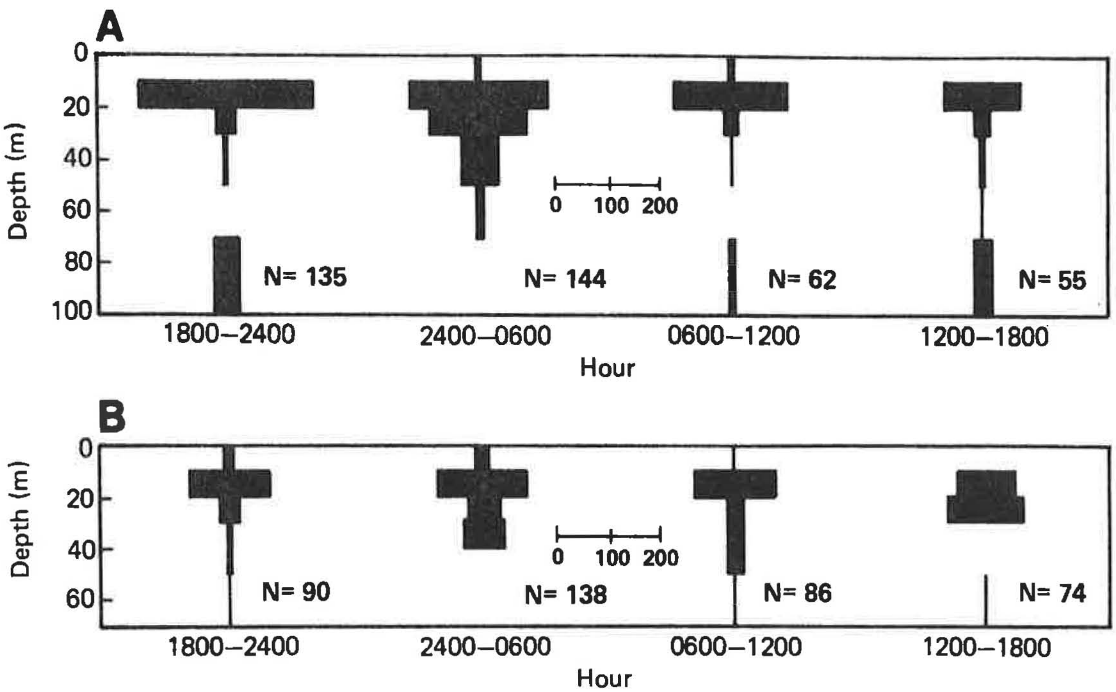

Figure 4. Vertical distribution at different times of day for walleye pollock at: A. a station in the Outer Shelf Domain of the eastern Bering Sea; B. a station in the Inner Shelf Domain of the eastern Bering Sea (from Walline 1981b). Width of bar is proportional to abundance in numbers per 100 m^3.

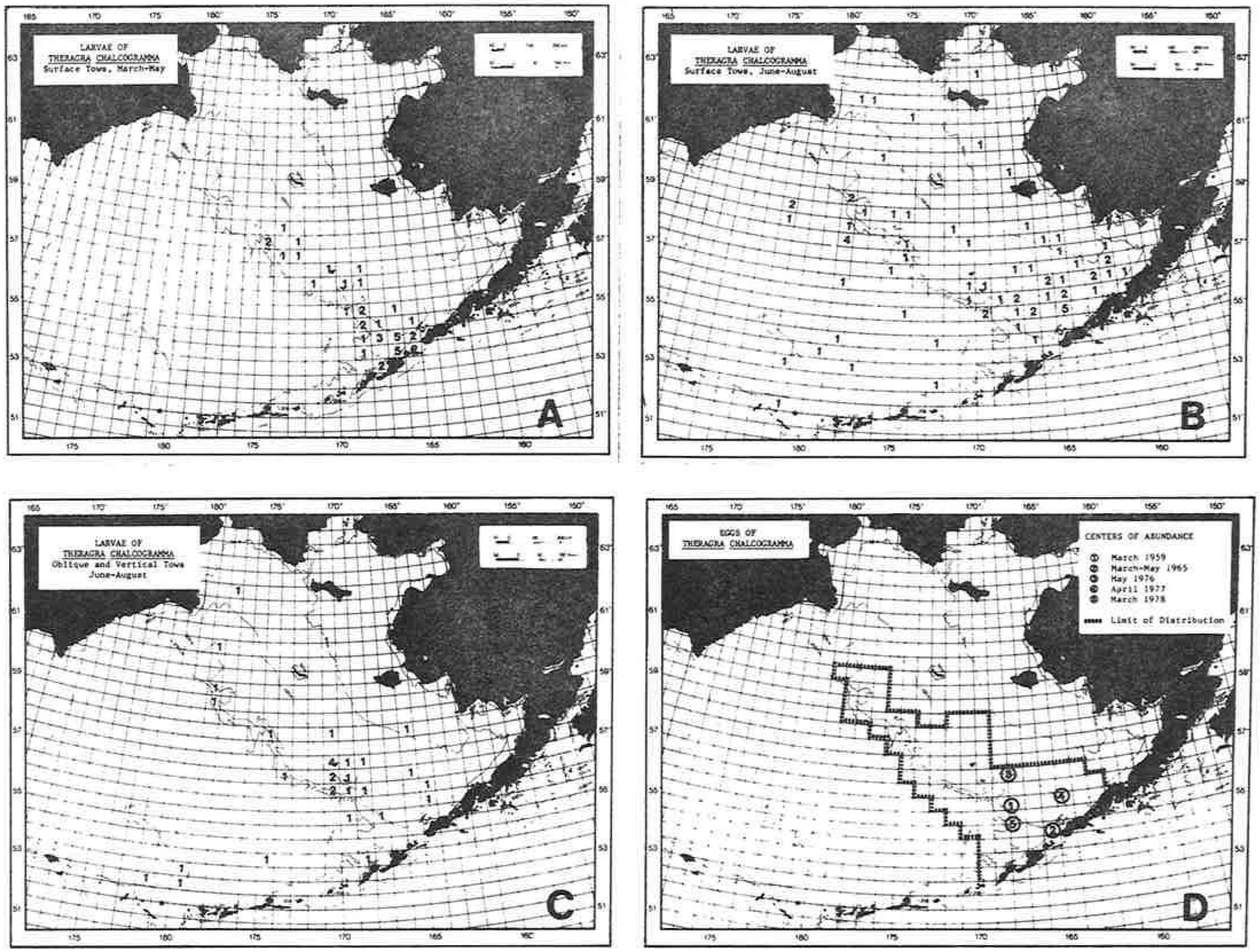

Figure 5. Number of stations at which larvae of _Theragra chalcogramma_ have been caught: A. surface tows, March-May; B. oblique or vertical tows, March-May; C. surface tows, June-August; D. oblique or vertical tows, June-August (from Waldron 1981).