

National Marine Fisheries Service

U.S DEPARTMENT OF COMMERCE

AFSC PROCESSED REPORT 2001-01

Specific Gravity and Vertical Distribution of Walleye Pollock (*Theragra chalcogramma*) Eggs

January 2001

This report does not constitute a publication and is for information only. All data herein are to be considered provisional.

ERRATA NOTICE

This document is being made available in .PDF format for the convenience of users; however, the accuracy and correctness of the document can only be certified as was presented in the original hard copy format.

Inaccuracies in the OCR scanning process may influence text searches of the .PDF file. Light or faded ink in the original document may also affect the quality of the scanned document.

Specific Gravity and Vertical Distribution of Walleye Pollock (Theragra chalcogramma) Eggs

By

Arthur W. Kendall, Jr.

Alaska Fisheries Science Center 7600 Sand Point Way NE Seattle WA 98115, USA

January 2001

Abstract

Walleye pollock (*Theragra chalcogramma*), an abundant and valuable gadid, occurs throughout the temperate and subarctic North Pacific and adjacent seas and spawns pelagic eggs in numerous defined areas within this range. These areas have different depths and hydrographic conditions. The eggs and then larvae drift with prevailing currents toward presumed juvenile nursery areas. Water temperature and currents often vary with depth, so the vertical position of the eggs can affect their rate of development, and rate and direction of drift. The specific gravity of the eggs determines their vertical position. Results of studies of the vertical distribution and specific gravity of walleye pollock eggs that have been conducted in five spawning habitats (Funka Bay, Japan; Shelikof Strait, Gulf of Alaska; Bering Sea basin; Bering Sea slope; and Eastern Bering Sea shelf) are reported. I found that the specific gravity and vertical distribution of eggs varied among these spawning areas. These differences allow the eggs to reside at a depth which will minimize development time and enhance their probability of hatching in a food-rich environment. These variations in specific gravity may reflect genetic differences among spawning populations.

Introduction

The Vertical Distribution of Pelagic Fish Eggs

Planktonic eggs, which are produced by most marine fish, float within precise depth ranges (e.g., Ahlstrom 1959, Coombs et al. 1981, Haug et al. 1986). These depth ranges often change in predictable ways as the eggs develop. This requires complex, but poorly understood, interactions between the specific gravity of seawater and that of the eggs (Craik and Harvey 1987). Maternal versus external environmental influences on egg specific gravity are similarly poorly known. The vertical distribution of eggs of a species may vary with local hydrography (Haug et al. 1986). Presumably the specific gravity of the eggs is adaptive and allows the eggs to hatch at depths favorable for feeding of the larvae, since larval prey is usually vertically stratified (Ellertson et al. 1981), and larvae are visual feeders needing light levels found during daytime above about 50 m (Paul 1983, Munk et al. 1989). Since currents often vary with depth, another reason for precise control of depth of eggs may be to ensure (or prevent) their drift in relation to suitable areas for the larvae. Ultraviolet radiation, which diminishes rapidly with depth, is damaging to fish eggs (Browman et al. 2000), so occurring too high in the water column would be disadvantageous.

Water, Salt and Density

Seawater is a solution of pure water (H_2O) and several salts, which are in practically the same proportions throughout the world s oceans. These salts change the properties of seawater relative to those of pure water. Some of these changes depend on the number of ions in the water, and not their particular type. These changes, brought about by the numbers of ions in solution, are called colligative properties, and include lowering of the freezing point (by definition pure water freezes at 0°C, while seawater freezes at about -1.9°C) and increasing specific gravity or density (by definition pure water at 4°C has a specific gravity of 1, while seawater has a specific gravity of about 1.028). For many applications in oceanography, precise knowledge of the specific gravity of a parcel of seawater is required. It is easier to measure other colligative properties, and calculate specific gravity using well-established empirical

relationships. Based on the fact that all seawater has very nearly the same mixture of ions, the total amount of contained salt (salinity) is calculated based on electrical conductivity and temperature. Salinity and temperature are then used to calculate specific gravity, which is expressed as sigma t ([sigma t = (specific gravity-1) × 1000]; for example, seawater with a specific gravity of 1.028 has a sigma t of 28).

Aquatic Animals in Relation to the Water They Live In

Animals can also be thought of as aqueous solutions separated from the environment by a relatively impermeable barrier (the skin). The liquid in animals is a solution of pure water, salts and organic molecules. This liquid exists as blood serum and other fluids which all have the same ionic concentration. In marine fishes, this concentration is less than that of the seawater in which they exist. That is, marine fish are hypotonic relative to seawater. The freezing point depression of marine fish blood is about -0.74 °C, which corresponds to a salinity of about 14 psu (practical salinity units: typical seawater has a salinity of 30-35 psu). Animals can also be thought of as chemical reactors, using water as one of the major ingredients in reactions involved with such functions as digestion, assimilation and respiration. For these reactions there needs to be continuous exchange between the water in the animal and the environment. To prevent dehydration, marine fish drink large quantities of water and excrete salt by way of salt secreting cells that are located primarily in the gills. They produce small quantities of hypotonic urine, as opposed to freshwater fish which produce huge quantities of urine since they have the opposite problem and must get rid of excess water while retaining salt.

Why Pelagic Fish Eggs Float

Pelagic marine fish eggs are buoyant, implying that their specific gravity is less than that of seawater. The fluid within the egg cell has practically the same ionic concentration as that of the female that spawned it, which is less than that of seawater and provides most of the buoyancy to the eggs (Craik and Harvey 1987). Lipids generally provide a minor portion of the buoyancy, whether they are dispersed throughout the egg or organized in one or more oil globules. Since most eggs do not float right at the surface, the egg membranes and cytoplasm

must be somewhat more dense than seawater. There is considerable variation in the specific gravity and depth distribution of fish eggs of different species and within-species variation also occurs. Neither the influence of the female, either genetic or environmentally induced, nor the influence of the environment on the egg after it is spawned on egg specific gravity is well known.

Fish Egg Development

Eggs begin development within the ovary by accumulating yolk (vitellogenesis). Shortly before spawning the eggs take on considerable liquid (hydration), which is isotonic with the female s blood. The egg cell is surrounded by two membranes. The inner one, the egg membrane, is impermeable to water and salt. The outer one, the chorion, is permeable to both salt and water. Following release of the egg and fertilization, the perivitelline space develops between the egg membrane and the chorion. The fluid in the perivitelline space is isotonic with the surrounding seawater (Davenport et al. 1981).

