

Behavioral responses of walleye pollock, *Theragra chalcogramma*, larvae to experimental gradients of sea water flow: implications for vertical distribution

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Received 6 March 2000

Accepted 5 March 2001

Key words: current speed, feeding, gravity, light, orientation, swimming, turbulence

Synopsis

Walleye pollock larvae under controlled laboratory conditions were exposed to vertical gradients of sea water flow in low and high light. Whether flow originated from the surface or the bottom, larvae responded by altering depth distribution, showing attraction to low flows, avoidance of higher flows and when flow was above a threshold level, loss of ability to orient, swim and feed. These results demonstrate that walleye pollock have the capability for responding to gradients of flow by adjusting their vertical distribution. Walleye pollock and many other pelagic fish larvae have weak swimming capabilities and are generally unable to directly control horizontal distributions in the sea by swimming in higher flow regimens. However, using vertical migration, larvae may select conditions of flow direction and speed which are favorable for feeding and predator avoidance and which indirectly allow them to control transport, aggregation and dispersion.

Introduction

Walleye pollock, *Theragra chalcogramma* Pallas, are widely distributed throughout the northern Pacific Ocean and the Bering Sea and form the basis for a major international fishery. Behavior of walleye pollock larvae, including vertical migration, can be a significant determinant of their distribution, growth and survival (Bailey & Macklin 1994, Megrey et al. 1996, Olla et al. 1996). Preliminary observations of walleye pollock larvae under conditions of flow both in the laboratory (Olla & Davis 1990) and the field (Schumacher & Kendall 1991, Kendall et al. 1994) have suggested that they may avoid higher levels of flow. Other laboratory studies have also suggested that marine fish larvae may avoid certain types of flow regimens (Batty 1987).

Walleye pollock in the sea have been observed to be associated with circulation features such as eddies and cold plumes that are composed of gradients of flow (Vastano et al. 1992, Schumacher et al. 1993,

Stabeno et al. 1996). While it has been suggested that survival of walleye pollock and other species of larvae may be enhanced by association with these circulation features, knowledge of how behavior of larvae affects patch formation and dispersal is limited (Hamner 1988, Franks 1992, Denman & Gargett 1995). Laboratory studies of patch formation in walleye pollock larvae have suggested that movement in response to selected environmental factors (e.g., gravity, light, temperature) may bring them into contact with prey patches, where they could then remain to feed as long as light intensity remained at or above levels necessary for feeding (Davis & Olla 1995). However, little consideration has been given to gradients of flow and how these may act in concert with gradients of gravity, light and temperature in an ever shifting order of precedence of behavioral responses by fish larvae to ultimately determine vertical distribution as well as growth and survival (Davis & Olla 1994, Olla et al. 1996). Larvae of walleye pollock and many other pelagic fish species have

weak swimming capabilities and are generally unable to directly control horizontal distributions in the sea by swimming in higher flow regimens (Blaxter 1996, Olla et al. 1996). However, using vertical migration, larvae may select conditions of flow direction and speed which are favorable for feeding and predator avoidance and which indirectly allow them to control transport, aggregation and dispersion (Forward et al. 1999, Hare et al. 1999).

The goal of this study was to test under controlled laboratory conditions the hypothesis that vertical gradients of flow under low and high light could regulate the vertical distribution of walleye pollock larvae. Orientation, swimming, feeding and depth distributions were measured to assess possible effects of flow gradients on larvae.

