Behavior Plays a Key Role in Controlling Distribution and Survival in the Early Life Stages of Walleye Pollock

Early life stages of marine fishes play a crucial role in determining the subsequent abundance of adult fish available for harvest. Small differences in mortality rates or growth rates during the often fragile stages of early development can ultimately result in major differences in recruitment rates. The capability to predict the fate of individuals spawned in a particular year depends on understanding the processes that influence mortality and growth rates and the processes that determine spatial and temporal patterns of abundance. These processes are in large measure influenced by the behavior of individual fishes.

The behavioral responses of fishes to abiotic and biotic factors are the result of the fishes' adaptations to selective pressures exerted during their evolutionary history. Understanding these behavioral adaptations is critical, because it is through behavior that fishes orient themselves in the water column, feed, avoid predation, and respond to environmental change—all driving forces for survival.

The Fisheries Behavioral Ecology Program of the Alaska Fisheries Science Center (AFSC) focuses on better understanding the role of behavior in controlling distribution, growth, survival, (and eventual recruitment) of the early life stages of walleye pollock, *Theragra chalcogramma.* The research is part of the Fisheries Oceanography Coordinated Investigations (FOCI) program, which is made up of fisheries biologists from the AFSC and physical oceanographers from the Pacific Marine Environmental Laboratory. The Fisheries Behavioral Ecology Program is based at the Mark O. Hatfield Marine Science Center in Newport, Oregon, where extensive seawater facilities and specialized environmentally controlled experimental systems allow researchers to selectively test various combinations of biological and physical factors that may potentially influence the various early life stages of walleye pollock. These laboratory studies test hypotheses generated from FOCI field observations and generate new hypotheses which, in turn, are examined in the field. This integrated, synergistic approach has proven valuable in revealing a number of basic relationships between environmental factors and behavioral responses that mediate distribution and potentially influence survival and recruitment.

The following article presents current results of the Fisheries Behavioral Ecology Program research of the early life stages of walleye pollock, with a focus on linkages between results of laboratory experiments and results of field studies conducted by other FOCI researchers. Studies are organized by life history stage: eggs, yolk-sac (prefeeding) larvae, feeding larvae, and juveniles.

EGGS

Laboratory studies on the egg stage of walleye pollock have concentrated on vertical distribution, which can be altered by changes in egg density. Field studies have shown that pollock eggs develop and hatch at depths below 150 m under essentially dark conditions.

We examined changes in density of developing pollock eggs by incubating them in columns of seawater with a gradient in density decreasing from bottom to surface. The gradient was created by adding seawater of continuously decreasing salinity into the columns. The eggs, which had been collected and fertilized during FOCI research cruises in the Gulf of Alaska, were air-shipped to the Hatfield Center in Newport, where they were added to the density gradient columns and maintained in the dark at a constant temperature of 6°C, replicating the condi-

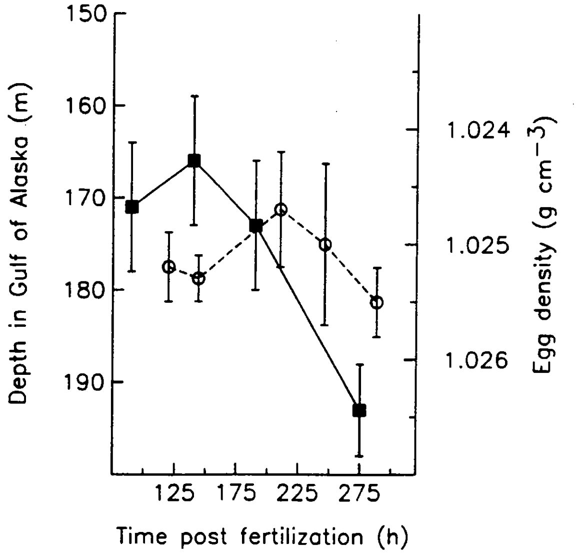

Figure 1. Changes in density of walleye pollock eggs relative to time postfertilization (mean ± 95% confidence intervals) in the laboratory (open circles) and depth distribution of comparable stage eggs (mean ± standard error) in the Gulf of Alaska (solid squares).

