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The effects of thin layers on the vertical distribution of larval Pacific herring, *Clupea pallasi*

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Abstract

Temporal and spatial heterogeneity of resources is likely to have dramatic effects on the behaviors of zooplankton and ichthyoplankton, which in turn are likely to have strong effects on ecological dynamics such as predation, growth, and mating. The objective of this study was to determine whether vertically thin layers of extreme prey concentration affect the vertical distribution of larval Pacific herring (*Clupea pallasi*). We employed 2-m tall experimental tanks equipped with video cameras that scanned the vertical extent of the tanks to investigate the effects of thin layers on the vertical distribution of 5- and 10-day-old herring larvae. Three treatments were established: (1) a thin layer of prey (rotifers, *Brachionus plicatilis*) through density (salinity) stratification, (2) homogeneous vertical distribution of both prey and density, and (3) density (salinity) stratification, but with a homogeneous distribution of prey. We found that in all treatments the majority of larval herring were at the surface, near the light, despite the absence of a peak in rotifer abundance at this depth in some instances. However, there were also clear effects of the thin layers—secondary subsurface peaks in herring abundance occurred at the mid-depths in the stratified tanks, in and around the thin layers. In addition, our results provide some evidence that thin layers specifically, rather than prey patches generally, influence the vertical distribution of larval herring, i.e., larvae may use the physical properties of thin layers to locate and distribute themselves, instead of reacting solely to the prey patches. Thus thin layers can affect directly the vertical distribution of larval herring, and perhaps indirectly their horizontal

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distribution, as herring larvae live in environments (e.g., estuaries) where advective transport is also often vertically heterogeneous.

Keywords: Ichthyoplankton; Larval fish behavior; Pacific herring (*Clupea pallasi*); Patchiness; Thin layer; Vertical distribution; Zooplankton

1. Introduction

Over a wide range of species, habitats, and scales, plankton are spatially variable, or patchy. Many field and experimental investigations have found patchy distributions of planktonic prey to be important for survival, growth, and recruitment of zooplankton and/or ichthyoplankton predators (e.g., Lasker, 1975; Lasker and Zweifel, 1978; Munk and Kiorboe, 1985; McClatchie, 1986). In addition, many models simulating planktonic predator–prey interactions show patchy prey distributions to be important for predator survival (Heath, 1989; Davis et al., 1991; Letcher and Rice, 1997).

One example of patchiness is thin layers, which are vertical strata within the water column on the order of tens of cm in thickness (Desiderio et al., 1993; Cowles et al., 1998; Holliday et al., 1998; Dekshenieks et al., 2001), with extreme biological, chemical and/or physical properties. Thin layers can extend horizontally for up to several kilometers and persist for as long as several days to several weeks (Nielsen and Bjornsen, 1990; Bjornsen and Nielsen, 1991; Rines et al., 2002). Thin layers are most often found in highly stratified waters.

Thin layers are formed through biological or physical processes, or through a combination of the two. These processes may include shear (Eckart, 1940; Franks, 1995), the disintegration of a thicker layer into a thin layer (Osborn, 1998), the sinking and accumulation of biological particles at micropycnoclines (Franks, 1995), the horizontal intrusion of water masses (Osborn, 1998), and preferential grazing (Franks, 1995).

With recent improvements in oceanographic sampling equipment and deployment techniques it has become possible to investigate thin layers (Cowles et al., 1993; Desiderio et al., 1993; Dekshenieks et al., 2001). Most studies investigating thin layers have focused on the development of sampling devices and the documentation of physical and biological thin layers (Pieper and Holliday, 1984; Desiderio et al., 1993; Cowles et al., 1998; Holliday et al., 1998; Jaffe et al., 1998), or chemical aspects of these layers (Hanson and Donaghay, 1998), and only hypothesize as to the ecological importance of thin layers. Although some studies have been conducted on the effects of phytoplankton thin layers on zooplankton grazers (Saiz et al., 1993; Bochdansky and Bollens, in press) they are few, and we are aware of no published studies that investigate the interactions between zooplankton and/or ichthyoplankton predators and thin layers of zooplankton prey.

