Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*)

THOMAS P. HURST,[1,]* **DANIEL W. COOPER,**[2] **JOEL S. SCHEINGROSS,**[1] **ERIN M. SEALE,**[1] **BENJAMIN J. LAUREL**[1] **AND MARA L. SPENCER**[1]

[1]*NOAA-NMFS Alaska Fisheries Science Center, Fisheries Behavioral Ecology Program, Hatfield Marine Science Center, 2030 S. Marine Science Dr., Newport, OR 97365 USA*
[2]*NOAA/NMFS Alaska Fisheries Science Center, Recruitment Processes Program, Bldg 4, 7600 Sand Point Way NE, Seattle, WA 98115-0070 USA*

ABSTRACT

The role of behavior, especially vertical migration, is recognized as a critical component of realistic models of larval fish dispersion. Unfortunately, our understanding of these behaviors lags well behind our ability to construct three-dimensional flow-field models. Previous field studies of vertical behavior of larval Pacific cod (*Gadus macrocephalus*) were limited to small, preflexion stages (≤11 mm SL) in a narrow range of thermal conditions. To develop a more complete picture of larval behavior, we examined the effects of ontogeny, temperature, and light on vertical responses of larval Pacific cod in experimental columns. While eggs were strictly demersal, yolk-sac larvae displayed a strong surface orientation as early as 1 day post hatch (∼ 5 mm SL). Consistent with field observations, small preflexion larvae (<10 mm SL) showed no response to varying light levels. However, there was a direct effect of temperature on larval behavior: Pacific cod larvae exhibited a stronger surface orientation at 4°C than at 8°C. The behavior of larger, postflexion larvae (>15 mm SL) in experimental columns was consistent with a diel vertical migration and independent of water temperature: fish were more widely distributed in the column, and median positions were consistently deeper at higher light levels. These laboratory observations are combined with observations from discrete-depth (MOCNESS) sampling in the Gulf of Alaska to characterize the vertical distribution of larval Pacific cod and contrast ontogenetic patterns with walleye pollock (*Theragra chalcogramma*). The vertical movements of larval Pacific cod described here will be applied in the development of dispersal projections from Gulf of Alaska spawning grounds.

INTRODUCTION

The vertical distribution of fish larvae in the water column has direct implications for their survival by regulating encounters with predators and prey and influencing distance and direction of transport (Fiksen *et al.*, 2007; Miller, 2007). The concept that diel and ontogenetic changes in the vertical distribution of larvae are critical for transport to suitable nursery grounds has been well established through the study of estuarine and, more recently, tropical reef fishes and invertebrates (Cronin and Forward, 1979; Norcross and Shaw, 1984; Paris and Cowen, 2004). These organisms have served as useful models as the prevailing flow fields and specific settlement habitat requirements of these groups suggest that local populations are likely to be dependent upon larval retention and self-recruitment (Cronin and Forward, 1979; Cowen *et al.*, 2000; Bradbury *et al.*, 2008). Where diel and ontogenetic changes in vertical distribution of temperate and boreal marine larvae have been examined, these changes have been interpreted as responses to predator–prey biological interactions (Neilson and Perry, 1990; Reiss *et al.*, 2002; Sebates, 2004).

Recent interest in understanding and conservation of sub-population stock structure in widespread marine species has placed a renewed emphasis on determining dispersal patterns of early life stages (Sponaugle *et al.*, 2002; Laurel and Bradbury, 2006). At the same time, the construction of detailed three-dimensional flow field models of coastal oceans has allowed for more precise modeling of drift trajectories (Hinrichsen *et al.*, 2005). However, the application of stratified flow

Correspondence. e-mail: thomas.hurst@noaa.gov

models to larval dispersal depends upon a thorough understanding of the vertical distribution of larvae including ontogenetic changes, diel periodicity, and responses to environmental conditions (Naylor, 2006). Unfortunately, for most marine fish species, insufficient knowledge of larval behavior precludes effective integration of biological and physical models of dispersal. As a result, many studies continue to apply simplified models of vertical movements (Paris and Cowen, 2004) or treat larvae as passive particles travelling at fixed depths (Hinrichsen *et al.*, 2005; Lanksbury *et al.*, 2007). Furthermore, as differences in vertical distribution of co-occurring larvae can result in divergent drift trajectories (Hare and Govoni, 2005), models must be based upon species-specific behavioral patterns.

To date, descriptions of vertical behavior patterns of fish larvae have depended largely upon discrete-depth field sampling. In addition to facing the high variability in catch rates of marine plankton (Gray, 1996a), field surveys are dependent upon the ranges of physical and biological conditions encountered during sampling, limiting the ability to examine behavior from a multifactorial perspective. Hence, except for the most intensively studied species, field data are likely to be insufficient to fully resolve aspects of vertical behavior relevant to dispersal.