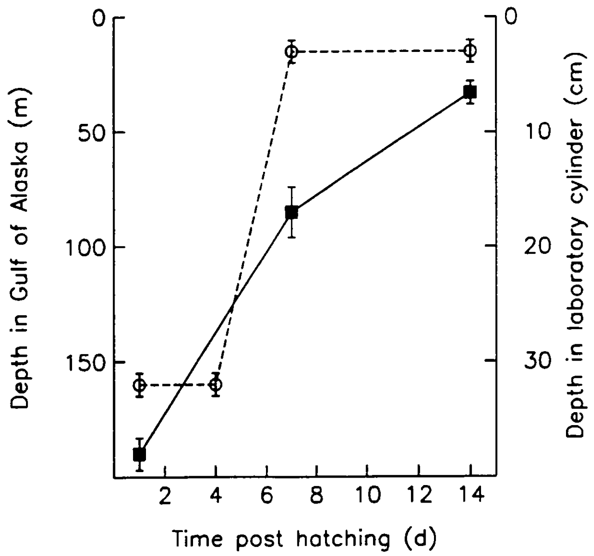

Figure 2. Depth (mean ± 95% confidence intervals) of larval walleye pollock relative to time posthatching in laboratory cylinders in the dark (open circles) and depth (mean ± standard error) of comparable stage larvae in the Gulf of Alaska (solid squares).

tions naturally encountered at depth in the Gulf of Alaska. The pattern of increasing egg density observed as hatching approached (i.e. 275 hours after fertilization) was similar to the increases in depth distribution of developing eggs that were observed in the Gulf of Alaska (Fig. 1). This general agreement between laboratory and field observations indicates that changes in the vertical distribution of walleye pollock eggs in the sea over the course of development are mostly likely attributable to changes in density associated with embryonic development.

YOLKSAC LARVAE

At sea, walleye pollock yolksac larvae generally are found at depths greater than 150 m, where they remain for the first 5 to 6 days posthatching (Fig. 2). During this stage, nutritional requirements are met by the yolk. With their poorly developed swimming abilities, yolksac larvae remain in deep water, thereby avoiding the many predators that forage in the upper photic zone.

The results of our laboratory experiments suggest that the occurrence of yolksac larvae in deep water is at least partly attributable to their response to gravity, expressed as positive geotaxis. We observed groups of newly hatched larvae in 30-cm tall cylinders of seawater with a density gradient as described above for the egg experiments. The larvae were maintained under constant dark conditions, with positions in the column observed during a 2-week period. Detection of larvae in the dark was facilitated by using low-intensity red light for brief periods, which allowed us to observe depth, duration of swimming activity, and angle of orientation.

Yolksac larvae at 1 and 4 days posthatching swam downward repeatedly from a depth at which they were neutrally buoyant (Fig. 2). By 5 to 7 days posthatching, at a time when larvae reach feeding readiness (the number of days depending on temperature), larvae switched from positive to negative geotaxis and swam continually upward (Fig. 2). The change in orientation of pollock larvae in the laboratory closely corresponds to the time of upward migration to the photic zone of larvae in the Gulf of Alaska. Based on swimming ability established in the laboratory (net upward movement of 0.1 - 0.2 cm per second), yolksac larvae have the capability of swimming into the upper water column from 150 m in 21-42 hours, well within the time that feeding must commence.

FEEDING LARVAE

Once competent to feed, walleye pollock larvae are found primarily in the upper 40 m of the water column, where they exhibit diel vertical migration, generally occurring at deeper depths during the day and shallower depths at night (Fig. 3). In the laboratory, we tested the response of feeding larvae to varying light levels as a potential mechanism eliciting this pattern.

For these experiments, vertical distribution of larvae was observed in 150-cm tall cylinders under varying light regimes. Constant temperatures (9°C) were maintained, and uniform prey densities of rotifers were established, limiting the influence of temperature and food on larval behavior. Light was provided by 100-W tungsten lamps suspended over the cylinders. Lower light intensities were created with layers of screen placed beneath the lamps. Positions in the cylinders were observed under dark, low light, and high light conditions. In darkness and under light of low intensity ($\leq$2.5 µmol photons m^{-2} s^{-1}), feeding larvae moved upward in the cylinders and were distributed close to the surface. They also swam towards the surface if the experimental columns were illuminated from below, suggesting that negative geotaxis was the primary stimulus for upward movement in both low light and in darkness. However, when exposed to light of high intensity ($>$13 µmol photons m^{-2} s^{-1}), negative phototaxis took precedence over negative geotaxis, resulting in larvae moving downward and away from the highest light intensities. The vertical distribution observed in the laboratory was in general agreement with the vertical distribution of walleye pollock larvae observed in the sea under comparable light levels (Fig. 3).