Materials and methods

Capture and rearing methods for walleye pollock eggs and larvae have been described by Davis & Olla (1995). Briefly, adult walleye pollock were captured in a trawl in the Gulf of Alaska and eggs and sperm were collected from an assortment of ripe fish and mixed in containers of sea water. Fertilized eggs were incubated on shipboard for 2–3 d and then transported to the laboratory in Newport, Oregon for rearing and experimentation. Eggs, embryos and larvae of walleye pollock were reared at a concentration of 201^{-1} in acrylic tanks ($75 \times 25 \times 15$ cm) containing 20 l filtered ($0.45 \mu\text{m}$) uv-sterilized sea water (30–32 ppt S). Water was changed ($\frac{1}{2}$ culture volume) every 24 h and rotifers *Brachionus plicatilis* were introduced in fresh sea water as food to a concentration of 10 ml^{-1} . Cultures were maintained in a constant temperature room at 6.0°C in darkness until 5 d after hatching when embryos became feeding-ready larvae, then under a photoperiod of 14 h light ($0.6 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; daylight fluorescent, 5000°K) and 10 h dark. In the sea, walleye pollock free embryos normally remain at depth in darkness until they become feeding-ready larvae, at which time they migrate to shallow depths to begin feeding in lighted conditions (Davis & Olla 1994). Previous studies with walleye pollock larvae in the laboratory have determined that they avoided light intensities above $13 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and required light above $0.004 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ to feed (Olla et al. 1996). Walleye pollock larvae in the sea occurred at light intensities that were similar to those observed in the laboratory (Kendall et al. 1987, 1994). Levels of

flow that are preferred by walleye pollock larvae have not been determined experimentally and walleye pollock larvae have weak swimming abilities with cruising speed ranging from 0.1 to 0.2 cm s^{-1} (Olla et al. 1996). A review of swimming speeds in pelagic fish larvae less than 10 mm in length found cruising speeds of 0.4 – 3.0 cm s^{-1} (Blaxter 1986). Flows in Shelikof Strait, Gulf of Alaska ranged from 0 to 40 cm s^{-1} and larvae tended to concentrate in flow convergence zones and eddies which had reduced flow (Schumacher & Kendall 1991, Stabeno et al. 1996). For this study, gradients of low flow varied from 0 to 3 cm s^{-1} , corresponding to observed swimming speeds for pelagic fish larvae and originated from the surface and the bottom of water columns.

Responses to vertical gradients of light and flow in larvae (6.4 – 7.8 mm TL) were tested in acrylic cylinders (15 cm diameter \times 110 cm depth) in a constant temperature room (6°C) 13 and 20 d after hatching. Replicate cylinders ($n = 6$) were filled with 19.4 l filtered sea water and rotifers (1 ml^{-1}), and were surrounded by black matte cotton material to control stray light. Twelve to 15 larvae were placed in each column 18 h prior to an experiment. Gradient treatments were administered in the order of: (1) low light, (2) high light, (3) high light and flow originating from the surface, (4) low light and surface flow, (5) low light, (6) low light and flow originating from the bottom, (7) high light and bottom flow, and (8) high light. Larvae were exposed to an experimental condition for 30 min and then 12 larvae in each column were visually observed and data were recorded in a notebook for: (1) the depth for each larva relative to a scale marked on the columns, (2) presence of swimming and feeding activity and (3) orientation angle measured with a protractor as angle of deviation from horizontal. These observations of larvae were pooled for each replicate water column and the results were reported for the six replicate columns on a particular day.

Gradients of light (Figure 1a) were produced from directly above the columns using fluorescent light (5000°K ; low light, 3.2 – $0.5 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; high light, 60.0 – $14.0 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). A gradient of circular flow originating from the surface was produced using an air stream (4.0 standard 1 min^{-1}) directed towards the water surface through 7 mm ID vinyl tubing positioned 5 cm above the water at a radius of 5.5 cm from the central axis of the acrylic column and oriented 30° downward towards the water surface. Rotifers ($220 \mu\text{m}$ length, $140 \mu\text{m}$ width) were distributed randomly throughout the column and acted