Laboratory experiments on the behavior of fish larvae can provide a valuable complement to field surveys in the characterization of vertical movements (Olla and Davis, 1990; Burke *et al.*, 1995; Forward *et al.*, 1996). Such experiments have been widely applied in the study of invertebrate larvae (Forward, 1988; Hays, 2003), allowing for isolation of environmental and biological factors that govern vertical movements. When compared to field-derived behavior models, laboratory-scale experimentation on the vertical responses of marine fish larvae has been shown to provide robust descriptions of basic behavioral patterns (Champalbert and Koutsikopoulos, 1995; Olla *et al.*, 1996).

Pacific cod (*Gadus macrocephalus*) is an important component of fisheries and foodwebs in the north Pacific Ocean and Bering Sea. Despite being managed as separate stock units (NPFMC, 2006), genetic analyses have identified only weak discrimination between the Gulf of Alaska and Bering Sea (Grant *et al.*, 1987; Cunningham *et al.*, 2009), suggesting some degree of exchange on an evolutionary time scale. However, the early life history of Pacific cod as it relates to population structure and recruitment dynamics remains largely unknown. One study by Brodeur and Rugen (1994) examined the vertical distribution of Pacific cod larvae in depth-discrete (MOCNESS) samples in the western Gulf of Alaska.

Fish were found in the upper water column and no significant differences in depth between day and night samples were observed. Unfortunately, the field samples contained exclusively small (≤11 mm) preflexion larvae, so no conclusions could be drawn about the vertical movements of larger postflexion larvae. Improved knowledge of the behavioral traits of Pacific cod larvae would allow an existing three-dimensional hydrographic model of the Gulf of Alaska (Hermann and Stabeno, 1996), previously applied to walleye pollock (Hinckley *et al.*, 1996, 2001), to be applied to questions of population connectivity in Pacific cod.

Here we present the results of laboratory experiments which describe the vertical distribution and behavior patterns of larval Pacific cod in the Gulf of Alaska. These experiments describe the vertical movements of yolk-sac and feeding-stage (preflexion and postflexion) larvae in response to variation in light level and (for feeding-stage larvae) temperature. Laboratory observations are combined with field data in the Gulf of Alaska to offer a more comprehensive description of the vertical behavior of Pacific cod larvae. Finally, we contrast vertical behavior patterns of early life stages of Pacific cod with those of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska.

METHODS

Laboratory experiments were designed to determine the movement patterns of larval Pacific cod in vertical water columns at different ambient light levels. Preliminary experiments were carried out in 2006. In 2007, a full series of experiments was conducted to examine the influences of ontogeny and temperature on vertical responses to light level. Summary data describing fish size, age, and number of replicates are presented in Table 1. Experimental procedures generally followed those of Olla and Davis (1990) and Davis (2001) for larval walleye pollock.

Fish were reared in the laboratory from eggs collected from spawning adults. Female and male Pacific cod were caught by commercial jigging gear from spawning grounds in Chiniak Bay, Kodiak Island, Alaska. The gametes were mixed and placed into 4-L incubation trays at 4°C. At 24 h post-fertilization, fertilized eggs were shipped in insulated containers filled with 4°C chilled seawater to Alaska Fisheries Science Center (AFSC) laboratory facilities in Newport, Oregon. Eggs were transferred to flow-through 4-L plastic trays and incubated at 4°C (2°C for preliminary trial). Hatching occurred 19–22 days post-fertilization, after which larvae were transferred into 100-L upwelling cylindrical tanks (460-L tanks

Table 1. Summary of laboratory experiments describing the effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod.

Temperature	Size class	N	dph	SL ± SD
Yolk-sac stage larvae				
4°C		6	1–4	4.9 ± 0.12
Feeding stage larvae				
8°C*		7	49–77	11–17[†]
4°C	Small	5	23–31	6.9 ± 0.5
4°C	Medium	9	61–68	9.0 ± 0.6
4°C	Large	9	87–94	18.8 ± 2.4
8°C	Medium	14	38–58	10.6 ± 0.8
8°C	Large	9	77–81	15.3 ± 1.9

*Preliminary experiments carried out in 2006.
[†]Fish were not measured in preliminary trials with feeding stage larvae. Based on measurements of other fish under identical rearing conditions, fish size was estimated to range 11–17 mm SL.

for preliminary trial) and acclimated to 4°C or 8°C. Light regime during larval rearing was maintained at 12 : 12 h light:dark, with light provided by overhead fluorescent bulbs at a level of 6.7×10^{-0} μE m^{-2} s^{-1} at the water surface. Larvae were reared on a combination of rotifers (*Brachionus plicatilis*; 4 prey mL^{-1}) and microparticulate dry food (Otohime A). Food levels in some rearing tanks were reduced as part of another experiment described elsewhere (B. Laurel, unpublished data). For those tanks, rotifer density during the first 3–6 weeks post-hatch was reduced to 0.5 prey mL^{-1}, contributing size variation among rearing tanks. No fish were tested while being reared on reduced prey density.