Other factors, however, further modify the way in which pollock larvae respond to gravity and light. In the laboratory, we induced turbulence by directing a compressed airstream toward the surface of the cylinders, simulating the turbulence of the sea surface during increased wind stress. This treatment elicited avoidance behavior as larvae moved downward. Vertical distribution of walleye pollock larvae in the Gulf of Alaska appears to support the importance of this type of interaction; an increase in wind speed caused the distribution of larvae to be depressed downward under all light conditions.

The laboratory studies outlined above demonstrate the complexity of extrinsic factors that affect the behavior of larval walleye pollock. Intrinsic factors, such as the health or condition of individual larvae, also influence behavior. We tested the effect of diet on larval behavior by feeding larvae lipid-rich or lipid-deficient prey. Larvae on the poor quality diet swam almost continuously to maintain vertical position and sank headfirst during rare resting bouts. This behavior pattern was associated with reduced growth, gas bladder size, and survival (Fig. 4). Larvae on the lipid-rich diet exhibited energetically efficient swimming behavior, with periods of swimming interspersed with short periods of resting, during which they remained nearly horizontal in orientation, indicating fully functioning gas bladders and increased buoyancy, relative to larvae in poor condition.

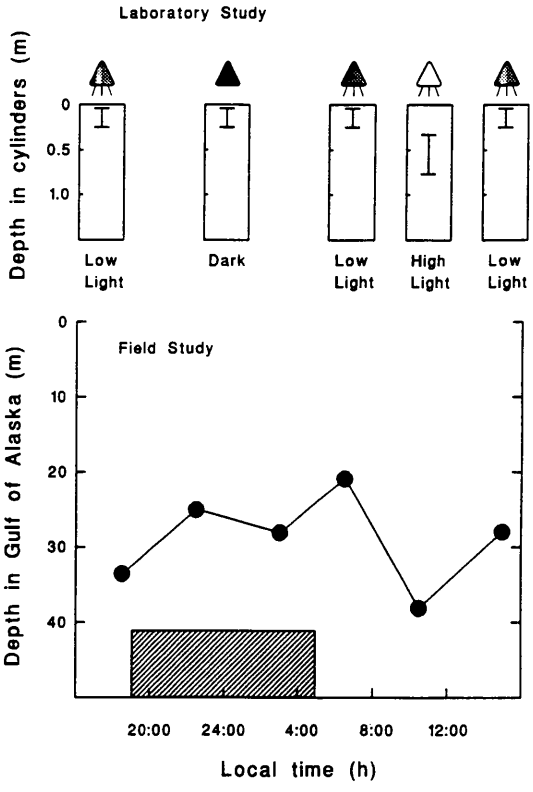

Figure 3. Vertical distribution (mean ± standard error) of walleye pollock larvae in experimental columns exposed to varying light regimes in the laboratory (upper graph), and average depth in the Gulf of Alaska at comparable time periods (lower graph).

Our experiments demonstrate that larval behavior is the result of an integration of several different factors, both extrinsic and intrinsic (Fig. 5). Understanding behavioral responses to any one of these inputs alone is not sufficient to predict what larvae will do in a natural environment.