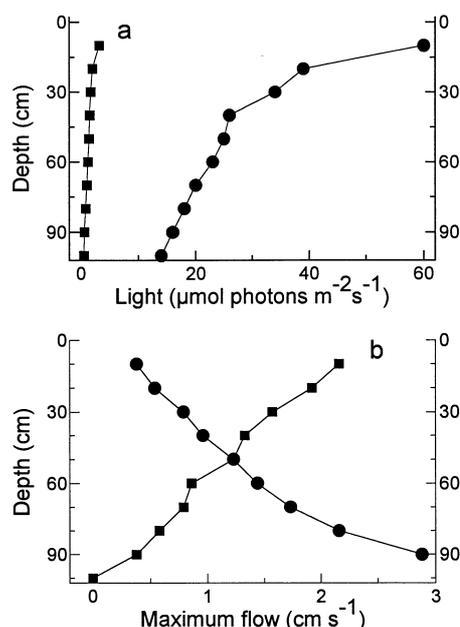


Figure 1. Light and flow gradient conditions in experimental vertical columns. a – depth (cm) profiles of light level ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$) in gradients of low light (■) and high light (●). b – depth (cm) profiles of maximum circular flow (cm s^{-1}) in gradients originating from the surface (■) and from the bottom (●). The large size of the data points includes mean ± 1 Standard Error of the Mean. See Materials and methods for description of flow measurements and patterns.

as flow tracers. Circular flow was observed between a radius of 6.0 and 2.5 cm from the central axis. Maximum circular flow of particles was sampled at a radius 5.5 cm from the central axis by measuring the time with a stop watch that a prey particle took to make one revolution of the water column and calculating the speed as cm s^{-1} , assuming a circumference of 34.56 cm. At a specific depth, speed of circular flow decreased from the maximum observed at 5.5 cm radius (Figure 1b) until upwelling flow was observed from a radius of 2.5 cm inward to the central axis. This upwelling occurred at 1.43 cm s^{-1} between 10 and 40 cm depth, 0.83 cm s^{-1} at 65 cm depth, 0.77 cm s^{-1} at 80 cm depth and was not apparent below 90 cm depth. A low velocity ($<0.15 \text{ cm s}^{-1}$) downwelling current was observed in the outer perimeter of the column (7.5–6.0 cm), but this was not quantified because of variable path lengths for particles that could not be accurately measured using visual observations.

A gradient of circular flow originating from the bottom which decreased up through the water column (Figure 1b) was produced with a magnetically-turned

stirring bar centered on the bottom (6 cm long, 80 rpm). The pattern of circular flow was similar to that observed for flow originating from the surface, while downwelling rather than upwelling was observed in the central area, and upwelling was observed in the perimeter of the column. Measurements of maximum circular flow were made in the same manner as described above. A downwelling current was observed from a radius of 2.5 cm inward to the central axis and occurred at 1.67 cm s^{-1} between 100 and 50 cm depth, 1.00 cm s^{-1} at 30 cm depth, 0.83 cm s^{-1} at 20 cm depth and was not apparent above 10 cm depth. A low velocity ($<0.15 \text{ cm s}^{-1}$) upwelling current was observed near the outer perimeter of the column (7.5–6.0 cm), but this was not quantified because of variable path lengths for particles that could not be accurately measured using visual observations.

Results

Changes in vertical distribution of walleye pollock larvae (6.4–7.8 mm total length) in response to light intensity and flow were similar for 13 and 20 d after hatching ($p > 0.10$; Friedman ANOVA) and therefore, measures from replicate columns for both days were pooled for further analysis ($n = 12$). Light level and flow caused larvae to adjust position in the water column ($p < 0.001$; Friedman ANOVA) and multiple comparisons showed significant ($p < 0.05$) differences among treatments. In a vertical gradient of low light, walleye pollock larvae swam and fed near the surface in response to negative geotaxis (median depth = 5 cm, range = 2.5–7.5 cm; Figure 2), while high light caused larvae to move downward where they continued to swim and feed with negative phototaxis suppressing negative geotaxis (median depth = 15 cm, range = 12.5–17.5 cm).

Under low light when flow originated from the surface, larvae were displaced downward from depths in which they occurred when flow was absent, as they avoided high flow and negative geotaxis was suppressed (median depth = 22.5 cm, range = 20.0–40.0 cm; Figure 2). There they became entrained in the circular flow (1.92 – 1.33 cm s^{-1} ; Table 1), tumbled freely and were not able to swim or feed. When flow originated from the bottom in low light, larvae again moved downward below depths achieved when flow was absent and were distributed in low circular flow (0.50 – 0.60 cm s^{-1} ; Table 1) where they continued to swim and feed, apparently attracted to low flow over the

