Capabilities of Walleye Pollock Eggs, Larvae, and Juveniles to Respond to Environmental Factors and Determine Distribution

Fish populations vary substantially in size over time and space. These variations result from a myriad of diverse biological and physical factors impinging on all life stages and in all habitats, ranging from shallow inshore areas to the open ocean. The dearth of understanding of the role that these factors may play in population fluctuations has, in many instances, precluded the attainment of two of the primary goals of fisheries science – the prediction of population abundance and development of effective management practices.

Establishing linkages between biological and physical processes that influence recruitment, distribution, and survival of early life stages of walleye pollock, *Theragra chalcogramma*, is a primary focus of the Fisheries Oceanography Coordinated Investigations (FOCI) program of the Alaska Fisheries Science Center's (AFSC) Division of Resource Assessment & Conservation Engineering and the Pacific Marine Environmental Laboratory. As an integral part of FOCI, the AFSC's Fisheries Behavioral Ecology Program provides information on the role that behavioral responses may play in establishing such linkages. Research conducted within the Behavioral Program is performed at the Mark O. Hatfield Marine Science Center,

Newport, Oregon, under controlled laboratory conditions utilizing systems designed to either duplicate or closely simulate selected biological and physical factors critical to the recruitment, distribution, and survival of the species. Research questions addressed by program members are formulated directly from the results of field research performed by other FOCI researchers. In like manner, the results of the laboratory behavioral experiments are compared, integrated, and verified with the results of field research. In this way, cause-and-effect relationships can be established between various environmental factors and behaviors that mediate recruitment, distribution, and survival at different life stages.

The following article provides a first-hand account of research conducted by scientists within the Fisheries Behavioral Ecology Program, focusing on the egg, larval, and juvenile stages of walleye pollock.

Eggs

While it may not be surprising that larvae and juveniles are capable of controlling their position in the water column, our recent investigations on the vertical distribution of walleye pollock eggs have shown how early in their life history this control can begin. The vertical distribution of marine pelagic fish eggs is the net result of interactions between egg density and physical features of the water column, such as seawater density and currents. Since processes associated with embryonic development cause changes in egg density, the question that engaged our interest was whether extrinsic factors could act upon these processes and thereby affect buoyancy. Evidence for this was almost entirely lacking. The aim of our investigation was to determine if the densities of developing walleye pollock eggs were affected by light, suggesting a response capability in eggs that may be adaptive. We selected light as a stimulus since structures associated with vision arise early in embryonic development.

Eggs were collected and fertilized from six females and eight males on board ship in the Gulf of Alaska, held at 2°-4°C in darkness, and air shipped in insulated containers to the NMFS experimental facility in Newport. Two experiments were conducted using separate batches of eggs collected 2 weeks apart. Density of eggs was measured in 1-L graduated cylinders (6 X 45 cm) filled with a density gradient of seawater ranging in density from 1.0210 to 1.0330 g cm^{-3}. Filtered (0.20 μm), UV-treated seawater was diluted with distilled water, or seasalt was added to achieve the

required densities. Calibration of the gradients was accomplished prior to beginning experiments using a series of six glass spheres ranging from 1.0213 to 1.0293 g cm^{-3} at 6°C. The gradients remained stable for at least 14 days as verified by recalibration. Cylinders were kept in a constant temperature room (6° ± 0.5°C) under conditions of 1) constant darkness which simulated natural conditions at a depth of 200-250 m; or 2) diel light with a photoperiod of 14 hours light (28 μmol photons m^{-2} s^{-1}) supplied by white fluorescent lamps (5,000 K) and 10 hours dark, corresponding to light conditions in the field at time of collection. In both experiments, 15-20 eggs were introduced into each cylinder at 90-100 hours postfertilization, and positions of eggs (and corresponding densities) were noted periodically until hatching began. For each light condition, two replicate cylinders were used in the first experiment and three replicate cylinders were used in the second experiment. Observations of eggs under constant darkness were made using a low light (0.1 μmol photons m^{-2} s^{-1}) for no more than 2 minutes.

Results of both experiments were similar, with differences in egg density between light- and dark-exposed eggs evident within 12 hours after introduction into the density gradient columns. The eggs exposed to light became denser than those held in dark (Fig. 1). This pattern continued until 24 hours before hatching, when eggs held in the dark showed a precipitous increase in density. In both experiments, 80% of the eggs hatched in the columns under both light conditions. Our most recent experiments have shown that fertilized eggs only begin to respond when optic tissue is first clearly differentiated (90-100 hours postfertilization). Before this time, eggs showed no capability to alter density when exposed to light.