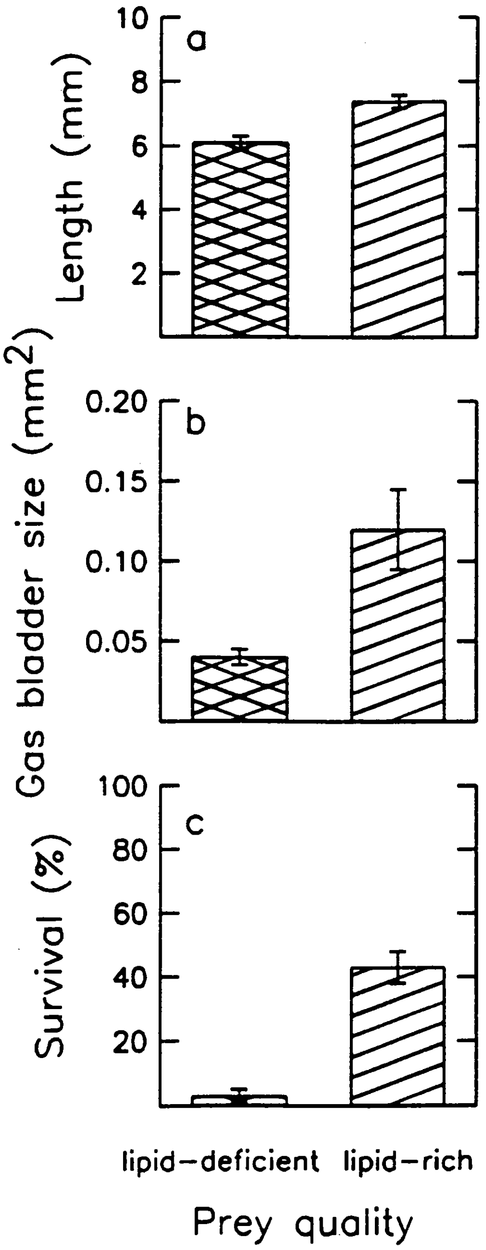

Figure 4. Mean length, gas bladder size, and % survival (± standard error) of larval walleye pollock maintained on lipid-deficient or lipid-enriched prey for a period of 34 days in the laboratory.

JUVENILES - VERTICAL DISTRIBUTION

As with larvae, behavioral responses of juveniles result from an integration of extrinsic and intrinsic factors (Fig. 5). A response to temperature, for example, has a dominant influence on vertical distribution, but may be moderated by responses to other environmental or intrinsic factors. Under thermally stratified conditions in the Bering Sea, juvenile walleye pollock appear to be generally distributed above the thermocline and below the neustonic layer. In the laboratory we tested the response of juveniles to varying light and temperature regimes in large (2.5- x 2.5- x 2.5-m) tanks. Continuously flowing seawater from temperature-controlled reservoirs was introduced at the bottom of the tanks and removed by an overflow drain at the top. Light was produced by 400-W metal halide lamps channeled through light boxes suspended over

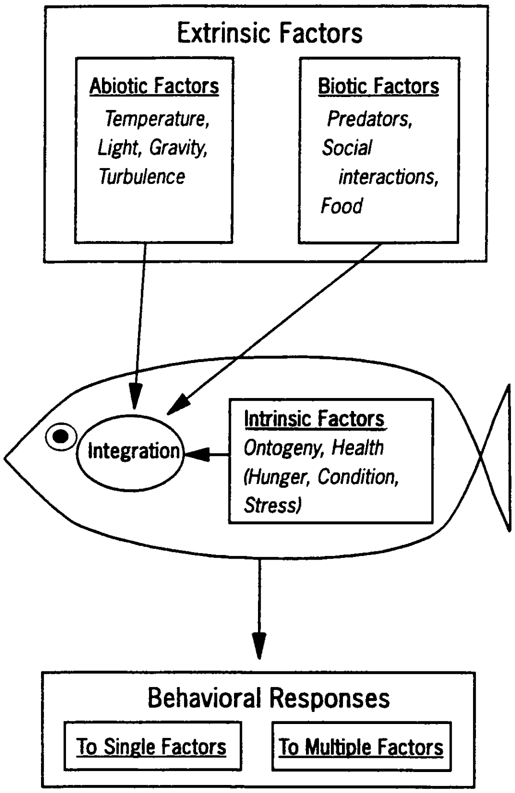

Figure 5. Some probable extrinsic and intrinsic factors for behavioral responses in walleye pollock larvae and juveniles.