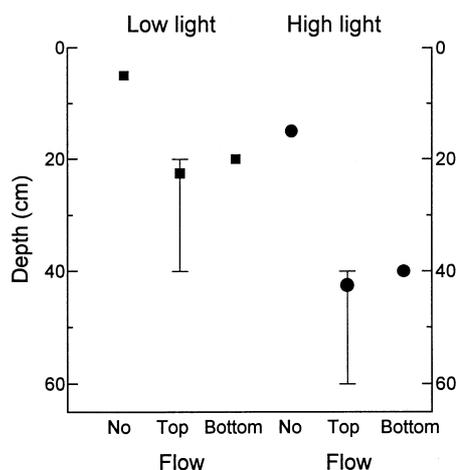


Figure 2. Depth (cm) chosen by walleye pollock larvae in response to low light (■) and high light (●) with no flow (no flow), flow originating from the surface of the column (top flow) and flow originating from the bottom of the column (bottom flow). For top flow treatments in low and high light, large data points are median and the total range of data is indicated by vertical lines and bars. All other treatments have single large data points which include median \pm total range of data.

Table 1. Depth ranges (cm; Depth) chosen by walleye pollock larvae in response to vertical gradients of light and flow. Treatment gradients were for: (1) low light and no flow, (2) low light and flow originating from the surface, (3) low light and flow originating from the bottom; and (4) high light and no flow, (5) high light and flow from the surface, and (6) high light and flow from the bottom. Depth ranges chosen by larvae correspond to ranges for light ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$; Light), maximum circular flow (cm s^{-1} ; Flow) and presence or absence (+/–) of swimming and feeding (Swim/Feed). See Materials and methods for description of flow measurements and patterns.

Treatment	Depth	Light	Flow	Swim/Feed
(1) Low light and no flow	2.5–7.5	3.2	0	+
(2) Low light + surface flow	20.0–40.0	2.0–1.5	1.92–1.33	–
(3) Low light + bottom flow	17.5–22.5	2.0	0.50–0.60	+
(4) High light and no flow	12.5–17.5	50.0	0	+
(5) High light + surface flow	40.0–60.0	26.0–23.0	1.33–0.86	+
(6) High light + bottom flow	37.5–42.5	26.0	0.92–1.03	+

effects of negative geotaxis (median depth = 20 cm, range = 17.5–22.5 cm).

Under high light with flow originating from the surface, larvae moved downward avoiding higher flow

and light, to exceed depths achieved in the absence of flow or when flow was present under low light (median depth = 42.5 cm, range = 40.0–60.0 cm; Figure 2). Circular flow at these depths was at levels at which the larvae could continue swimming and feeding ($1.33\text{--}0.86 \text{ cm s}^{-1}$; Table 1). When flow originated from the bottom in high light, larvae again moved lower in the water column, being attracted to low flow and avoiding higher light (median depth = 40.0 cm, range = 37.5–42.5 cm), comparable to when flow originated at the surface. At these depths, circular flow was at a level at which larvae could continue swimming and feeding ($0.92\text{--}1.03 \text{ cm s}^{-1}$).

In low and high light, larvae showed a greater range of depths of occurrence when flow originated from the surface than from the bottom and these ranges extended further downward from the median depths (Figure 2). Observations of larvae (12 replicate larvae in 6 treatments = 72 larvae observed) under all light and flow conditions showed that swimming and feeding behavior were not possible above 1.33 cm s^{-1} ($p < 0.05$; Sign test, $n = 12$), and that larvae did not occur in upwelling or downwelling currents, apparently choosing to avoid vertical motion and to remain in horizontal circular currents ($p < 0.05$; Sign test, $n = 12$). Larvae remained at depths where circular flows were below 1.33 cm s^{-1} , except in low light when flow originated from the surface ($1.92\text{--}1.33 \text{ cm s}^{-1}$; Table 1). Under all conditions in which they were able to swim, larvae ($n = 60$) showed orientation angles that ranged from 1 to 39° from horizontal, while larvae ($n = 12$) that were subjected to low light and flow from the surface and were not able to swim, showed angles of orientation that were significantly different from swimming larvae (median = 48° , range = $8\text{--}83^\circ$; $p < 0.007$, Friedman ANOVA).