Behavior of yolk-sac larvae

The experimental apparatus consisted of a 435-mm vertical glass cylinder with an inner diameter of 52 mm. The tube was filled to a depth of 360 mm with filtered sea water (salinity 33) chilled to 4°C. Marks on the outside of the column at 4-mm intervals allowed determination of the vertical position of each larva. The columns were placed 1 m below a bank of overhead fluorescent lights which provided daytime illumination of 2.75×10^1 μE m^{-2} s^{-1}. Nighttime illumination was $<1.0 \times 10^{-7}$ μE m^{-2} s^{-1}. Experimental columns were separated from each other by opaque dividers. Supplemental observations of the frequency and duration of swimming bouts, as well as the body orientation during swimming and resting were used to determine whether vertical position in the water columns was maintained through buoyancy regulation or active swimming (Davis and Olla, 1994).

Twelve newly hatched larvae (<5 h post-hatch) were captured from egg-incubation tanks with a pipette and transferred to each of six columns at 1500 (1200 nominally defined as hatching time). The fish were then exposed to a diel light cycle of 12 : 12 light:dark. Over the next 3 days, the positions of the fish in each replicate column were determined eight times. Nighttime observations were made with a dim, red-filtered light. Fish were not offered food during the experimental period, relying instead on internal yolk reserves which become depleted 4–6 days post-hatch (dph) in larval Pacific cod reared at 4°C (Laurel *et al.*, 2008).

From the vertical positions of all fish in each replicate column, the group median was calculated. The median position in each column at each observation point was used as the level of observation in subsequent analyses. The 25th and 75th percentiles of fish positions at observation point were used to illustrate the breadth of fish distribution in experimental columns.

Behavior of feeding-stage larvae

The experimental apparatus used for feeding-stage larvae (6–18 mm SL) consisted of a 1.2-m vertical acrylic tube with an inner diameter of 15.24 cm. The tube was filled to a depth of 110 cm with filtered sea water (salinity 33) chilled to the experimental temperature. The columns were marked at 5-cm increments to estimate the positions of fish in the column. The top edge of the column was covered with opaque tape and the columns were placed on a non-reflective cloth-covered platform. An Edison-style compact fluorescent bulb was positioned 25.4 cm above the column (35.6 cm from water surface). A sleeve of black fabric was hung between the light source and the water surface to minimize scattered light around the experimental column. Multiple experimental columns were separated by opaque dividers.

The entire experimental set-up was maintained in a temperature-controlled room. Due to heat from the light (when unfiltered), there was a slight temperature gradient present in the experimental columns at some points during the experiments. Surface temperatures (top 5 cm) were as much as 0.5° above the target test temperature. Column temperatures did not deviate from the target temperature below 30 cm depth. This slight temperature gradient was not believed to have significantly affected fish positioning in the columns. Fish positions in additional tests, in which the water column was vertically stirred, were not different from those in undisturbed columns. In addition, the ordering of light exposure treatments was randomized,

preventing a time bias from potential heating; there was no effect of order of light exposure treatments on median fish position.

Light intensities were varied over eight orders of magnitude in the experiment by placing neutral-density filters between the light source and the experimental column. Light levels were measured with a research radiometer. Experimental light levels (measured at the water surface) were 2.75×10^1, 6.76×10^0, 5.4×10^{-1}, 7.50×10^{-3}, and $<1.0 \times 10^{-7}$ μE m^{-2} s^{-1} (for the preliminary trial in 2006, light levels were 8.41×10^1, 1.62×10^1, 3.24×10^{-1}, 1.26×10^{-2}, and $<1.0 \times 10^{-7}$ μE m^{-2} s^{-1}). Experimental light levels cover much of the range potentially experienced by Pacific cod larvae in the Gulf of Alaska in spring, but the maximum level was slightly less than that estimated by Kendall *et al.* (1994) for mid-day surface waters ($>5 \times 10^1$ μE m^{-2} s^{-1} above 10 m depth).