The interactions between ichthyoplankton and thin layers is of particular interest because of (i) the prevalence of ichthyoplankton in bays and estuaries where thin layers are expected to occur, (ii) the commercial and ecological importance of many fish species, and (iii) the dependence of many larval fish species on prey such as copepods and their nauplii that might be expected to be found within thin layers. In addition, prey patchiness

has been shown to be important to larval fish survival (Lasker, 1975; Peterman and Bradford, 1987). Food limitation as a major source of larval fish mortality was suggested by Hjort (1914) and has been supported by many studies since (McGurk, 1984; Leggett, 1986), including some that indicate that the source of this mortality is likely due to predation rather than starvation per se (e.g., Houde, 1987; Purcell, 1990). It has been suggested that prey patchiness, by providing areas of high prey concentration, is a mechanism by which larval fish survive despite otherwise low prey concentrations in situ (Hunter and Thomas, 1974; Lasker, 1975; Houde and Schekter, 1978; Lasker, 1985).

In addition to directly influencing larval herring survival by enhancing feeding, thin layers may also indirectly influence survival by affecting the vertical distribution of larval herring in relation to other sources of mortality (e.g., predators, UV radiation). Thus, understanding the relationship between thin layers and larval fish, especially for ecologically or commercially important species such as Pacific herring (*Clupea pallasi*) is of great value. However, previous field studies of larval herring in relation to prey distribution were not relevant to thin layers because the sampling scale was too large (Sjoblom and Parmanne, 1978; Fortier and Leggett, 1983; Munk et al., 1989). Nor have any laboratory investigations examined the impacts of thin layers of prey on the vertical distribution of ichthyoplankton.

The objective of this study is to investigate, through laboratory experiments, the effect of thin layers of zooplankton prey on the vertical distribution of larval Pacific herring (*C. pallasi*), including how these effects vary with the age of the larval herring, and how this distribution is affected by physical versus biological aspects of thin layers.

2. Materials and methods

2.1. Rearing the herring

Fertilized Pacific herring eggs were obtained from Bodega Bay Marine Laboratories (Bodega Bay, CA) in February 2001, and January and February 2002. Embryos and larvae were kept in an environmentally controlled room at 12 °C with a 100 W light bulb providing a light/dark cycle of local sunrise and sunset. Embryos and larvae were kept in water with a salinity of 15 psu, which is very near the salinity of 16 psu shown to provide optimal survival (Alderdice and Velson, 1971). Embryos were covered by 1 in. of water and upon hatching larvae were separated by hatch date and transferred to 5-gal aquaria at an initial density of 50 l^{-1}. Daily water exchanges were made of 100% for embryos and 50% for larvae.

Three-day-old herring larvae were fed 0.3 rotifers (*Brachionus plicatilis*) ml^{-1}, 4-day-old larvae were given 0.6 rotifers ml^{-1}, and 5-day-old and older larvae were given 1.2 rotifers ml^{-1}. Those ages were chosen according to evidence that larval herring begin to practice feed during the yolk sac stage (Blaxter, 1962; Rosenthal and Hemple, 1970; Alderdice and Velson, 1971). Prey densities were chosen based upon evidence of good survivorship of larval herring at a prey density of 0.3 *Artemia* ml^{-1} (Werner and Blaxter, 1980), and the conversion from an *Artemia* density to a rotifer density was based upon their comparable nutritional values and relative sizes (Hoff and Snell, 1993). The

nutritional properties of the rotifers were assured by providing them with diets of Roti-rich® brand liquid invertebrate food and *Nannochloropsus oculata* in 2001, and yeast and DC Super Selco® brand supplement in 2002.