Discussion

Behavioral responses of walleye pollock larvae to selected environmental factors (e.g., gravity, light, temperature, prey distribution) in previous studies under laboratory conditions shifted according to strength and priority of the stimulus (Olla & Davis 1990, Davis & Olla 1995, Olla et al. 1996). In the absence of water flow, larvae swam toward the surface under low light (Olla & Davis 1990). This response was indicative of a negative geotaxis rather than a positive phototaxis, since larvae showed the same surface distribution when illuminated with low light from the bottom

of the water column. However, under higher light, larvae swam downward with a negative phototaxis taking precedence over negative geotaxis, to a level of lower light where negative geotaxis again became the primary orientation cue.

The predicted responses to light in the absence of flow were confirmed in the present study and the addition of gradients of flow added further behavioral choice for walleye pollock larvae. Based on preliminary observations under laboratory conditions of responses to wind mixing in the top 10 cm of the water column, the expectation was that larvae would avoid conditions of flow (Olla & Davis 1990). This expectation was supported in the present study by observations that larvae avoided upwelling or downwelling flow. Larvae also avoided high levels of horizontal circular flow that originated from the surface or the bottom. However, larvae were observed to tolerate or be attracted to low levels of circular flow, in contradiction to the original expectation (Olla & Davis 1990).

Larvae showed concurrent negative phototaxis and avoidance of high levels of flow under high light and a gradient of horizontal circular flow that originated from the surface. This resulted in downward movement into low levels of flow in which larvae could swim and feed. Under high light when circular flow came from the bottom, larvae showed negative phototaxis and apparent attraction to low flow as they moved downward until high circular flow became the primary environmental stimulus, causing larvae to avoid high flow and to remain in a narrow range of depths in which they could swim and feed.

Larvae shifted from negative geotaxis to apparent attraction to low levels of flow when they were exposed to circular flow originating from the bottom under low light. This shift in priority of response caused larvae to move downward until negative geotaxis and avoidance of high levels of flow became the priority environmental cues, with larvae remaining in a narrow range of depths in which they could swim and feed.

Larvae shifted from negative geotaxis to avoidance of high levels of flow when they were exposed to a gradient of horizontal circular flow originating from the surface under low light. This shift in priority of response caused larvae to move downward until they again responded to negative geotaxis, but had not moved deep enough to escape higher levels of flow which caused them to become entrained in the flow and unable to swim horizontally and feed. This lack of swimming ability in higher circular flows and low light indicated possible conditions in the sea under which

larvae would not be able to feed or maintain position through behavioral responses. Under these conditions, advection could sweep larvae away from favorable conditions for feeding and survival found in eddies and cold plumes (Incze et al. 1989, Schumacher & Kendall 1991, Vastano et al. 1992).

An earlier study with larvae of Pacific herring, *Clupea harengus pallasii*, showed that caution must be observed when measuring swimming performance in laboratory-reared larvae (von Westernhagen & Rosenthal 1979). Herring larvae that were captured in the field and observed in the laboratory swam at an average speed of 1.6 cm s^{-1} , while larvae that had been reared in the laboratory swam at an average speed of 0.9 cm s^{-1} . After field-caught larvae had been held in the laboratory for a few days, their swimming speeds decreased to those observed for larvae reared in the laboratory, suggesting that a significant factor controlling swimming performance was the level of environmental stimulation present in the laboratory (von Westernhagen & Rosenthal 1979). Stimulation would be provided by active prey, gradients of light and water mixing, and the presence of predators. Similar conclusions about altered swimming performance in larvae were also suggested for coral-reef fishes in the eastern Pacific Ocean (Leis & Carson-Ewart 1997). Swimming speeds for walleye pollock larvae have not been compared among field-caught and laboratory-reared individuals. Walleye pollock larvae in this study would not be expected to show a diminution of swimming performance based on lack of environmental stimuli, as more realistic environmental conditions were produced in the laboratory by including gradients of light and flow. In contrast, most laboratory studies of swimming in pelagic fish larvae have been conducted under conditions of no flow with constant light or darkness (Blaxter 1986).