Ten Pacific cod larvae (five in preliminary experiments) were captured from larval rearing tanks approximately 2 h after the last feeding of the day and transferred to experimental columns. Fish in columns were maintained in the dark overnight prior to initiation of the experiment. Fish were not fed while in the experimental columns. All fish were sequentially exposed to all five light levels for periods of 2 h between 0800 and 1800. The order of treatment presentation was randomly determined prior to each experiment with the constraint that all light changes were of at least two orders of magnitude. After a light level change, fish were allowed to acclimate to the new level for a period of 60 min, after which the positions of all 10 fish in the column were recorded three times at 30-min intervals. Fish positions were determined by visually scanning the column. During low light treatments, a dim, red-filtered light was used to locate larvae. To minimize disturbance from the light, observations were made in a single pass from the top to bottom of the column. Sizes of fish used in the experiment were determined by measuring a sub-sample of fish following experiments, or by measuring a sub-sample of fish from experimental rearing tanks.

Experiments were conducted at 4 and 8°C to describe the direct influence of temperature on vertical behavior. At each temperature, experiments were conducted with fish of different ages and sizes to examine the effect of ontogeny on behavior of Pacific cod larvae. Specific sizes used in experiments for small ($\leq$8 mm SL), medium (around 10 mm SL), and large ($\geq$14 mm SL) size classes are presented in Table 1. The small size class was only tested at 4°C. Within each size class, 5–14 replicate experiments were conducted at each temperature. Low numbers of fish

available for the preliminary experiments required that fish were reused in experiments, but they were allowed to recover for a minimum of 5 days before reuse. In the ontogenetic series, fish were used only once during experiments at a specific stage, but may have been reused in experiments on later ontogenetic stages. Fish were not reused across temperature treatments.

Frequency histograms of fish position in 10-cm-depth bins were used to illustrate cumulative patterns in fish distribution as a function of light level, water temperature, and ontogenetic stage. Statistical analysis was conducted using multifactor ANOVA with temperature ($N = 2$), size class ($N = 3$), and light level ($N = 5$) as main factors. Within temperature treatment and size class, light level was treated as a repeated measure. From the raw data on individual fish positions in the experimental columns, the median fish position in the column at each light level was used as the level of observation in statistical analyses to eliminate the potential for pseudo-replication. The 25th and 75th percentiles of fish positions at each light level were used to illustrate the breadth of fish distribution in experimental columns.

RESULTS

Behavior yolk-sac larvae

Within 24 h of hatching, larval Pacific cod expressed a marked surface orientation in experimental columns (Fig. 1). In the first 48 h post-hatch, median fish

Figure 1. Vertical position of Pacific cod yolk-sac larvae in experimental columns during the first 4 days post-hatch. Points are average median fish position in six replicate columns and error bars represent average 25th and 75th percentiles of fish distribution. Open symbols represent observations made in the light and filled symbols represent observations made in the dark. The bar along the x-axis represents the light–dark cycle in the experiment.
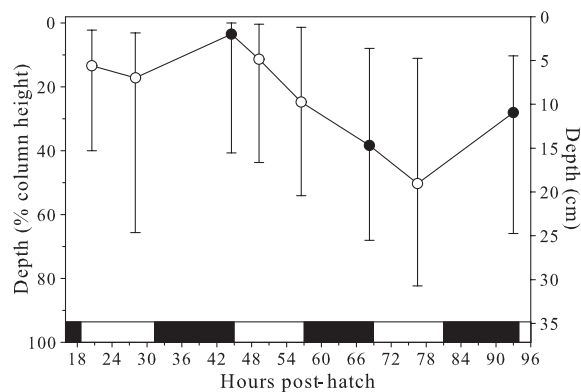
positions were consistently in the upper 7 cm of the water column. Positions of individual fish in the water column became more variable after 48 h post-hatch, with some fish periodically resting on the bottom of the columns. However, when not in contact with the bottom, most fish remained in the upper half of the water column. During the yolk-sac stage, there were no consistent differences in vertical position between day and night.

Observations of the movements of individual larvae indicated that they tended to be near-neutrally buoyant after hatching. But at 3 dph, fish appeared negatively buoyant and sank between swimming bouts. Fish maintained position in the upper portions of the water column through intermittent, active upward swimming during the day and night.

Behavior of feeding-stage larvae

Preliminary experiments in 2006 demonstrated that larval Pacific cod varied their depth distribution in experimental columns in response to variation in ambient light levels. Fish remained near the surface of the column at light levels of 10^{-1} μE m^{-2} s^{-1} and below. However, average depth of occurrence was significantly deeper at higher light levels (Table 2).

The series of experiments conducted in 2007 demonstrated that depth distribution of larval Pacific cod in experimental columns was explained by the interactive effects of light, ontogeny, and water temperature (sig-

Table 2. Analysis of variance of depth distribution of larval Pacific cod in experimental columns. Within temperature and size treatments, light level is treated as a repeated measure. The dependent variable is the median fish position at each observation point in experimental trials.