Walleye Pollock Spawning and Egg Distributions

Walleye pollock, *Theragra chalcogramma*, an abundant and economically important fish of the North Pacific, spawns pelagic eggs in predictable areas and at predictable times throughout its extensive range (Bailey et al. 2000) (Fig. 1). These areas have a variety of hydrographic and bathymetric characteristics. Among the various spawning areas, walleye pollock eggs have different specific gravities and depth distributions (Table 1). Regardless of the absolute values, in most areas walleye pollock eggs seem to rise in the water column during the middle stages of development. In Funka Bay, Japan, walleye pollock spawn over a protracted period, but primarily in January and February (Kendall and Nakatani 1992). Spawning occurs over depths of 100-120 m, and eggs are found at 10-30 m (Kamba 1977) (Fig. 2), where sigma t is 26.4-27.2. The specific gravity of eggs from Funka Bay is mainly 1.022-1.023 (Nakatani 1988) (Fig. 3). In Shelikof Strait, Gulf of Alaska, spawning occurs primarily in early April at depths of 200-300 m (Kendall and Picquelle 1990, Kendall et al. 1994). Water temperatures where the eggs develop are about 5°C, and sigma t ranges from 25.4 to 26.2

(Kendall and Kim 1989) (Fig. 4). Eggs are found mainly at depths between 150 and 200 m (Kendall et al. 1994) (Fig. 5). Eggs in Shelikof Strait rise in the water column in middevelopment (Kendall et al. 1994) (Fig. 6), and in laboratory experiments are shown to become more dense as hatching approaches (Olla and Davis 1993). Although there are several spawning areas in the Bering Sea, depth of spawning and egg occurrence is not well known. Two major distinct spawnings occur in the southeast Bering Sea: one in late winter over the basin (>1500 m), and one in April-May over the continental shelf (<170 m) (Dell Arciprete 1992). Spawning and egg distribution is much deeper (400-500 m) over the basin than over the shelf where spawning is in water < 180 m, and eggs are found above 100 m (Serobaba 1974; Nishiyama et al. 1986; Haldorson, L. Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. comm., 20 October 1998) (Figs. 7-10), and there is some indication that they rise in the water column during middle stages of development (Fig. 11). Temperatures at the time and depth of spawning in the Bering Sea basin are about 3-4°C, while those on the shelf are 0-2°C. Sigma t in basin waters is 26-27 while on the shelf it is 25.2-25.8.

Thus, in some areas spawning occurs at much shallower depths (southeast Bering Sea shelf, Funka Bay) and reduced specific gravity than in others (Shelikof Strait, Bering Sea basin); eggs would sink to the bottom (where predation is probably more intense) if they had the same specific gravity and depth distribution in these as they have in spawning areas that are deeper or have more dense water. Less is known about the vertical distribution of walleye pollock eggs in other major spawning areas such as the Sea of Okhotsk and areas of the western Bering Sea.

The Relevance of Differences in Egg Characteristics

Presumably adaptive reproductive strategies of walleye pollock include large spawnings at predictable times and places. Other reproductive characteristics, such as egg buoyancy should also be adaptive, and may promote the coincidence of larvae and optimal feeding conditions. Walleye pollock eggs develop in midwater over a considerable period of time (e.g., incubation requires 14 days at 5°C and 21 days at 3°C). Egg mortality is substantial, reaching about 30% per day (Brodeur et al. 1996). It would seem that accelerating the rate of development, and thus

shortening this period of vulnerability would be advantageous. Within a fish species, including walleye pollock, egg development rate is largely dependent on temperature. Secondarily, and among species, egg development rate is related to egg size: larger eggs develop more slowly (Ware 1975). In walleye pollock (Hinckley 1990), as in other fish, larger eggs result in larger larvae. There is probably a trade-off between producing large larvae that can consume a wider range of prey, stave off starvation longer, and be more capable of avoiding predators, and producing smaller larvae from smaller eggs that would pass through the incubation period faster, and thereby reduce the period of egg mortality.

In walleye pollock, spawning occurs in late winter or early spring so larvae will be at first feeding stage during the spring bloom, when prey production is at its seasonal maximum. Within spawning populations of walleye pollock, spawning seems to be consistent from year-to-year rather than varying with environmental conditions. Again, there is probably a trade-off between spawning early when water temperatures are at their seasonal minima and spawning too late to intercept the spring bloom. Thus, life history characteristics should include having the eggs reside at a depth where temperatures are maximal (to minimize the length of the incubation period and thus reduce egg mortality), while spawning at a time of year that will allow the larvae to take advantage of the spring bloom. Since water column characteristics are different among the various spawning locations of walleye pollock, as is the timing of the spring bloom, adaptive differences in egg specific gravity and depth distribution among the populations should be expected.

A major fisheries question involves whether these spawnings of walleye pollock are genetically distinct. Determining whether differences in egg buoyancy are environmentally induced or whether they are genetically set bears directly on this question.

Bering Sea Egg Studies

Although it has not been a priority activity, over the years the Fisheries Oceanography Coordinated Investigations (FOCI) group at the AFSC has conducted some research on the question of specific gravity and vertical distribution of walleye pollock eggs in the Bering Sea (Tables 2, 3 and 4; Fig. 12).

Methods and Materials

Specific Gravity Measurements

In 1986, 1998, and 1999 a density gradient column was used to measure the specific gravity of live walleye pollock eggs collected in the plankton. In 1986 these measurements were made aboard ship; in 1998 and 1999 the measurements were made in Seattle, Washington. In 1999 the eggs were collected in the upper and lower parts of the water column; in 1986 and 1998, the tows were not depth-stratified. In 1999 similar experiments were conducted on artificially spawned eggs to investigate the effects of spawning in water of different salinities (28, 30, 32 psu) on egg specific gravity. Following spawning and early development aboard the ship (1999), or sorting from the plankton samples (1998 and 1999), the eggs were transported to the laboratory in Seattle in insulated glass-lined bottles. In Seattle, they were maintained in a dark (lights were on only during operations in the room) constant-temperature room (3°C) in 4 1 glass jars in the three test salinities, or in water with salinity similar to that where the eggs were collected. Water was renewed every few days, and dead eggs were removed.

Eggs (5-15 per experiment) were placed in a density gradient column (at 3°C also) for specific gravity measurements. The eggs were held in the column for varying periods (2-24 hr) and their heights in the column noted, usually about 1 hr after the eggs were introduced to the column, and about 12 hr later. Heights in the column were converted to specific gravity by plotting the heights of several specific-gravity calibrated glass floats that were also in the column. After their specific gravity was determined, the eggs were preserved individually in 5 % formalin, their diameters measured, and their stage of development assessed microscopically according to the 21-stage scheme of Blood et al. (1994). Stage of development was converted to age in hours at 3°C based on temperature/age relationships in Blood et al. (1994). Egg stages were also grouped according to the 6 age groups of Kendall and Kim (1989) for statistical comparisons. Water column temperature and density was derived from Conductivity-Temperature-Depth (CTD) casts associated with the plankton tows that collected the walleye pollock eggs.

Vertical Distribution

In 1986 a cruise to the Bering Sea included some discrete-depth Tucker tows in the basin. As reported in Dell Arciprete (1992), during this cruise such tows were made at six stations: two of these were in the Donut Hole, three were near the Island of Four Mountains, and one was between these areas. At each station at least two depths were sampled: the surface to 400 m in 100 m increments, and from that depth to 100 or 200 m deeper. In 1988, a discrete-depth Tucker trawl tow was made at one station over the slope north of Unimak Island in which four depth intervals were sampled: 30-101, 91-133, 150-200, and 186-227 m.

In the 1990s, MOCNESS (Multiple-Opening-Closing-Net and Environmental Sensing System: Weibe et al. 1976) tows, conducted primarily for other purposes, were used to examine the vertical distribution of walleye pollock eggs that they contained. In 1994 and 1995, walleye pollock eggs were collected in MOCNESS tows at 11 stations in basin, slope and shelf waters in April and May. Depth schemes of these tows were quite variable and did not always encompass the entire water column. Vertical distribution of walleye pollock larvae from tows on three occasions over the shelf in 1995 were reported by Brase (1996); the vertical distribution of eggs taken in the tows made on 30 April is reported here. That MOCNESS tows are made over the shelf of the Bering Sea in April specifically to investigate the vertical distribution of walleye pollock eggs (results of these tows will be reported elsewhere).