Alteration of egg density in response to light may have ecological importance for the distribution and survival of marine bathypelagic fish eggs. These changes could represent an adaptation whereby eggs avoid the upper lighted layers of the sea where predation and the effects of ultraviolet light on growth may be significant. Vulnerability of eggs to predation can be a function of light

available for their detection by predators. Ultraviolet light has been measured at 3 m depth in the sea at intensities sufficient to create significant damage to DNA. Mechanisms for the detection of light by eggs and adaptive responses resulting from light detection may represent novel classes of behavioral and physiological responses. Light-induced changes in egg density indicate a capability of walleye pollock eggs to respond to external stimuli and thereby alter their position in the water column in an ecologically meaningful way.

Larvae

While field studies on walleye pollock larvae have shown ontogenetic differences in vertical distribution and diel patterns of vertical movement in the upper photic zone, no clear cause-and-effect relationships between changes in distribution and environmental factors have been shown. Our objectives were to determine under controlled laboratory conditions 1) the age at which larvae were first capable of responding to environmental factors; and 2) the role that various factors, including light, gravity, turbulence, and temperature gradients, might play in vertical distribution and movements.

The earliest stages of larvae from immediately posthatching until 8 days posthatching were observed in the same experimental columns that were described above for the egg experiments.

We found that larvae held under constant dark were positively geotactic beginning at hatching and continuing for 4-5 days posthatching (Fig. 2). During this period, larvae are not developmentally capable of feeding and derive their nutrients from the yolk sac. As a result of behavioral responses to gravity, yolk-sac larvae swim downward in the absence of light, insuring that they remain under dark conditions
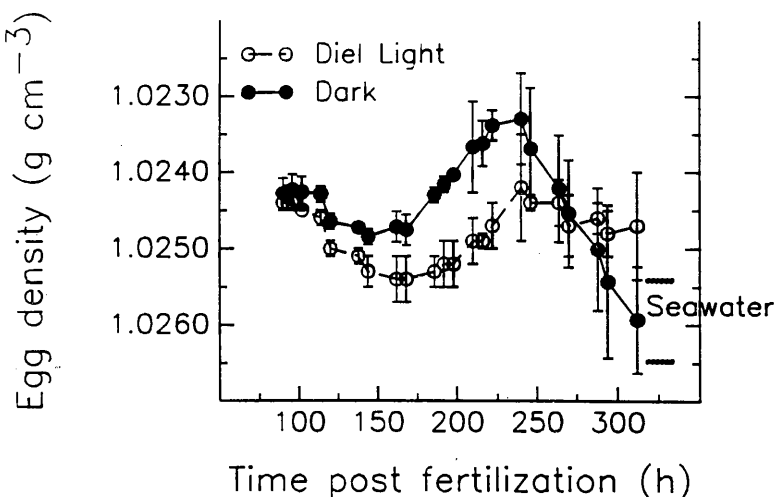

Figure 1. Effect of diel light and constant dark on density of walleye pollock eggs. Values are mean ± 95% confidence interval for 15-20 eggs in each of three replicate columns for each light condition. Range of values for density of seawater in the Gulf of Alaska is given between lines on lower right side of graph.
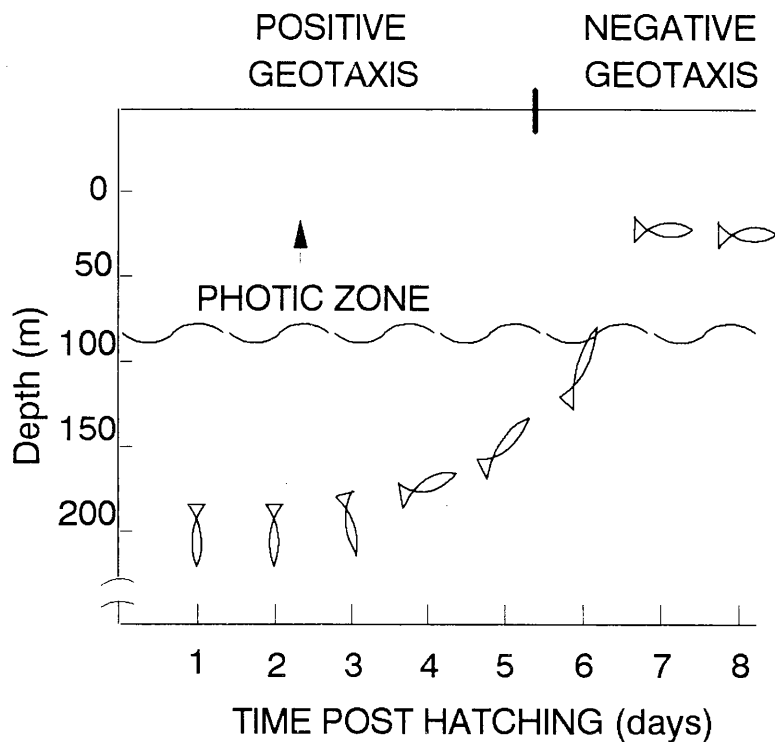
Figure 2. Geotactic orientation and postulated depth distribution for walleye pollock yolk-sac larvae in the sea from 1 to 8 days posthatching.