Source	d.f.	MS	F	P
Preliminary experiment (8°C)				
Error among replicates	6	146.7		
Light level	4	433.2	4.05	0.012
Error	24	99.5		
4°C Experiments				
Size class	2	8766.9	45.619	<0.001
Error among replicates	20	192.2		
Light level	4	1749.2	14.376	<0.001
Light × size	8	1190.0	9.780	<0.001
Error	80	121.7		
8°C Experiments				
Size class	1	676.8	1.290	0.269
Error among replicates	21	524.8		
Light level	4	2733.5	11.7056	<0.001
Light × size	4	701.8	3.005	0.023
Error	80	230.8		

nificant temperature × size and light × size interactions, Table 2). Examination of the two temperature treatments separately reveals the development of a behavioral response to light with ontogeny.

Within the 4°C trials, the effect of light level on median depth of occurrence varied with ontogeny (significant light × size interaction; Table 2). Small fish remained concentrated near the surface of the water column independent of light level ($P = 0.296$; Fig. 2a). During experiments with the medium and large size classes, light level had a significant effect on fish position in the columns ($P < 0.001$). This effect was most pronounced among the large fish, which remained concentrated in the surface waters at low light levels but were more deeply and uniformly distributed throughout the columns at high light levels (Fig. 3c).

Although small fish were not tested at 8°C, a similar ontogenetic pattern in behavioral response to light was observed between experiments with medium and large larvae (significant light × size class interaction; Table 2). Among medium-sized fish there was a slight, but non-significant, trend toward shallower depths under darker conditions ($P = 0.150$). Among large fish, median depth of occurrence was significantly shallower and fish were more concentrated near the surface in the dark than at higher light levels ($P < 0.001$), as observed in the 4°C trials.

The main difference observed between temperature treatments was that medium fish were more densely concentrated and occurred closer to the surface at 4°C than at 8°C (average 4.3 cm versus 33.9 cm below the surface, respectively; $P < 0.001$; Fig. 2b). Among large fish, there was no effect of temperature on distribution ($P = 0.164$). At both temperatures large fish were concentrated near the surface in the dark and showed a broad, deeper distribution in the light (Fig. 2c).

DISCUSSION

Discrete-depth sampling of fish and invertebrate larvae using towed nets has become a routine methodology used in fisheries oceanography, as studies seek to determine how position in the water column influences growth, survival, and distribution of offspring. Although discrete-depth field sampling studies provide direct observations of larvae in their environment, their ability to fully describe ontogenetic and environmentally-influenced responses can be limited by sampling circumstances. Laboratory experimentation can aid in determining dispersal patterns through improved understanding of the proximate factors directing vertical movements. Such experiments have

Figure 2. Vertical position of Pacific cod feeding larvae in experimental columns as a function of light level, ontogenetic stage, and water temperature. Groups of fish were exposed to each light level for a 2-h period in a randomized order between 0800 and 1800. The panels represent experiments conducted with small (≤8 mm SL), medium (~10 mm SL), large (≥14 mm SL) size larvae. See Table 1 for specific size and age data. Triangles represent experiments conducted at 4°C; circles represent experiments at 8°C. Points are the average of median fish position in 5–14 replicate columns and error bars represent average 25th and 75th percentiles of fish distribution.
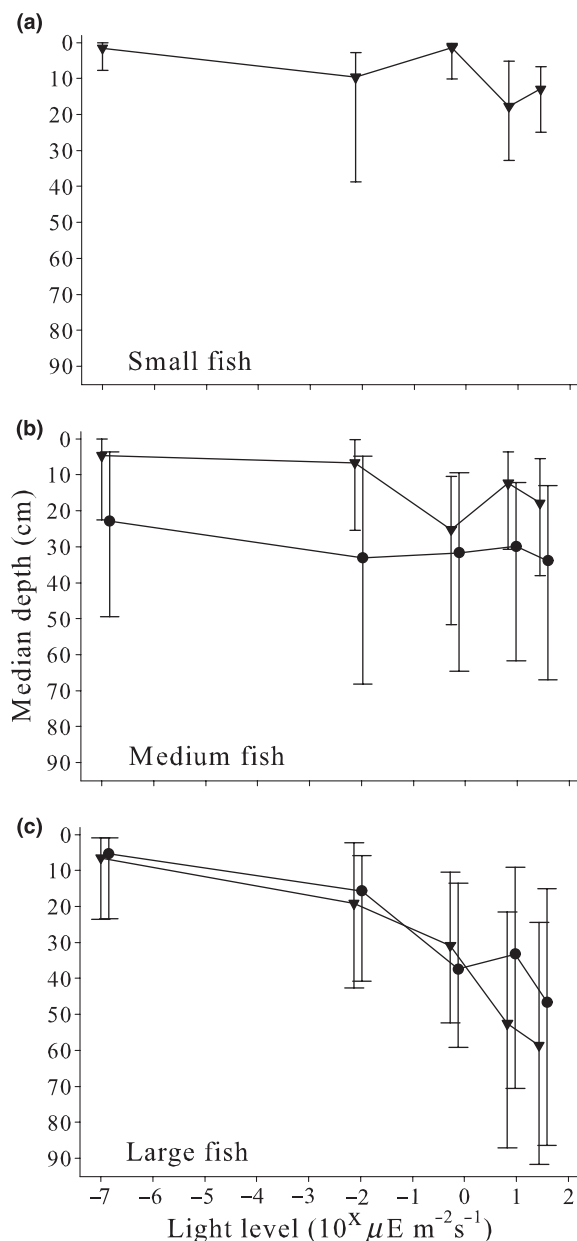
been extensively applied in studying the transport patterns of invertebrate larvae (Forward, 1988), but their application to fish larvae has been more limited (Boehlert and Mundy, 1988; Clay *et al.*, 2004). Our laboratory studies of Pacific cod larvae demonstrated a direct effect of temperature variation on preflexion larvae and an ontogenetic change in the vertical response to light level among postflexion larvae. The vertical movements of early life stages of Pacific cod, as described by these experiments and *in situ* observations, are important to determining oceanic drift patterns and appear to differ from those of co-occurring walleye pollock.