2.2. Experimental design and setup

Ten experiments were conducted, five each on two age classes of larval herring: young (5-day-old) and older (10–12-day-old). Four columnar Plexiglas® tanks (200×7.6×5.1 cm) located in a cold room set to 12 °C were used for each experiment. All tanks were lit with a 100 W GE grow bulb outfitted with a light diffuser, and local dawn and dusk cycles were simulated as closely as possible. On one occasion the visible light intensity was measured at the surface and the bottom of each tank using an LI-COR underwater quantum sensor, model #LI-192SA. Averaged across tanks the visible light intensity at the surface was 0.58×10^{15} Quanta s^{-1} cm^{-2} and at the bottom was 0.072×10^{15} Quanta s^{-1} cm^{-2}. These light levels are approximately 11.6% and 1.4% of natural visible radiation at noon during winter at the Romberg Tiburon Center (122°35.30′W; 37°55.65′N), which corresponded to depths of approximately 2.4 and 4.8 m in San Francisco Estuary, respectively, representing the lower half of the euphotic zone, which extended to a depth of approximately 5.2 m (Speekmann et al., 2000).

Prior to each experimental setup the tanks were rinsed with fresh water and soaked in deionized (D.I.) water for at least 6 h. Thin layers were created through density stratification achieved through salinity manipulation: three layers were established of salinities 12 psu (0–68 cm), 15 psu (the thin layer, 68–93 cm), and 18 psu (93–200 cm). While establishing salinity stratification, mixing was minimized by slowly pouring water of the appropriate salinity sequentially through each of eight evenly spaced valves on the side of the tank (at depths of 3, 29, 57, 85, 113, 140, 168, and 197 cm) from the lowest to highest valve, such that newly added water never fell more than 28 cm to the water's surface. Homogeneous salinity treatment tanks were filled in a similar manner, but more quickly and with water of salinity 15 psu. Tanks were filled simultaneously over ca. 3 h in near darkness. Rotifers were added to the water prior to filling the experimental tanks and introduced along with the water during the filling process. In cases where a thin layer of highly concentrated rotifers was desired, all rotifers were added to the water that was used to fill the mid-depths of the tank (68–93 cm). In cases where a homogenous distribution of rotifers was desired, the rotifers were mixed equally into the total volume of water used to fill the tank. The initial placement of the rotifers was the only technique employed to control rotifer distributions. Each experiment began with the introduction of 10 larval herring to the top of each tank, 1 h prior to dawn. The duration of each experiment was 11 h.

Ten experiments were undertaken (Table 1). The first six experiments were to determine if the distribution of larval herring is affected by a biological (high concentration of rotifer prey) and physical (salinity stratification) thin layer. Despite nearly identical experimental designs, experiments 1 and 2, and experiments 3 through 6, are separated for analysis due to differing sampling techniques, as described below. The purpose of experiments 7 through 10 was to separate the effects of biological and physical thin layers on the vertical distribution of larval herring.

Table 1
Summary of experiments conducted

Treatments	Herring age (days)	Experiment date
Experiment 1		
Homogeneous, Physically and biologically stratified	5	March 19, 2001
Experiment 2		
Homogeneous, Physically and biologically stratified	10	March 24, 2001
Experiment 3		
Homogeneous, Physically and biologically stratified	5	January 17, 2002
Experiment 4		
Homogeneous, Physically and biologically stratified	5	January 23, 2002
Experiment 5		
Homogeneous, Physically and biologically stratified	10	January 28, 2002
Experiment 6		
Homogeneous, Physically and biologically stratified	10	February 1, 2002
Experiment 7		
Homogeneous, Physically stratified only	12	February 22, 2002
Experiment 8		
Homogeneous, Physically stratified only	12	February 23, 2002
Experiment 9		
Homogeneous, Physically stratified only	5	March 6, 2002
Experiment 10		
Homogeneous, Physically stratified only	5	March 7, 2002

The first two experiments included one using young herring (5-day-old) (experiment 1) and the other using older herring (10-day-old) (experiment 2). These were carried out on March 19, 2001 and March 24, 2001, respectively. For each experiment all tanks were filled with 1 μm bag-filtered San Francisco Estuary water with salinities adjusted with D.I. water, 16,000 rotifers and 200 ml of *N. oculata* (as food for the rotifers). Two tanks were prepared with a homogeneous salinity profile and homogeneous distributions of rotifers and *N. oculata*, creating an expected rotifer density of 2 ml^{-1} throughout (“homogeneous tanks”). The other two tanks were prepared with a stratified salinity profile and with the mid-layer containing all of the *N. oculata* and rotifers, creating expected rotifer densities of 16 ml^{-1} in the mid-layer and 0 ml^{-1} in the other two layers (“stratified tanks”) (Table 1).