Results

Specific Gravity (Table 3)

Plankton-caught walleye pollock eggs were used for specific gravity measurements as follows: 97 eggs in 1986, 61 eggs in 1998 and 326 eggs in 1999. The eggs in 1986 were collected in February over deep water of the basin of the Bering Sea and over the slope; those in 1998 and 1999 were collected in April in shelf waters. In 1986 and 1998 the eggs were collected in oblique tows. In 1999 the eggs were from depth-stratified tows: the upper 20 m of the water column and the lower 20 m (17 April: 55° 31' N, 163° 32' W, depth: 75 m, upper 20 m

and lower 20 m; 18 April: 55° 52' N, 163° 22' W, depth: 94 m). Also in 1999, specific gravity was determined for eggs (from females collected over the shelf of the Bering Sea on 18 April 1999 at 55° 26.93 N, 164° 6.98 W where water depth was 99 m) that were artificially spawned into water of three different salinities (28, 30, 32 psu) and reared to hatching at these salinities. The eggs used for experiments in 1986 were less than 300 hr old (11-286 hr), while those used in 1998 (235-537 hr) and 1999 (shallow/deep tows: 140-537 hr; three rearing salinities: 72-461 hr) were older. This was because experiments were conducted on board ship during the cruise in 1986, but the eggs were brought back to Seattle for the experiments in 1998 and 1999.

Area (Basin, Slope, Shelf): Analysis of variance was used to test for differences in specific gravity among areas with egg diameter and age group as covariates. Eggs from the basin were in age groups 1-6, those from the slope in age groups 1-5, while those from the shelf were in age groups 4-6. There were no significant relationships between egg diameter and specific gravity (Fig. 13) or age group. The specific gravity of the eggs from over the basin in 1986 ranged from 1.0256 to 1.0283, while the specific gravity of those from slope waters ranged from 1.0262 to 1.0283 (Fig. 14). There was no significant difference in specific gravities of eggs from the basin and slope for age groups 1, 2 and 3. For eggs from the basin and slope, there was a significant interaction between the two areas, there was a tendency for older eggs to have greater specific gravities in both areas. The specific gravities of eggs collected over the shelf in 1998 ranged from 1.0217-1.0266. These egg densities were significantly less than those of the eggs from the basin and slope (Fig. 14). There was no effect of age on specific gravity of eggs from the shelf in 1998 ranged from 1.0217-1.0266. These egg densities were significantly less than those of the eggs from the basin and slope (Fig. 14). There was no effect of age on specific gravity of eggs from the shelf, although only age groups 4-6 were tested.

The water column in the basin and slope area where the eggs were collected in 1986 and 1988 was quite complex, with a temperature maximum at 150-250 m, where temperatures ranged from 3.9° to 4.1° C (Appendix B:1-4). Below a surface mixed layer, which was about 100 m thick, salinity and density increased steadily. At the 200-400 m depths where most eggs occurred (see later), temperatures were 3.6° - 4.1° C and density was sigma t 26.65-26.92 in the basin and sigma t 26.20-26.55 over the slope. The ranges of measured egg densities from the

basin and slope areas were slightly greater than the ranges observed in the water column, but indicated that the eggs were probably close to neutrally buoyant at the depths where they occurred.

The water depth at the shelf site of egg collection in 1998 was 85-96 m. The water was well mixed with temperatures of 3.4°C, salinities of 32 psu, and sigma t of 25.4-25.5 (specific gravity 1.0245-1.0255) (Appendix B:16-18). The measured specific gravity of eggs from this location was mainly less than 1.0245, meaning that the eggs were less dense than the surrounding seawater, which would cause them to rise toward the surface.

Rearing Salinity (28, 30, 32 psu): There was no consistent relationship between egg diameter and rearing salinity, although there were some differences in diameter of age group 2 eggs. There is a complex interaction between rearing salinity and age (Fig. 15). At age group 3, the youngest measured, eggs reared at 28 and 32 psu were slightly lighter than those reared at 30 psu, however, at age group 6 those at 28 were lighter than those at 30 which in turn were lighter than those at 32 psu. Thus, rearing salinity did not seem to cause major changes in egg specific gravity. These eggs were spawned from fish collected over the shelf, and regardless of the salinity the eggs were spawned and reared in, their specific gravities are similar to those of eggs caught in the plankton in this region. They are all lighter than eggs collected over the basin and slope. The water column over the Bering Sea shelf in April 1999, where the adults were collected, was practically uniform in regard to temperature and density (Appendix B:19-20). Temperature was about 1.4°C and density was about sigma t 25.52. Salinity was about 31.9 psu.

Depth of collection (upper and lower 20 m of the water column over the shelf): Again there was no relationship between egg diameter and specific gravity for eggs collected in either the deep or shallow tows. There is little pattern of specific gravity in relation to depth of collection (Fig. 16). Overall it appears that eggs collected higher in the water column have lower specific gravities than those collected deeper. However, in looking at each age group the pattern is complex. For example, at station 46, eggs in age groups 3 and 6 from the shallow tow were lighter than those from the deep tow. However, at age group 5 the eggs from the deep tow were lighter than those from the shallow tow. Eggs from the shallow tow at station 37 were always lighter than those from the deep tow (data only for age groups 4-6); however, the

difference was not always significant. Since the water column where the eggs were collected was well mixed; that is, the temperature and specific gravity did not vary with depth (Appendix B:19-20), the specific gravity of the eggs would not be expected to vary with depth.

Vertical Distribution (Table 4)

In 1986, sufficient numbers of eggs were collected at two basin stations to examine their vertical distribution. Eggs were rare above 200 m. They were most abundant in the 300-400 m stratum, although sampling was not conducted deeper than 400 m at one station, or deeper than 500 m at the other station (Fig. 17, Appendix A: Figs. 1 and 2). As mentioned above, there was a temperature maximum at 150-250 m and temperature ranged from 3.6 to 4.1° C at the depths where most eggs occurred (Appendix B: Figs. 1-3). At the basin station in 1988, eggs were more evenly distributed with depth, but were most abundant in the 150-200 m stratum (Fig. 17, Appendix A: Fig. 3). The temperature profile of the water where the eggs were collected in 1988 was quite complex (Appendix B: Fig. 4). Below a cold (< 3°C) and fresh (< 33 psu) surface mixed layer that was about 45 m deep, temperature, salinity and density increased rapidly. Between 50 and 150 m, temperature fluctuated considerably with depth between 3.1° and 3.4°C. At about 150 m there was another sharp increase in temperature with a maximum of about 3.9°C at 200 m. Below that temperature decreased steadily while salinity and density increased steadily to 500 m, the maximum depth of measurements.