Ontogenetic patterns

Pacific cod eggs are negatively buoyant and semi-adhesive, remaining on or near the sediment surface (Alderdice and Forrester, 1971). This restriction to the benthos is supported by the extreme rarity of cod eggs in extensive plankton sampling of Alaskan coastal waters (Matarese *et al.*, 2003). Hatching occurs 21–26 days after fertilization at 4°C (Forrester and Alderdice, 1966; Laurel *et al.*, 2008). In laboratory experiments, strong surface orientation was observed among yolk-sac larvae at a size of 4–5 mm SL. In depth-stratified collections in the GOA, Pacific cod larvae as small as 4 mm SL were concentrated in surface waters above 45 m (Brodeur and Rugen, 1994; D. Cooper, unpublished data). This surface orientation appears to keep larvae above the level of the developing seasonal thermocline. However, similar depth distributions were observed in years without a developed thermocline, indicating that surface concentration was not solely dependent upon vertical temperature (and density) gradients (Gray, 1996b). Laboratory experiments demonstrated that yolk-sac larvae were neutrally to negatively buoyant, maintaining a vertical position with periodic bouts of oriented swimming.

There was little evidence of vertical movement of preflexion larvae in response to varying light levels in either laboratory experiments or field collections. In experiments with yolk-sac and 'small' feeding stage larvae, depth distribution was independent of light level. In 2 yrs of MOCNESS collections, Brodeur and Rugen (1994) found that weighted mean depths of Pacific cod larvae (≤11 mm SL) were slightly, but not significantly, deeper in night collections than during day collections. Analysis of additional MOCNESS data in the Gulf of Alaska indicates that day–night depth distributions were highly variable and failed to provide strong support for diel changes in depth distribution among preflexion larvae (D. Cooper, unpublished data).
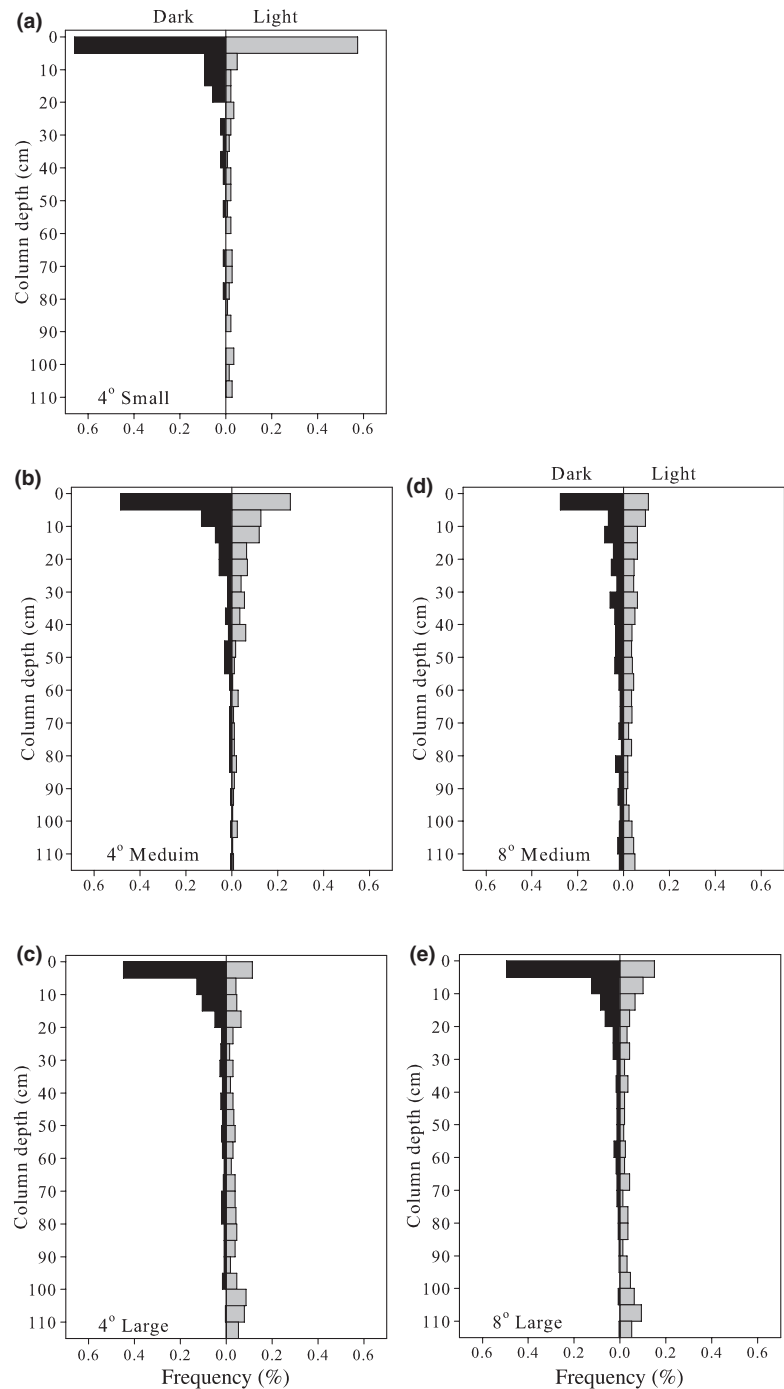
Figure 3. Representative patterns of vertical distribution of Pacific cod feeding larvae in experimental columns in the dark ($<1.0 \times 10^{-7}$ μE m^{-2} s^{-1}) and light (2.75×10^1 μE m^{-2} s^{-1}) at 4°C (left column) and 8°C (right column). Small fish were only tested at 4°C. Size classes are defined in Table 1.

As observed in other species (Lough and Potter, 1993; Kendall *et al.*, 1994; Bradbury *et al.*, 2006), larval Pacific cod exhibited an ontogenetic change in vertical movements in response to light levels. Laboratory experiments demonstrated a change in behavior around the time of flexion (10–17 mm SL, Matarese *et al.*, 1989) after which larval behavior is consistent with a diel vertical migration. Experiments conducted