at depth. We would expect that under dark conditions, susceptibility to predators would be lower than would be the case in the upper photic zone.

At 5-6 days posthatching, when larvae were first capable of feeding, the response to gravity reversed and larvae became negatively geotactic (Fig. 2). In the sea, this change in behavior would result in upward migration to the photic zone where prey are abundant and where larvae rely upon vision to find and capture prey.

Beginning at 13 days posthatching, responses of larvae to vertical gradients of light, gravity, turbulence, and temperature were studied in 20-L plexiglass cylinders (15 X 150 cm), located in a constant temperature (9° ± 0.5°C), light-controlled room. For each experimental treatment, six independent replicate columns were established, with each replicate consisting of 50-70 larvae (2.5-3.5 L^{-1}) held in each cylinder for up to 12 days and fed with rotifers (20 mL^{-1} initially). Rotifer concentrations, measured by counting five 1-mL samples per third of the cylinder, did not vary with depth during any treatment, allowing us to assume that larval distributions were not altered by the distribution of food. A vertical light gradient was supplied from two 100-W tungsten lamps (3,900 K) suspended above two cylinders. Intensity (μmol photons m^{-2} s^{-1}) ranged from 70 at the water surface to 45 at 120 cm depth. Gradients of lower light intensity were produced by placing layers of neutral density fiberglass screening between the lights and the cylinders, creating intensities (μmol photons m^{-2} s^{-1}) ranging from 2.5 at the surface to 1.6 at 120 cm depth and 13.2 at the surface to 8.0 at 120 cm depth. Lower intensities were produced with a 25-W tungsten lamp (3,900 K) yielding a surface intensity of 0.01 μmol photons m^{-2} s^{-1}. Surface turbulence, as a gentle horizontal circular water motion, was produced by directing a compressed airstream at the surface of the water, with turbulence extending to 10 cm depth as determined by observing mixing of prey organisms. Thermoclines were created by introducing chilled seawater (0°C) into the bottom of the cylinders until one-third of the water had been replaced through overflow from the top of the cylinders. During thermocline conditions, temperature ranged from 9°C in the top half to 3°C in the bottom third of the cylinder with this condition persisting for 2 hours after cold water introduction. Distribution of larvae was measured in cylinders by direct visual inspection during simulated daylight conditions. During low-light or night conditions, the cylinders were illuminated with 20-W infrared lamps (Wratten 87 filter; 780 nm) and the larvae were observed by infrared-sensitive video camera.