In 1994 and 1995, MOCNESS tows made in April and May over the basin, slope and shelf yielded walleye pollock eggs. The tows in 1994 were in the basin (four tows), over the slope (one tow) and over the shelf (one tow); in 1995, they were over the shelf (five tows). Depths at sampling stations ranged from 60 to 2,005 m (Table 4). On the shelf, where water depth was less than 250 m, the mean depth of the eggs was 27 m or less (Fig. 17, Appendix A: Figs. 4-9). In water deeper than 800 m the lower part of the water column was not sampled; thus, these results may be biased toward shallower mean egg depths. At the one slope station where water depth was 837 m, sampling extended to 526 m (Appendix A: Fig.10), and the mean depth of eggs was 413 m. At the basin stations where water depth exceeded 1,500 m, maximum sampling depth was less than 400 m and mean egg depths were less than 200 m (Appendix A:

Figs. 11-14). There seemed to be a decrease in mean egg depth as the season proceeded, but this may have resulted from sampling in shallower water later in the year.

The CTD geographically closest to the slope MOCNESS tow in 1994 was taken on 29 April, whereas the MOCNESS tow was taken on 16 April (Appendix B: Fig. 5). Nevertheless, the water column probably did not change much in the intervening 13 days. Temperature at the surface was about 3.7°C, and decreased sharply with depth to a minimum of about 3.45°C at about 45 m, and thereafter it increased to a maximum of about 3.85°C at 110-120 m. Salinity and density increased steadily with depth; density at the surface was sigma t 25.7 and it was 26.3 at 200 m, the deepest value recorded.

At the basin stations in 1994, temperature, salinity and density measurements at three stations are only available from the upper 100 m of the water column (Appendix B: Figs. 6-8). Temperature in the upper 100 m was about 3.4-3.6 °C, with considerable fine-scale structure. Salinity and density indicated a surface mixed layer about 18 m deep; below this, both variables increased sharply to about 80 m and thereafter increased steadily to the maximum depth of measurements. At the one station where measurements were taken deeper (to 700 m) similar structure and values were seen in the upper 100 m (Appendix B: Fig. 9). Below that temperature increased sharply to a maximum of 3.8 °C at 220 m and then decreased steadily with depth. Below a surface mixed layer of ~50 m, density and salinity increased steadily with depth.

At the shelf station in April 1994 salinity and density was minimal at the surface (0-20 m) and increased at greater depths (Appendix B: Fig. 10). In a shallow mixed layer (~15 m deep), temperature was about 3.35°C, and then it decreased sharply to a minimum of 3.24°C at 20 m. It then increased to a maximum of 3.76°C at 120 m. Density at the surface was sigma t 25.2 and increased below the mixed layer, reaching sigma t 26.4 at 180 m.

In late April 1995, the shelf stations were still cold and fresh in the upper 30 m of the water column (Appendix B: Figs. 11-12). Temperatures near the surface were cold at less than 1.5°C. Density was about sigma t 25.35-25.40.

By the time of the sampling on the shelf in May 1995, a thermocline was starting to develop in the upper 40 m of the water column (Appendix B: Figs.13-15). The surface layer was

still cold (< 2.5 °C), but deeper waters were even colder. Density near the surface was sigma t 25.3-25.5.

Discussion and Conclusions

Walleye pollock spawns pelagic eggs in predictable areas and at predictable times throughout its extensive range in the North Pacific Ocean and adjacent seas. The specific gravities of the eggs are adapted for the different spawning areas to minimize the duration of the egg stage, and to position larvae in an optimal feeding environment. Eggs spawned in Funka Bay are the least dense, followed by those spawned over the eastern Bering Sea shelf, Shelikof Strait, and the slope and basin areas of the eastern Bering Sea (Fig. 18). The vertical distribution of the eggs follows a similar pattern in that eggs from Funka Bay are very close to the surface followed by those from the eastern Bering Sea shelf (< 30 m), the eastern Bering Sea slope and basin (although the depth distribution of eggs in these areas is not well known), and Shelikof Strait where they are mainly below 180 m (Fig. 19). In Funka Bay the eggs are spawned near the mouth of the bay, float near the surface, and drift into the bay where the larvae find optimal feeding (Nakatani 1988). Over the basin and slope of the eastern Bering Sea there is a temperature maximum at 150-300 m and walleye pollock eggs have specific gravities of the water at these depths; vertically stratified tows indicate they are found there. Spawning on the Bering Sea shelf occurs under quite different hydrographic conditions, and later in the year (April) than spawning in the Bering Sea basin (February). The water column where spawning occurs over the Bering Sea shelf is shallow (< 100 m), well mixed and densities are less than those in the Bering Sea basin and slope areas (Fig. 20). Egg spawned in Bering Sea shelf waters are less dense than those spawned in the Bering Sea basin and slope and are less dense than the water in which they are spawned. This allows these eggs to rise to the surface, where temperatures are warming, and the spring bloom, which will provide food for the larvae, is starting. In Shelikof Strait the eggs are spawned and remain deep in the water column (180-200 m), where temperatures are maximal (Fig. 21). In both the Bering Sea shelf and Shelikof Strait middle stage eggs are shallower than early or late stage eggs (Fig. 22). On the Bering Sea shelf, the eggs to rise to the surface in these middle stages and stay above the pycnocline through

hatching; however, in Shelikof Strait the eggs remain well below 100 m. In Funka Bay, eggs continue to rise throughout development (Nakatani 1988), while specific gravity of walleye pollock eggs in Shelikof Strait increases toward hatching (Olla and Davis 1993) and older eggs are found deeper than younger eggs (Kendall et al. 1994). Presumably recently hatched larvae from the Bering Sea basin and slope spawnings rise into the photic zone for feeding in the same way larvae from Shelikof Strait do, while larvae from Funka Bay and the Bering Sea shelf spawnings hatch directly in the photic zone.

The mechanisms regulating specific gravity of pelagic fish eggs are poorly understood. The degree to which minute differences in specific gravity are genetically or environmentally controlled are largely unknown. How much of this control is due to events occurring in the ovary before spawning, or to the eggs immediately after spawning is likewise uncertain. Since in walleye pollock it seems that these differences adapt the eggs and larvae to survive in the particular circumstances associated with the various spawning areas, it would seem that they are at least partially under genetic control. Egg specific gravity then could be a phenotypic characteristic of walleye pollock populations that would indicate that they are genetically distinct.

Acknowledgments

Many people were involved in making the collections reported on here. Their efforts in making these collections, and allowing me use of these collections and other data is gratefully acknowledged (from Alaska Fisheries Science Center except as noted). Kevin Bailey made collections and specific gravity measurements on eggs collected in the Bering Sea in winter 1986. Patricia Dell Arciprete (University of Washington at the time) made collections of eggs in 1988. Lew Haldorson (University of Alaska) counted eggs collected by Audra Brase (University of Alaska at the time) in MOCNESS tows in 1995, and kindly supplied me with these data. Jeff Napp supervised egg collections in 1998. Debbie Blood supervised collections of eggs from plankton samples and reared eggs from adults in 1999, and staged and measured the eggs from the density gradient experiments and reviewed an earlier draft of this paper. Rachel Cartwright helped with specific gravity measurements in 1999, and Steve Porter provided

much technical support for rearing the eggs in Seattle in 1998 and 1999. Kathy Mier provided the statistical analyses used here. Susan Picquelle helped produce Figures 1 and 12. Ned Cokelet and Dave Kachel (Pacific Marine Environmental Laboratory) helped secure and analyze the hydrographic data used here.

Citations

Ahlstrom, E.H.

1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull., U.S. 60:107-146.

Bailey, K.M., T.J. Quinn, P. Bentzen, and W.S. Grant.

2000. Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. Adv. Mar. Biol. 37:179-255.