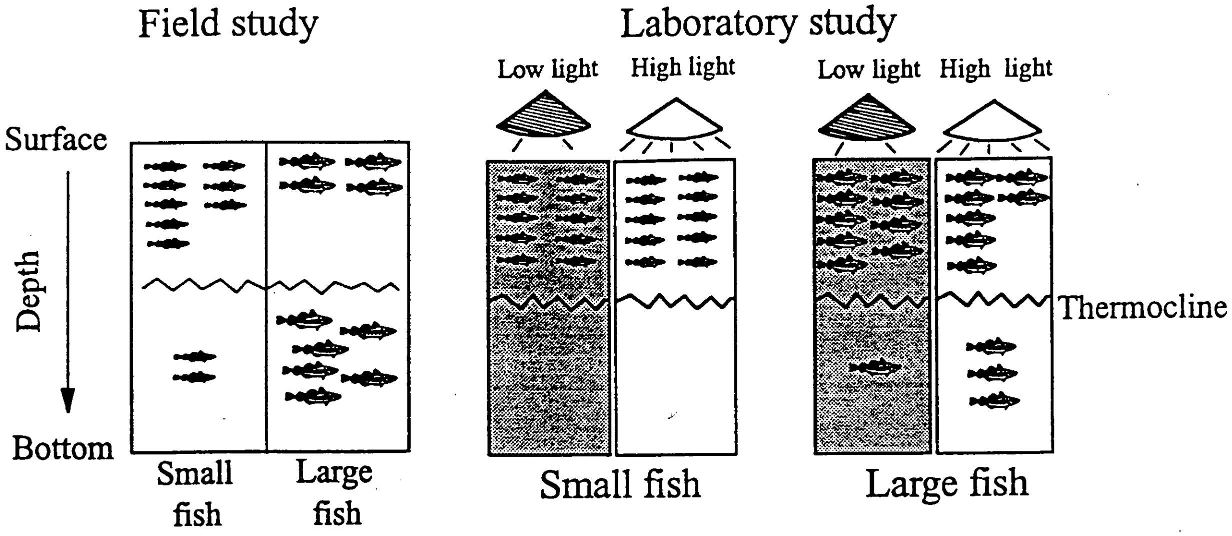

Figure 6. Relative distribution of juvenile walleye pollock above and below the thermocline in the Bering Sea (left) and in the laboratory (right) under low and high light conditions. Results are presented from small fish (<70 mm) and large fish (>70 mm) for both studies.

the tanks. Light intensities were increased by 22x with the addition of four 1000-W lamps. Temperature gradients of varying strength were created by chilling water in the storage reservoirs, then adding cold water to the bottom of the tank. A series of 15 thermistors implanted in the side wall of the tanks allowed continuous monitoring of the vertical thermal structure. Temperature gradients persisted for periods of at least 3 days.

In this experimental setup, juveniles avoided bright light (>100 µmol photons m^{-2} s^{-1}) by moving downward in the water column, similar to the response of larvae. This behavior was consistent with field observations demonstrating a downward dispersal of juveniles during the day and concentration in upper water layers at night. The presence of a thermocline, however, altered the response of juveniles to light, with smaller fish (<70 mm) being more affected by temperature than larger fish (>70 mm). In general, juveniles avoided cold water by moving upward into the warmer layers above the thermocline. When exposed to both thermal stratification and bright light, avoidance of cold water took precedence over avoidance of bright light, with most fish remaining above the thermocline (Fig. 6). Larger juveniles, however, expressed a greater tendency to avoid bright light, resulting in more time spent beneath the thermocline. This integration of ontogeny, light, and temperature in modifying vertical distribution was consistent with observations in the Bering Sea, where juvenile walleye pollock generally remained above the thermocline, but where larger juveniles were more likely than smaller ones to move into deeper water (Fig. 6).

Vertical distribution in the Bering Sea also appeared to depend upon the abundance of zooplankton, a potential food source. When zooplankton abundance was low, distribution of juveniles increased beneath the thermocline; when zooplankton abundance was high, distribution was primarily above the thermocline (Fig. 7). We tested the potential roles of short-term hunger and long-term variability in physical condition on vertical distribution in the laboratory. For fish that had been deprived of food for 24 hours, the introduction of food beneath a thermocline resulted in rapid excursions into cold water to feed (Fig. 7).