with medium-sized larvae (8–11 mm SL) at both temperatures showed a modest response to light, with fish generally occurring at shallower depths in the dark. In experiments with large larvae (>15 mm SL), there was a clear pattern of residence at significantly greater depths under higher light levels. The movement between surface waters at low light and deeper waters at high light occurred equally at both 4 and

8°C. These observations suggest that postflexion Pacific cod exhibit a traditional diel vertical migration (Neilson and Perry, 1990). Unfortunately, because Gulf of Alaska field samples included only small preflexion fish, the occurrence of this migration pattern in the field could not be confirmed with independent empirical evidence. Interestingly, these observations contrast with those of Boehlert et al. (1985) for Pacific cod along the Oregon coast. In 1 yr of sampling, Pacific cod larvae averaging 14.2 mm SL (corrected for preservation) were found significantly deeper at night (50–60 m) than during the day (10–20 m). The discrepancy between studies could be the result of population-specific differences in behavioral patterns or interactions with environmental factors.

Environmental influences

Laboratory experiments demonstrated a direct effect of temperature on the vertical behavior of larval Pacific cod. In experiments with medium-sized fish, those reared and tested at 8°C were found significantly deeper than those reared and tested at 4°C. Although small fish were not tested at 8°C, observations in rearing tanks indicated a similar temperature effect on behavior among small feeding stage larvae (personal observations). The strong upward response exhibited at the lower temperatures may reflect a behavioral rule associated with a thermal preference. Because warmer waters (with rare exceptions) predictably overlay cooler waters in marine environments, this behavior would result in movement toward the warmest available waters. In fact, such behavioral rules are considered more reliable than kinesis- or taxis-based responses as they do not depend upon the ability of the larvae to perceive a temperature gradient (Neill, 1979). For example, during field sampling in 1988 the seasonal thermocline had not yet formed (D. Cooper, unpublished data). However, this response would be successful at maintaining fish in the most rapidly warming waters near the surface. Interestingly, as larvae age, vertical responses to light level appear to take precedence over the temperature response, suggesting a change in the ultimate factors regulating vertical positioning in the water column.