Blood D.B., A.C. Matarese, and M.M. Yoklavich.

1994. Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 92: 207-222.

Brase, A.J.L.

1996. Temporal variation in feeding of larval walleye pollock, *Theragra chalcogramma*, in the southeast Bering Sea. M.Sc. Thesis, University of Alaska, Fairbanks, AK, 87 p.

Brodeur, R.D., S.J. Picquelle, D.M. Blood, and N. Merati.

1996. Walleye pollock egg distribution and mortality in the western Gulf of Alaska. Fish. Oceanogr. 5 (Suppl. 1): 71-80. Browman, H.I., C. Alonso Rodriguez, F. Béland, J.J. Cullen, R.F. Davis, J.H.M. Kouwenberg, P. Kuhn, B. McArthur, J.A. Runge, J.-F. St-Pierre, and R.D. Vetter.
2000. The impact of ultraviolet radiation on marine crustacean zooplankton and ichthyoplankton: a synthesis of results from the estuary and Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. 199: 293-311.

Coombs, S.H., R.K. Pipe, and C.E. Mitchell.

1981. The vertical distribution of eggs and larvae of blue whiting (*Micromestistius poutassou*) and mackerel (*Scomber scombrus*) in the eastern North Atlantic and North Sea. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:188-195.

Craik, J.C.A., and S.M. Harvey.

1987. The causes of buoyancy in eggs of marine teleosts. J. Mar. Biol. Assoc. U.K. 67:169-182.

Davenport, J., S. Lonning, and J. Kjorsvik.

1981. Osmotic and structural changes during early development of eggs and larvae of the cod *Gadus morhua* L. J. Fish Biol. 19:317-331.

Dell Arciprete, O.P.

1992. Growth, mortality, and transport of walleye pollock larvae (*Theragra chalcogramma*) in the eastern Bering Sea. MS Thesis, U. Washington. 105 p.

Ellertson, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgard, and V. Oiestad.
1981. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:317-319.

Haug, T., E. Kjorsvik, and P. Solemdal.

1986. Influence of some physical and biological factors on the density and vertical distribution of Atlantic halibut *Hippoglossus hippoglossus* eggs. Mar. Ecol. Prog. Ser. 33:207-216.

Hinckley, S.

1990. Variation in egg size of walleye pollock *Theragra chalcogramma* with a preliminary examination of the effect of egg size on larval size. Fish. Bull., U.S. 88: 471-483.

Kamba, M.

1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175-197.

Kendall, A.W., Jr., L.S. Incze, P.B. Ortner, S. Cummings, and P.K. Brown.

1994. Vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Fish. Bull., U.S. 92: 540-554.

Kendall, A.W., Jr., and S. Kim.

1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. <u>In</u> R.J. Beamish and G.A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 169-180. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Kendall, A.W., Jr., and T. Nakatani.

1992. Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan. Fish. Bull., U.S. 90:129-138.

Kendall, A.W., Jr., and S.J. Picquelle.

1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish Bull., U. S. 88:133-154.

Munk, P., T. Kiorboe, and V. Christensen.

1989. Vertical distribution of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environ. Biol. Fish. 26:87-96.

Nakatani, T.

1988. Studies on the early life history of walleye pollock *Theragra chalcogramma* in Funka Bay and vicinity, Hokkaido. Mem. Fac. Fish. Hokkaido Univ. 35: 1-46.

Nishiyama, T., K. Hirano, and T. Haryu.

1986. The early life history and feeding habits of larval walleye pollock *Theragra* chalcogramma (Pallas) in the southeast Bering Sea. INPFC Bull. 45:177-227.

Olla, B.L., and M.W. Davis.

1993. The influence of light on egg buoyancy and hatching rate of the walleye pollock, *Theragra chalcogramma*. J. Fish. Biol. 42: 693-698.

Paul, A.J.

1983. Light, temperature, nauplii concentration and prey capture by first feeding pollock, *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175-179.

Serobaba, I.I.

1974. Spawning ecology of the walleye pollock, *Theragra chalcogramma*, in the Bering Sea. J. Ichthyol. 14:544-552.

Ware, D.M.

1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Bd. Can. 32:2503-2512.

Weibe, P.D., K.H. Burt, S.H. Boyd, and A.W. Morton.

1976. A multiple opening/closing net and environmental sensing system for zooplankton. J. Mar. Res. 34:313-326.

List of Tables

Table 1. Comparisons of specific gravity and depth distribution of walleye pollock eggs from various locations.

Table 2. Collections of walleye pollock eggs for specific gravity and vertical distribution from the Bering Sea.

Table 3. Walleye pollock egg specific gravity in the Bering Sea.

Table 4. Walleye pollock egg vertical distribution in the Bering Sea, based on NOAA sampling 1986-1995.

Table 5. Dates and locations of CTD casts associated with walleye pollock egg specific gravity and vertical distribution collections.

List of Figures

Figure 1. Geographic distribution (shading) and spawning areas (dots) of walleye pollock, after Bailey (pers. comm). Areas of comparison of egg specific gravity and vertical distribution are indicated by arrows.

Figure 2. Vertical distribution of walleye pollock eggs in Funka Bay, Japan. From Kamba (1977).

Figure 3. Specific gravity of walleye pollock eggs in Funka Bay, Japan. From Nakatani (1988).

Figure 4. Vertical distribution of walleye pollock eggs and water column density from Shelikof Strait, Gulf of Alaska. From Kendall et al. (1994).

Figure 5. Vertical distribution of walleye pollock eggs from Shelikof Strait, Gulf of Alaska. The abundance of eggs was greatest during Series 1 and 2, and decreased steadily after that. From Kendall et al. (1994).

Figure 6. Changes in vertical distribution of walleye pollock eggs from Shelikof Strait, Gulf of Alaska with development. From Kendall et al. (1994).

Figure 7. Transect used by Serobaba (1974) to sample vertical distribution of walleye pollock eggs across the southeastern Bering Sea shelf.

Figure 8. Vertical distribution of walleye pollock eggs across the Bering Sea shelf. From Serobaba (1974).

Figure 9. Vertical distribution of walleye pollock eggs over the southeastern Bering Sea shelf. From Nishiyama et al. (1986). See Figure 12 for collection locations.

Figure 10. Vertical distribution of walleye pollock eggs over the southeastern Bering Sea shelf, by developmental stages. From Nishiyama et al. (1986). See Figure 12 for collection locations.

Figure 11. Vertical distribution of walleye pollock eggs over the southeastern Bering Sea shelf. From Haldorson (L. Haldorson, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. comm., 20 October 1998). See Figure 12 for collection locations.

Figure 12. Locations of collections used for walleye pollock egg vertical distribution and specific gravity measurements in the Bering Sea. The 200 and 1000 m isobaths are shown. Station designations correspond to those in Tables 3-5. Plus-signs are stations where eggs were collected for specific gravity experiments. Circles are stations where vertical distribution tows were made in 1986 and 1988. Triangles are where vertical distribution tows were made in 1994 and 1995. The eastern 74 is where the tow was made in 1995. The square is where the vertical distribution tow of Haldorson (L. Haldorson, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. comm., 20 October 1998) was made. Circles connected by line (N1-N2) represent the range of locations of vertical distribution tows of Nishiyama et al. (1986). The star is where the trawl for spawning adults was made in 1999.