The results from this study support the hypothesis that gradients of flow could regulate the vertical distribution of walleye pollock larvae in the sea. Clearly, gradients of flow produced by wind mixing are a dominant feature of fish larvae habitats in the ocean (Incze et al. 1990, Davis et al. 1991, Schumacher & Kendall 1991, Denman & Gargett 1995). As wind speed increased in Shelikof Strait, Gulf of Alaska, walleye pollock larvae swam approximately 10 m downward under conditions of darkness and low and high light (Kendall et al. 1994). Studies with other marine fish larvae have indicated the possible role of wind mixing in regulation of vertical distribution. Herring, *Clupea harengus*, swam deeper in response to increased wind mixing in the sea

(Heath et al. 1988) and in the laboratory (Batty 1987). Atlantic cod, *Gadus morhua*, moved deeper in the water column as wind mixing increased (Ellertsen et al. 1984, Lough & Mountain 1996), and the same was true for haddock, *Melanogrammus aeglefinus* (Lough & Mountain 1996).

There are many examples of field studies in which it was observed or postulated that transport, migration and dispersal in pelagic and demersal fish larvae may often be regulated to a certain extent by the interactions of various flow regimens and swimming behavior. Types of mechanisms involved in transport included vertical migration, differential swimming abilities among species, control of buoyancy and rheotactic responses to flow (Cowen et al. 1993, Champalbert & Marchand 1994, Breitburg et al. 1995, Xie & Eggleston 1999, Hare et al. 1999, Armsworth 2000). Control of horizontal distribution and the ability to remain in patches of food and avoid predators may also be related to the swimming capabilities of fish larvae (Davis et al. 1991, Davis & Olla 1995).

Cruising speeds for pelagic species of fish larvae less than 10 mm in length in the laboratory ranged between 0.4 and 3.0 cm s⁻¹ (Blaxter 1986). This limited swimming capability appears to be sufficient for indirect control of horizontal distribution, maintenance of distribution in patches and transport through the use of vertical migration into depths where favorable current direction and speeds could facilitate horizontal movement, even for pelagic fish larvae of species with life histories that are dependent on cross-shelf transport and moving into estuaries for optimal growth of juveniles (Forward et al. 1999, Hare et al. 1999). Since walleye pollock larvae have relatively weak swimming capabilities, it would be predicted that they do not have the capacity to directly control their horizontal distribution in the sea by swimming long distances in a horizontal direction, but that some degree of control could be obtained through vertical migration into depths where favorable current directions and speeds were present to facilitate horizontal transport. However, the ability for behavior in walleye pollock larvae to control distribution may be limited in areas where water flow is rapid. Disruption of patches of walleye pollock larvae in Shelikof Strait, Gulf of Alaska was linked to disturbances in current fields and resultant advection (Incze et al. 1989, 1990) and lower survival of larvae was linked to the presence of strong wind mixing events (Bailey & Macklin 1994). In contrast, greater swimming capacity with cruising speeds between 4.9 and 23.7 cm s⁻¹ was observed in larvae less than 10 mm

in length for reef fishes in the western Pacific Ocean in the field and in the laboratory in flumes (Leis & Carson-Ewart 1997, Fisher et al. 2000). Reef fish larvae clearly have the capability to swim horizontally and directly control their horizontal distributions in flow fields (10–15 cm s⁻¹) that are typically found near coral reef habitats and this capability would be necessary for larvae that position themselves over and settle into the limited target areas of reefs (Leis & Carson-Ewart 1997).