The results of these experiments indicated that behavioral responses to light, temperature stratification, turbidity, and turbulence all played a role in determining the precise depth that larvae selected (Fig. 3). Under darkness and low-light conditions, larvae concentrated in the top layers of the cylinders, while under high light, larvae moved downward. Larvae moved downward away from turbulence and upward away from the thermocline layer. It is possible that intrinsic factors, such as hunger, may also influence the precise depth that larvae select by lowering avoidance thresholds towards various physical factors, similar to what we have observed for juvenile walleye pollock (see below). The greater the level of hunger, the greater the risk a larva will take to find prey. It is evident from our experiments that behavioral responses play a role in determining distribution, the result
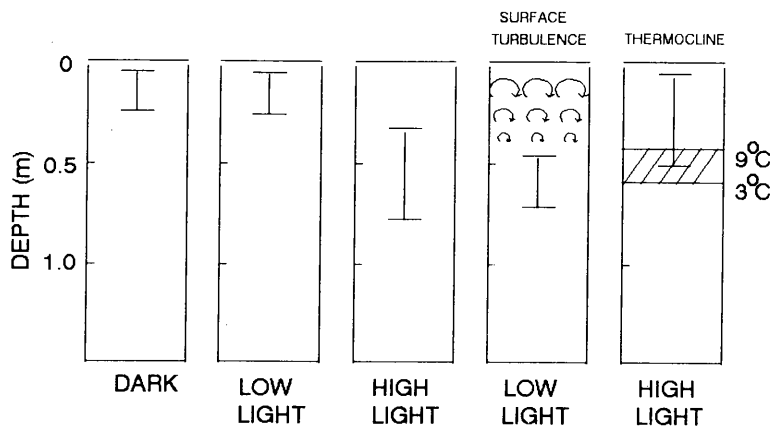
Figure 3. Changes in depth distribution for walleye pollock larvae in the laboratory corresponding to dark, low light (0.5 µmol photons $m^{-2}s^{-1}$), high light (20 µmol photons m^{-2} s^{-1}), gentle surface turbulence, and thermocline conditions. Bars indicate ranges of distribution.
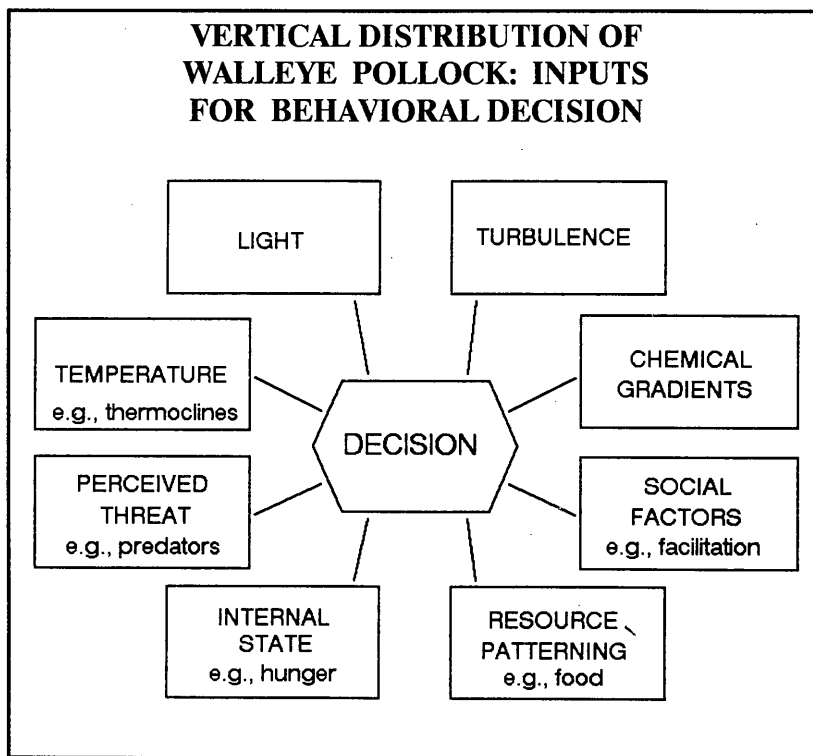

Figure 4. Probable inputs for behavioral decisions controlling vertical distribution of walleye pollock larvae.

of a complex process within the nervous system which integrates various inputs to yield decisions (Fig. 4).

Juveniles

As with larvae, we set out to examine the influence of selected environmental factors on the distribution of juvenile walleye pollock. Experiments on how behavioral responses to light, temperature, and food availability influenced vertical distribution were performed in a 15,000-L tank (2.5 X 2.5 X 2.5 m) constructed of insulated fiberglass. A plexiglass viewing window (2.4 X 2.4 X 0.07 m) made up one wall of the tank. Illumination was provided by two light pipes suspended above the tank with the light source consisting of two 400-W metal halide lamps (6,000 K). Light intensity (µmol photons m^{-2} s^{-1}) during simulated daylight ranged from 25 at the surface to 7 at the bottom. Sand-filtered seawater (30-32 ppt S) circulating through a chilling system flowed into the tank through a false bottom.