Figure 13. Diameters of walleye pollock eggs from the Bering Sea shelf (triangles), basin (circles) and slope (squares) used in specific gravity experiments in relation to stage of development.

Figure 14. Least squares means and standard errors of walleye pollock egg specific gravities by age group from the shelf (dotted line), slope (solid line) and basin (dashed line) of the eastern Bering Sea.

Figure 15. Least square means and standard errors of specific gravity of walleye pollock eggs from the Eastern Bering Sea shelf reared at three salinities (28, 30, 32 psu) by age group.

Figure 16. Least square means and standard errors of specific gravity of walleye pollock eggs by age group collected at two stations and two depths over the southeastern Bering Sea shelf.

Figure 17. Vertical distribution of walleye pollock eggs from the Bering Sea basin, slope and shelf based on Tucker trawl sampling in 1986 and 1988, and MOCNESS sampling in 1994 and 1995. Mean egg depth, maximum sampling depth and water depth are shown.

Figure 18. Means and ranges of specific gravity of walleye pollock eggs from several locations.

Figure 19. Means and ranges of vertical distribution of walleye pollock eggs from several locations.

Figure 20. Specific gravity and vertical distribution of walleye pollock eggs (mean and range) from Shelikof Strait, Gulf of Alaska, the Bering Sea basin and the southeastern Bering Sea shelf in relation to average water column specific gravity at the time of egg occurrence (from Ned Cokelet, PMEL, NOAA, pers. comm.).

Figure 21. Vertical distribution of walleye pollock eggs (mean and range) from Shelikof Strait, Gulf of Alaska, the Bering Sea basin, and the southeastern Bering Sea shelf in relation to average water column temperature at the time of egg occurrence (from Ned Cokelet, PMEL, NOAA, pers. comm.).

Figure 22. Model of changes in vertical distribution of walleye pollock eggs from the Bering Sea shelf during development (from Nishiyama et al. 1986).

Table 1. Comparisons of specific gravity and vertical distribution of walleye pollock eggs from various locations.

		Specific gravit	у			
	Water		Eggs		Depth distribution	
Location	Range	Range	Mean	SD	Range (m)	Source
Funka Bay, Japan					0-30	Kamba 1977
Funka Bay, Japan	1.02641-1.02717	1.020-1.026				Nakatani and Maeda 1984
Ainuma, Japan		1.019-1.024				Nakatani 1988
Shelikof Strait, Gulf of Alaska		1.0227-1.0266				Olla and Davis 1993
Shelikof Strait, Gulf of Alaska	1.02531-1.02563	1.024-1.031			150-210	Kendall et al. 1994
Eastern Bering Sea basin	1.02665-1.02692	1.0217-1.0266	1.0265	0.0006	> 200	This study, Bailey ¹ , Dell'Arciprete 1992
Eastern Bering Sea slope			1.0269	0.0007	100-200	This study, Bailey ¹ , Dell'Arciprete 1992
Eastern Bering Sea shelf					0-40	Nishiyama et al. 1986
Eastern Bering Sea shelf					0-100	Serobaba 1974
Eastern Bering Sea shelf					0-60	Haldorson ²
Eastern Bering Sea shelf	1.0254-1.0256	1.0215-1.0268	1.0239	0.0011		This study

¹K. M. Bailey, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle WA 98115, pers. comm.

²L. Haldorson, School of Fisheries and Ocean Sciences, University of Alaska, 11120 Glacier Highway, Juneau AK 99801, pers. comm., 20 October 1998.

Table 2. Collections of walleye pollock eggs for specific gravity and vertical distribution from the Bering Sea.

 $\sim 10^{-10}$

Cruise	Атеа	Dates	Type of samples	Initial investigator	Net used	Towing scheme
2MF86	Basin	2/21-2/26/86	Specific gravity	Bailey	Tucker trawl	three stations, 100 or 200 m increments.
2MF86	Basin	2/17-2/26/86	Vertical distribution	Dell'Arciprete	Tucker trawl	six stations, 100 m increments.
2MF86	Slope	2/27/86	Specific gravity	Bailey	Tucker trawl	one station, 0-400 m.
10C88	Basin	4/2/88	Vertical distribution	Dell'Arciprete	Tucker trawl	one station, four increments: 30-227 m.
4MF94	Basin	4/22-4/24/94	Vertical distribution	Lee	MOCNESS	four stations, maximum sampling depth: 399 m.
4MF94	Slope	4/16/94	Vertical distribution	Lee	MOCNESS	one station, maximium sampling depth: 526 m.
4MF94	Shelf	4/27/94	Vertical distribution	Lee	MOCNESS	one station, maximium sampling depth: 182 m.
6MF95	Shelf	4/23-4/30/95	Vertical distribution	Lee	MOCNESS	two stations, maximum sampling depth: 79 m.
6MF95	Shelf	4/30/95	Vertical distribution	Brase	MOCNESS	one station, six sampling depths: 10, 20, 30, 40, 50, 60 m (triplicates).
7MF95	Shelf	5/5-5/9/95	Vertical distribution	Lee	MOCNESS	three stations, maximum sampling depth: 115 m.
3MF98	Shelf	4/28/98	Specific gravity	Kendall	Tucker trawl	two stations, oblique tows.
1MF99	Shelf	4/18/99	Specific gravity	Kendall	Tucker trawl	two stations, two depth strata (0-20 m, 40-80 m).
1MF99	Shelf	4/18/99	Specific gravity	Kendall	Midwater trawl	one station, eggs from several females spawned into three salinities (28, 30, 32 psu)

Table 3.	Walleye po	llock egg specific	c gravity in t	he Bering Sea.
----------	------------	--------------------	----------------	----------------