Longer- term effects of food deprivation were tested by maintaining groups of juvenile pollock on one of six rations, then observing their behavior in a gradual thermal gradient. To create this gradient, we chilled and added water to the experimental tanks in 2^{0} intervals, resulting in a relatively smooth transition from about 9.5°C at the surface to about 2°C at the bottom. Groups of juveniles were videotaped during nonfeeding periods, with an image analysis system used to denote the vertical position and corresponding temperature for each fish. Food deprivation clearly affected the extent of movement into cold water. Fish maintained on high rations remained primarily in warmer surface waters (Fig. 7). Under rations that were low enough to inhibit growth, fish occurrence in colder water significantly increased. When completely deprived of food for extended periods, juveniles occupied temperatures that averaged 3^{0}-4^{0}C colder than fish held under high food conditions (Fig. 7). Searching behavior also varied with the extent of food deprivation. Across a broad range of ration levels, searching activity initially increased as food availability declined, then decreased again as rations dropped to starvation levels.

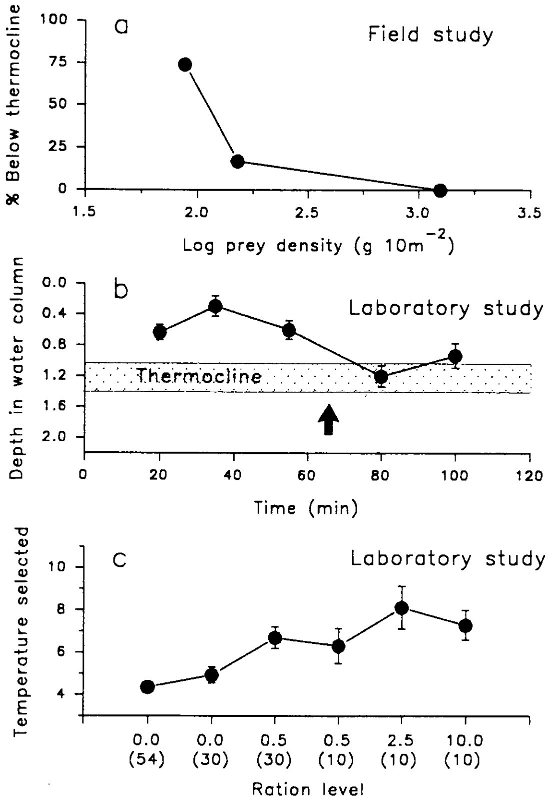

Figure 7. (a) Mean percentage of juvenile walleye pollock captured beneath the thermocline at stations in the Bering Sea, with increasing prey densities. (b) Mean depth (± SE) of juvenile walleye pollock in a stratified water column in the laboratory before and immediately after (arrow) the introduction of food beneath the thermocline. (c) Mean temperature (± SE) selected in a vertical thermal gradient by walleye pollock juveniles held under varying rations; upper numbers are the % body weight provided as food each day, and numbers in parentheses are the duration in days of the ration treatment.

These results suggest that the first act of defense against hunger in juvenile walleye pollock is to increase activity and expand the area searched for food, including transient excursions beneath the thermocline at temperatures that are otherwise avoided. However, if an increase in food searching does not prove to be profitable and low food availability continues, juvenile walleye pollock possess within their behavioral repertoire the ability to behaviorally thermoregulate and thereby lower metabolic requirements, conserving diminishing energy reserves.

JUVENILES - SOCIAL INTERACTIONS

On the most basic level, juvenile walleye pollock have an innate attraction for conspecifics. This social attraction is demonstrated by simple laboratory experiments in which juvenile pollock form schools when they are not actively searching for food or responding to predators. As with factors influencing vertical distribution, this innate social attraction operates in concert with, or in opposition to, other intrinsic and extrinsic factors to determine the extent of schooling behavior (Fig. 8). For example, predation threat operates in conjunction with innate attraction, resulting in more cohesive schools. We have tested this effect in the laboratory by measuring the distance between each fish in a group before and after a predator model is plunged into the tank, simulating an imminent attack.

In contrast to fright, hunger has an opposing influence, resulting in less cohesive schools as individuals disperse to search for food. The way in which food is distributed can also influence the cohesiveness of pollock schools. We tested this effect in the laboratory by monitoring the behavior of fish conditioned to patchy or dispersed food. Groups of pollock were videotaped in 3000-l circular tanks with a series of automatic feeders positioned around the periphery. Dispersed, unpredictable foraging conditions were simulated by dispensing single food pellets over random periods of time from randomly selected feeders.