Ultimately, the in situ vertical distribution of larval Pacific cod is likely driven by a variety of abiotic and biotic factors acting in concert. Local hydrographic variations may contribute to variations in depth distribution. Differences in salinity could affect buoyancy of yolk-sac stages, or temperature variations might affect metabolic efficiencies, prompting behavioral mitigation. Similarly, biotic forcing factors, such as spatio-temporal variability in the densities of predators or prey, could also prompt different behavioral responses. Future field sampling should be directed toward confirming diel movement patterns among GOA postflexion larvae and determining the depth

Table 3. Comparison of vertical distribution and behavior of early life stages of Pacific cod (Gadus macrocephalus) and walleye pollock (Theragra chalcogramma) in the Gulf of Alaska.

Stage	Pacific cod	Walleye pollock
Spawning sites	Shelf break[*]	Deep basins/channels[*]
Eggs	Demersal[†,‡]	Bathypelagic drifting[§,¶,**]
Yolk-sac larvae	Immediate rise to near-surface[††]	Gradual rise to near-surface[‡‡]
	No diel vertical migration[††,§§]	No diel vertical migration[‡‡]
Feeding larvae	Higher at lower temperatures[††]	Above thermocline[‡‡]
	Diel vertical migration[††]	Diel vertical migration[‡‡,¶¶]
	DVM initiated at 10 mm[††]	DVM initiated at 6 mm[‡‡]
Juveniles	Primarily coastal nurseries[***,†††]	Primarily pelagic[†††,‡‡‡]

[*]Dunn and Matarese (1987).
[†]Thomson (1963).
[‡]Alderdice and Forrester (1971).
[§]Olla and Davis (1993).
[¶]Kendall et al. (1994).
[**]Brodeur et al. (1996).
[††]This study.
[‡‡]Davis and Olla (1994).
[§§]Brodeur and Rugen (1994).
[¶¶]Olla and Davis (1990).
[***]Abookire et al. (2007).
[†††]Laurel et al. (2007).
[‡‡‡]Brodeur and Wilson (1996).

range of migrations and potential effects of other environmental factors.

Comparison with walleye pollock

The vertical distribution patterns of early life history stages of Pacific cod described here differ in significant ways from those of GOA walleye pollock, the dominant gadoid in the region (Table 3). Pacific cod spawn over rocky substrates at depths of 20–200 m, depositing eggs on the substrate at shallower depths than the bathypelagic eggs of walleye pollock, which spawn in deep basins and along the shelf break (Dunn and Matarese, 1987). Differences in spawning site and egg buoyancy may be linked to transport requirements for reaching primary nursery habitats. Juvenile Pacific cod primarily inhabit shallow coastal embayments with submerged macrophytes (Abookire *et al.*, 2007; Laurel *et al.*, 2007) whereas juvenile walleye pollock are primarily pelagic (Brodeur and Wilson, 1996).

After hatching, both species migrate upward to surface waters. While this ascension occurs immediately for Pacific cod, it appears more gradual for walleye pollock. Interestingly, during the feeding larval stage, the two species appear to converge upon a similar behavioral strategy of diel vertical migration (although walleye pollock appear to initiate migrations at a smaller size). This convergence of behavior suggests that shared constraints such as foraging requirements (Porter *et al.*, 2005) or predator avoidance (rather than transport requirements) are the ultimate drivers of vertical distribution of this stage in these species (Zaret and Suffern, 1976; Hays, 2003).

CONCLUSIONS

The combination of manipulative laboratory experiments with discrete-depth field sampling of larvae represents a powerful approach to determining the behavior of early life stages as they relate to survival and dispersal. As observed for other well studied species, the vertical distribution of Pacific cod larvae in the ocean reflects a multi-faceted behavioral regulation that depends upon ontogenetic stage, water temperature, and light level. Future studies will refine our understanding of behavioral patterns based on responses to prey availability and turbulence as well as evaluate potential differences between Gulf of Alaska and Bering Sea stocks. Knowledge of the factors regulating vertical distribution will significantly improve the ability to model drift patterns of Pacific cod larvae with existing three-dimensional models of Gulf of Alaska and Bering Sea flow fields (Hermann and Stabeno, 1996). These analyses will be instrumental in determining the degree to which spawning activity is related to localized recruitment in Gulf of Alaska Pacific cod.

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