Experimental results									
	Coll	ection data		Egg age	Number of	Eg	gg diameters	Specifc gravity	
Cruise	Атеа	Station	Date	group	measurements	Mean	Range	Mean Range	
2MF86	Basin	Z6	2/21/86	1	3	1.54	1.52-1.56	1.0261 1.0257-1.0265	
				2	10	1.55	1.42-1-68	1.0264 1.0261-1.0272	
				3	1	1.48		1.0272	
2MF86	Basin	G2	2/26/86	1	14	1.54	1.42-1.62	1.0260 1.0256-1.0264	
				2	12	1.55	1.46-1.64	1.0256 1.0258-1.0270	
				3	5	1.62	1.54-1.68	1.0263 1.0257-1.0272	
				4	9	1.57	1.50-1.64	1.0274 1.0267-1.0283	
				5	4	1.55	1.52-1.60	1.0273 1.0269-1.0276	
		20							
2MF86	Basın	E3	2/24/86	3	3	1.57	1.54-1.60	1.0267 1.0266-1.0267	
				4	1	1.72		1.0272	
2MF86	Slope	7.7	2/27/86	1	1	1.60		1 0262	
	S.op.			2	3	1.53	1 43-1 60	1 0264 1 0262-1 0266	
				3	8	1.55	1 42-1 64	1 0264 1 0262-1 0267	
				4	4	1.55	1.50-1.61	1.0207 1.0262-1.0207	
					-	1.57	1.52 1.60	1.0277 1.0208-1.0281	
				5	0	1.57	1.52-1.00	1.0275 1.0205-1.0285	
2MF86	Slope	Z8	2/27/86	2	4	1.53	1.48-1.58	1.0265 1.0265-1.0265	
				5	7	1.58	1.56-1.67	1.0268 1.0266-1.0275	
				6	2	1.58	1.58-1.58	1.0272 1.0268-1.0275	
3MF98	Shelf	ED70, ED71	4/28/98	3	4	1.45	1-41-1.49	1.0241 1.0238-1.0243	
				4	33	1.51	1.39-1.71	1.0240 1.0218-1.0266	
				5	18	1.54	1.37-1.78	1.0236 1.0217-1.0266	
1ME00	Shelf	27 shallow	4/17/00	4	2	1.40	1 45 1 52	1 0006 1 0000 1 0041	
11411.22	Shen	57 shanow	4/1////		21	1 54	1 41 1 60	1.0230 1.0232-1.0241	
				5	21	1.54	1.41-1.09	1 0232 1.0208-1.0233	
				0	25	1.55	1.37-1.09	1.0239 1.0216-1.0203	
1MF99	Shelf	37 deep	4/17/99	2	1	1.69		1.0238	
				4	9	1.57	1.45-1.65	1.0244 1.0236-1.0259	
				5	16	1.57	1.45-1.72	1.0239 1.0227-1.0262	
				6	17	1.53	1.33-1.69	1,0240 1,0220-1,0250	
1MF99	Shelf	46 shallow	4/18/99	3	16	1.56	1.45-1.61	1.0234 1.0220-1.0248	
				4	6	1.50	1.37-1.57	1.0236 1.0214-1.0253	
				5	2	1.57	1.57-1.57	1.0245 1.0240-1.0250	
				6	32	1.57	1.37-1.76	1.0225 1.0201-1.0254	
1ME00	Sholf	46 deen	4/18/00	2	12	1.62	1 45 1 72	10746 10739 10757	
11411.2.2	OTEL	-o deep	-17/10/77	<i>З</i> Л	7	1.02	1 37-1-65	1.0240 1.0230-1.0237	
				4	7	1.04	1.57-1.05	1.0240 1.0241-1.0249	
				5	14	1.00	1.37-1.03	1.0235 1.0227-1.0247	
				0	14	1.50	1.33-1.09	1.0230 1.0222-1.0248	
1MF99	Shelf	47 (28 psu)	4/18/99	2	13	1.55	1.53-1.61	1.0234 1.0231-1.0236	
				4	15	1.56	1.53-1.61	1.0230 1.0225-1.0234	
				5	23	1.54	1.37-1-61	1.0222 1.0207-1.0236	
				6	8	1.55	1.49-1.57	1.0226 1.0217-1.0243	
1MF99	Shelf	47 (30 psu)	4/18/99	2	9	1.55	1.53-1.57	1.0242 1.0237-1.0248	
				3	35	1.55	1.49-1.61	1.0239 1.0234-1.0245	
				4	18	1.55	1.45-1.57	1.0242 1.0226-1.0247	
				5	25	1.54	1.45-1.57	1.0232 1.0223-1.0245	
				6	21	1.53	1.49-1.57	1.0232 1.0201-1.0248	
1 ME00	Shalf	17 (22 mart)	4/18/00	r	5	1 55	1 53 1 57	10721 10700 10340	
11411.22	Shell	т (52 psu)	7110177	5	2	1.55	1.55-1.57	1.0251 1.0200-1.0248	
				6	2	hatched	1.07 1.07	1 0241 1.0239-1.0200	
				~	4	10101100		1.0211 1000071.0272	

				Mean egg	Bottom	Max. tow			N	et depths (m)				
Cruise	Station	Date	Habitat	depths (m)	depth (m)	depth	1	2	3	4	5	6	7	8	9
2MF86	V5-V8	2/24/86	Basin	337	3237	400	0-100	100-200	200-300	300-400					
2MF86	V9-V12	2/26/86	Basin	353	3182	500	0-100	100-200	200-300	300-400	400-500				
10C88	43	2/4/88	Basin	164	1637	227	30-101	91-133	150-200	186-227					
4MF94	9	4/16/94	Slope	413	837	526	399-526	300-397	200-300	1-200					
4MF94	74	4/22/94	Basin	44	1759	199		150-199	98-149	74-98	59-73	43-59	28-42	15-28	0-14
4MF94	71	4/22/94	Basin	193	1547	399		199-399		75-102	60-74	45-60	30-44	16-29	3-16
4MF94	85	4/23/94	Basin	74	2005	202		150-202	101-150	75-100	60-74	43-59	30-42	12-30	0-12
4MF94	82	4/23/94	Basin	117	1781	200		149-200	100-147	74-99	59-74	43-59	29-42	13-29	0-13
4MF94	135	4/27/94	Shelf	10	205	182		148-182	98-149	75-97	61-74	44-60	30-43	13-29	0-11
6MF95	74	4/23/95	Shelf	27	67	56		39-56	29-39	19-29	11-19	1-11			
6MF95	139	4/30/95	Shelf	18	83	79		57-79	45-57	34-42	22-33	16-21	3-16		
7MF95	21	5/5/95	Shelf	19	60	50		41-50	31-40	21-30	9-21	1-10			
7MF95	41	5/8/95	Shelf	21	72	69		58-69	45-58	32-45	22-32	13-21	0-11		
7MF95	53	5/9/95	Shelf	25	123	115		99-115	82-99	66-81	49-65	35-48	23-34	1-23	

Table 4. Walleye pollock egg vertical distribution in the Bering Sea, based on NOAA sampling 1986-1995.

Cruise/Year	CTD Station	Egg station	Date	Latitude	Longitude	Gear	Appendix
1986							
2MF86	33	V5-V8, E3	2/24/86	54 03.1	171 27.5	CTD	B1
2MF86	40	V9-V12, G2, Z6	2/26/86	53 39.0	171 24.8	CTD	B2
2MF86	42	Z7, Z8	2/27/86	54 28.1	167 15.2	CTD	B3
1988							
10C88	103	43	2/4/88	54 50.6	168 03.1	CTD	B4
1994	8						
4MF94	30	71	4/22/94	54 59.1	168 09.9	CTD	B5
4MF94	31	74	4/22/94	55 05.8	168 16.1	CTD	B6
4MF94	40	82	4/23/94	55 08.7	168 24.1	CTD	B 7
4MF94	41	85	4/23/94	54 49.9	168 35.8	CTD	B8
4MF94	42	88	4/23/94	55 05.5	168 39.9	CTD	B9
4MF94	67	135	4/27/94	54 40.1	165 25.4	CTD	B10
1995	k:						
6MF95	36	74	4/23/95	55 04.0	164 32.3	CTD	B11
6MF95	44	139	4/30/95	56 27.4	164 36.7	CTD	B12
7MF95	19	21	5/5/95	55 04.2	164 31.6	CTD	B13
7MF95	22	41	5/8/95	56 35.9	164 37.9	CTD	B14
7MF95	25	53	5/9/95	56 02.2	166 23.9	CTD	B15
1998							
3MF98	86		4/27/98	55 27.58	164 32.66	CTD	B16
3MF98		70	4/28/98	55 16.63	164 17.19	CAT	B17
3MF98		71	4/28/98	55 07.48	164 37.11	CAT	B18
1999							
1MF99		37	4/17/99	55 31.63	163 32.54	CAT	B19
1MF99		46	4/18/99	55 51.74	163 22.06	CAT	B20

Table 5. Dates and locations of CTD casts associated with walleye pollock egg specific gravity and vertical distribution collections.