Patchy conditions were created by dispensing clumps of pellets. Results of these experiments demonstrated that juvenile walleye pollock forage in socially interactive groups when food occurs in ephemeral patches. In contrast, when food is widely dispersed juvenile pollock forage more independently, ignoring conspecifics. As a result, group cohesiveness decreases (Fig. 8).

Our laboratory studies on the effect of innate attraction, predation, feeding, and food distribution upon school cohesiveness in juvenile walleye pollock have potentially important implications for understanding the behavior and distribution of fish in the field. For example, under high predation risk we would predict that juvenile pollock schools would form highly cohesive and dense groups, as individuals attempt to minimize their vulnerability to predators (Fig. 8). When areas of abundant food are encountered, we would expect juvenile pollock schools to become less cohesive as fish spread out to search for prey. When exploiting a widely dispersed prey, fish should spread out even further and forage more or less independently or in loose aggregations. In contrast, when prey occur in distinct clumps or swarms, juvenile pollock schools should be more cohesive, with individuals exploiting the discovery of food patches by others in the group.

Social behaviors such as group cohesion also vary ontogenetically. In the laboratory, smaller juveniles form less cohesive groups and are less active than larger juveniles. The benefits of group foraging may not outweigh the costs (such as energy expended in maintaining contact with the group) for smaller juveniles, resulting in more independent behavior.

SUMMARY

The results of our extensive series of laboratory experiments demonstrate that behavior of early life stages of walleye pollock depends upon a complex and continually changing hierarchy of extrinsic and intrinsic factors. The consistency of results in the laboratory with observations in the field suggests that experimental methods are appropriate for testing the influence of environment on behavior. By using focused laboratory experiments that test a single factor or a combination of factors, we have developed a preliminary base for understanding the mechanisms underlying distribution in the naturally complex environment in the sea. We believe that establishing linkages between behavioral capabilities of early life stages and key environmental factors can further our understanding of the underlying mechanisms that control distribution, recruitment, and ultimately, survival of young walleye pollock.

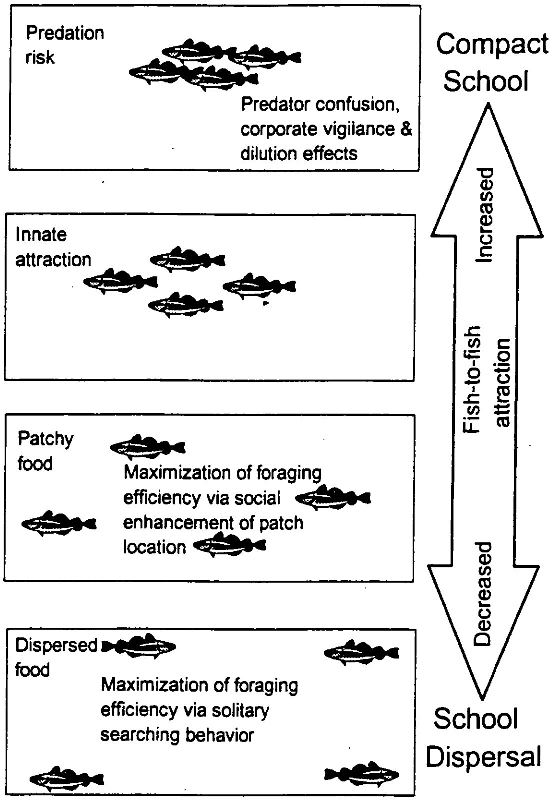

Figure 8. Relative cohesiveness of juvenile walleye pollock schools under varying conditions that either increase or decrease fish-to-fish attraction.

This article was written by BORI OLLA, MICHAEL DAVIS, CLIFFORD RYER, and SUSAN SOGARD, members of the Fisheries Behavioral Ecology Program in the AFSC's Resource Assessment and Conservation Engineering Division at the Mark O. Hatfield Marine Science Center, Newport, Oregon. It is based on a manuscript being prepared for publication in a FOCI compendium.