To form a thermocline, chilled seawater was introduced upward through hundreds of holes in the false bottom, displacing ambient tank water which overflowed the top. This flow of chilled water was gradual and, within 45 minutes, 7,500 L of chilled seawater displaced an equal amount of ambient tank water. A sharp thermal discontinuity resulted (3°-9°C) within 0.3 m depth between 1.0 and 1.3 m. The established thermocline persisted for up to 24 hours after formation. Food was introduced through a tube that extended to a depth of 1.5 m, positioned so that it would be below the thermocline. Walleye pollock juveniles were fed bite-sized pieces

of the same artificial diet on which they were maintained. Four separate experiments were performed on groups of six fish.

It was clear from our results that vertical distribution was influenced by the interaction of light, thermal stratification, hunger, and food availability (Fig. 5). Under low light, fish swam in the lower half of the tank, while under high light, they concentrated in the lowest quarter of the tank. After introduction of the thermocline, juveniles swam in the upper third of the tank under low light, while high light caused them to concentrate near the thermocline layer. The introduction of food below the thermocline caused fish to swim below and feed in the cold water. This pattern, especially with regard to thermal stratification and food availability, agreed substantially with what was observed for juveniles under natural conditions by other FOCI scientists.

Juveniles respond not only to their environment but to conspecific behavior as well, which may also influence patterns of distribution. Our investigations of juvenile social behavior have centered on group foraging, where the food detection and feeding behaviors of one individual attract others to the site of a prey patch (i.e., local enhancement). We examined questions of group foraging by designing an experimental system that permitted food to be delivered in discrete pulses (patches) without visual and mechanical cues preceding introduction. Food in this system was only accessible to the fish for brief periods (7-9 seconds) and the time and point of introduction was randomized. When juveniles foraged for these temporally and spatially unpredictable ephemeral food patches, similar to how they might forage in nature, individual fish found more patches when in groups than when alone (Fig. 6). However, this strategy of group foraging was abandoned when food did not occur in patches, but was introduced in a widely dispersed configuration. This implies that the spatial distri-
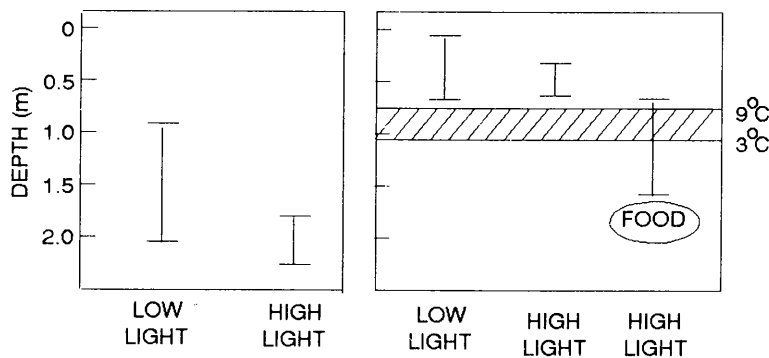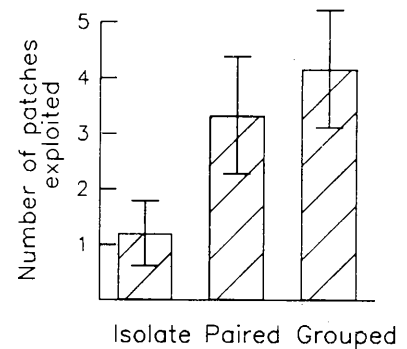

Figure 6. Number of food patches exploited by juvenile walleye pollock as isolates, in pairs, or in groups. Values are mean ± 1 SE for six replicate fish.

bution of prey may determine the size and cohesiveness of juvenile aggregations in the oceanic environment.

In summary, laboratory studies on egg, larval, and juvenile stages of walleye pollock have demonstrated that they possess the behavioral capability to alter their position in the water column in response to environmental gradients and either select favorable conditions or avoid unfavorable conditions. It is clear therefore, that models designed to predict the distribution and recruitment of walleye pollock should include behavioral response capabilities to environmental variables and changes associated with ontogeny.

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Figure 5. Changes in depth distribution for walleye pollock juveniles in the laboratory corresponding to low light (7.0 μmol photons $m^{-2} s^{-1}$), high light (320 μmol photons $m^{-2} s^{-1}$), and thermocline and feeding conditions. Bars indicate ranges of distribution.