Figure 1. – Geographic distribution (shading) and spawning areas (dots) of walleye pollock, after Bailey (pers. comm). Areas of comparison of egg specific gravity and vertical distribution are indicated by arrows.



Figure 2. – Vertical distribution of walleye pollock eggs in Funka Bay, Japan. From Kamba (1977).



Figure 3. - Specific gravity of walleye pollock eggs in Funka Bay, Japan. From Nakatani (1988).



Figure 4. – Vertical distribution of walleye pollock eggs and water column density from Shelikof Strait, Gulf of Alaska. From Kendall et al. (1994).



Figure 5. -- Vertical distribution of walleye pollock eggs from Shelikof Strait, Gulf of Alaska. The abundance of eggs was greatest during Series 1 and 2, and decreased steadily after that. From Kendall et al. (1994).


Figure 6. -- Changes in vertical distribution of walleye pollock eggs from Shelikof Strait, Gulf of Alaska with development. From Kendall et al. (1994).



Figure 7. – Transect used by Serobaba (1974) to sample vertical distribution of walleye pollock eggs across the southeastern Bering Sea shelf.



Figure 8. – Vertical distribution of walleye pollock eggs across the Bering Sea shelf. From Serobaba (1974).







Figure 10. – Vertical distribution of walleye pollock eggs over the southeastern Bering Sea shelf, by developmental stages. From Nishiyama et al. (1986). See Figure 12 for collection locations.



Figure 11. – Vertical distribution of walleye pollock eggs over the southeastern Bering Sea shelf.
From Haldorson (L. Haldorson, Juneau Center, School of Fisheries and Ocean
Sciences, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers.
comm., 20 October 1998). See Figure 12 for collection locations.



Figure 12. – Locations of collections used for walleye pollock egg vertical distribution and specific gravity measurements in the Bering Sea. The 200 and 1000 m isobaths are shown. Station designations correspond to those in Tables 3-5. Plus-signs are stations where eggs were collected for specific gravity experiments. Circles are stations where vertical distribution tows were made in 1986 and 1988. Triangles are where vertical distribution tows were made in 1994 and 1995. The eastern 74 is where the tow was made in 1995. The square is where the vertical distribution tow of Haldorson (L. Haldorson, Juneau Center, School of Fisheries and Ocean Sciences, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. comm., 20 October 1998) was made. Circles connected by line (N1-N2) represent the range of locations of vertical distribution tows of Nishiyama et al. (1986). The star is where the trawl for spawning adults was made in 1999.

39



Figure 13. – Diameters of walleye pollock eggs from the Bering Sea shelf (triangles), basin (circles) and slope (squares) used in specific gravity experiments in relation to stage of development.



Least square means and standard error bars.

Figure 14. – Least squares means and standard errors of walleye pollock egg specific gravities by age group from the shelf (dotted line), slope (solid line) and basin (dashed line) of the eastern Bering Sea.



Least square means with standard error bars.

Figure 15.- Least square means and standard errors of specific gravity of walleye pollock eggs from the Eastern Bering Sea shelf reared at three salinities (28, 30, 32 psu) by age group.



Least square means with standard error bars.

Figure 16. – Least square means and standard errors of specific gravity of walleye pollock eggs by age group collected at two stations and two depths over the southeastern Bering Sea shelf.



Bottom depth where tow was taken (m)

Figure 17. – Vertical distribution of walleye pollock eggs from the Bering Sea basin, slope and shelf based on Tucker trawl sampling in 1986 and 1988, and MOCNESS sampling in 1994 and 1995. Mean egg depth, maximum sampling depth and water depth are shown.











Figure 20. – Specific gravity and vertical distribution of walleye pollock eggs (mean and range) from Shelikof Strait, Gulf of Alaska, the Bering Sea basin and the southeastern Bering Sea shelf in relation to average water column specific gravity at the time of egg occurrence (from Ned Cokelet, PMEL, NOAA, pers. comm.).



Figure 21. – Vertical distribution of walleye pollock eggs (mean and range) from Shelikof Strait, Gulf of Alaska, the Bering Sea basin, and the southeastern Bering Sea shelf in relation to average water column temperature at the time of egg occurrence (from Ned Cokelet, PMEL, NOAA, pers. comm.).



Figure 22. – Model of changes in vertical distribution of walleye pollock eggs from the Bering Sea shelf during development (from Nishiyama et al. 1986).



Appendix A: Vertical distribution profiles of walleye pollock eggs

1. From 2MF86, Stations V5-V8, Bering Sea basin.

2. From 2MF86, Stations V9-V12, Bering Sea basin.

3. From 1OC88, Station 43, Bering Sea basin.

4. From 4MF94, Station 135, Bering Sea shelf.

5. From 6MF95, Station 74, Bering Sea shelf.

6. From 6MF95, Station 139, Bering Sea shelf.

7. From 7MF95, Station 21, Bering Sea shelf.

8. From 7MF95, Station 41, Bering Sea shelf.

9. From 7MF95, Station 53, Bering Sea shelf.

10. From 4MF94, Station 9, Bering Sea slope.

11. From 4MF94, Station 74, Bering Sea basin.

12. From 4MF94, Station 71, Bering Sea basin.

13. From 4MF94, Station 85, Bering Sea basin.

14. From 4MF94, Station 82, Bering Sea basin.































Appendix B: Temperature, salinity, density profiles associated with vertical distribution profiles of walleye pollock eggs.

1. Bering Sea basin, 24 Februrary 1986, CTD station 33.

2. Bering Sea basin, 26 Februrary 1986, CTD station 40.

3. Bering Sea slope, 27 Februrary 1986, CTD station 42.

4. Bering Sea basin, 4 April 1988, CTD station 103.

5. Bering Sea slope, 29 April 1994, CTD station 79.

6. Bering Sea basin, 22 April 1994, CTD station 30.

7. Bering Sea basin, 22 April 1994, CTD station 31.

8. Bering Sea basin, 23 April 1994, CTD station 40.

9. Bering Sea basin, 23 April 1994, CTD station 41.

10. Bering Sea shelf, 27 April 1994, CTD station 67.

11. Bering Sea shelf, 23 April 1995, CTD station 36.

12. Bering Sea shelf, 30 April 1995, CTD station 44.

13. Bering Sea shelf, 5 May 1995, CTD station 19.

14. Bering Sea shelf, 8 May 1995, CTD station 22.

15. Bering Sea shelf, 9 May 1995, CTD station 25.

16. Bering Sea shelf, 27 April 1998, CTD station 86.

17. Bering Sea shelf, 28 April 1998, Egg station 70.

18. Bering Sea shelf, 28 April 1998, Egg station 71.

19. Bering Sea shelf, 17 April 1999, Egg station 37.

20. Bering Sea shelf, 18 April 1999, Egg station 46.




















Appendix B7









Appendix B10



•

Appendix B11



Appendix B12





Appendix B14





Appendix B16



Appendix B17: 3MF98, Egg station 70, Bering Sea shelf



Appendix B18: 3MF98, Egg station 71, Bering Sea shelf



Appendix B19: 1MF99, Egg station 37, Bering Sea shelf



Appendix B20: 1MF99, Egg station 46, Bering Sea shelf