Walleye pollock larvae in this study lost orientation and ceased to swim normally and feed above an upper threshold level of flow. This novel observation suggested that there are rather specific conditions of flow that are required for survival in walleye pollock larvae. The extent to which this may be true for other species of pelagic fish larvae is unknown and not likely to be determined unless laboratory experiments include higher levels of flow or observations are made in the field, which is generally difficult given the low density of larvae in the sea. For walleye pollock larvae, any decrease in ability to orient, swim and feed would certainly decrease their nutrition status and condition, resulting in developmental changes, loss of buoyancy control and further loss of swimming and predator avoidance capabilities (Davis & Olla 1992, Olla & Davis 1992). There may also be the potential for increased energy costs associated with the presence of higher flows and this has not been evaluated experimentally. Considering the pervasive occurrence of gradients of flow in the sea, the responses of walleye pollock larvae to gradients of flow in the laboratory emphasizes the importance of including gradients of flow in future studies of the distribution, feeding and survival of pelagic fish larvae. Growth and survival may be decreased when walleye pollock larvae avoid higher levels of flow and move into depths with insufficient light for feeding or advection moves them from favorable areas into flow that inhibits swimming and feeding (Incze et al. 1989, 1990). Alternatively, under lower levels of flow, movement of walleye pollock larvae in response to selected environmental factors (e.g., gravity, light, temperature, mixing) may bring them into contact with prey patches that are associated with circulation features (e.g., eddies and cold plumes), where they then could remain in aggregations to feed as long as light intensity remained at or above levels necessary for feeding (Schumacher & Kendall 1991, Vastano et al. 1992, Davis & Olla 1995, Olla et al. 1996).

Feeding in fish larvae has been observed in the laboratory to be enhanced by intermediate levels

of isotropic flow in the form of turbulent mixing, expressed as the turbulent dissipation rate, with these studies being conducted under conditions of little or no non-random flow characteristic of water currents (see review by Dower et al. 1997). In the present study, while low to intermediate levels of turbulence were noted by observing random motion of prey particles in association with the gradients of flow, turbulence was not measured directly as the turbulent dissipation rate. This study has been a first attempt to simulate two relatively simple flow gradients that varied with depth. The inhibition of swimming and feeding in walleye pollock larvae by higher levels of flow emphasized that previous studies in the laboratory of fish larvae feeding in turbulence without accompanying non-random flow may not have been very realistic, given the co-occurrence in the sea of gradients of turbulence and flow.

Only a few studies of the effect of turbulence on feeding in fish larvae have been conducted in the field and conflicting patterns of response were observed. A long-standing idea, 'the stable ocean hypothesis' suggested that increasing turbulence likely had a negative effect on feeding, where a positive relationship was noted between survival of larvae and the frequency of calm, low wind speed periods which allowed for the maintenance of high prey concentrations (Lasker 1975, Vlymen 1977, Owen 1989). In contrast, other studies have suggested either that increasing turbulence produced an enhancement of feeding in fish larvae (Sundby & Fossum 1990), or that there was a dome-shaped relationship between intensity of turbulence and feeding in larvae (Cury et al. 1994, MacKenzie et al. 1994). As turbulence increased, prey capture rate increased until an optimum level of turbulence was reached, beyond which foraging behavior of the larvae was inhibited, prey patches dispersed and prey capture rate decreased. Optimal foraging in fish larvae may be significantly altered by the effects of turbulence and flow. Shifts in foraging and capture behaviors may occur as turbulence or flow increases, the energetic costs of foraging may increase, and capture may shift to more vulnerable prey (Dower et al. 1997). These hypotheses are testable in both the laboratory and the field.

In summary, the complex behavior of walleye pollock larvae in response to gradients of flow supported the hypothesis that flow may regulate vertical distribution and feeding in walleye pollock larvae. Walleye pollock larvae were unable to orient, swim and feed under higher levels of flow and avoided these regimens whenever possible, instead remaining in conditions of

low flow. Because of possible behavioral preferences for conditions of low flow balanced with negative geotaxis or negative phototaxis, it would seem necessary to determine the tolerance for flow in marine fish larvae prior to being able to perform realistic studies of the role of flow and mixing in the life histories of larvae. This could be accomplished by testing fish larvae in appropriate gradients of flow and light where behavioral choice may be observed.

Acknowledgements

We thank Debbie Blood for collection of walleye pollock eggs, Rich Titgen for transport of eggs, and Mara Spencer and Michele Ottmar for rearing algae and rotifers and technical assistance with rearing fish larvae. This work is a contribution to NOAA's Fisheries-Oceanography Coordinated Investigations, FOCI-0412.

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