The setup of the third through sixth experiments was similar to that of experiments 1 and 2, except that D.I. water mixed with Instant Ocean® was used to fill the tanks, and *N. oculata* was not included. Experiments 3 and 4 were conducted on young (5-day-old) larvae on January 17 and 23, 2002, respectively, and experiments 5 and 6 were conducted on older (10-day-old) larvae on January 28 and February 1, 2002, respectively (Table 1).

Experiments 7 through 10 each included two tanks that were homogeneous, as in experiments 3 through 6 (including a homogeneous salinity profile and a homogeneous distribution of rotifers), and two tanks that were stratified with respect to salinity only, with a homogeneous distribution of 2 rotifers ml^{-1} throughout (“physically stratified only” tanks). Experiments 7 and 8 were conducted on older (12-day-old) larvae on February 22 and 23, 2002, respectively, and experiments 9 and 10 were conducted on young (5-day-old) larval herring on March 6 and 7, 2002, respectively (Table 1).

Persistent salinity stratification was achieved, with the salinities of different layers within all tanks maintained throughout each experiment (Figs. 1–3). The apparent deepening of haloclines over time is an artifact of the removal of some water (taken for rotifer counts) before the final temperature and salinity measurements were taken. Although temperature did vary between experiments (11.3 to 15.3 °C), it varied no more than 2.7 °C over the course of a given experiment.

2.3. Sample collection and analysis

During experiments 1 and 2 the vertical position of the larval herring was monitored once per hour by eye for a total of 10 h and that of rotifers was monitored by collecting 20 ml samples once every 4 h from the eight evenly spaced valves and analyzed microscopically as described below.

In an effort to minimize disturbance and to allow frequent, non invasive sampling of the rotifer distribution, an experimental vertical migration apparatus similar to that used by Batty (1983, 1994) was used to determine the vertical distribution of larvae and rotifers during experiments 3 through 10. Each tank was set up with a monochrome video camera (Cohu) with a macro/zoom lens. Light for each camera was provided by an infrared light-emitting diode (LED) and a plano-convex lens (used to columnate the light from the LED) was placed between the LED and the tank. The camera and light system was mounted in a motorized linear bearing/rail system and was run up the length of the tank, with the lens zoomed out, to monitor the vertical distribution of the larval herring, and run down the length of the tank, with the lens zoomed in, to monitor the vertical distribution of rotifers. The depth of field of the camera was in excess of the depth of the tank. Video was recorded on videocassette time-lapse recorders (VCR, Panasonic, model AG-6124) with a date/time recorder. The motor, camera, lights and VCR were manually controlled with a switch located outside of the experimental room. The system was turned on once an hour, and took 6 min to traverse and record the entire length of the tank.

Prior to the start and upon completion of each experiment 20 ml samples were taken from each valve on each tank to be used to truth the rotifer counts from the video, i.e., to convert these counts to numbers of rotifers ml^{-1}. These samples were counted by eye, using a dissecting microscope. Salinity and temperature profiles were taken for each tank prior to and immediately following each experiment with a hand-held oxygen, conductivity, salinity and temperature system (YSI®, model 85).

Video recordings of both rotifers and herring were analyzed visually. In the case of the herring the depth of each organism was noted. In the case of the rotifers the video was stopped at each 10 cm depth increment and the total number of rotifers visible was recorded. In all instances the sample time and date were also logged.

Fig. 1. Representative rotifer and herring distributions (as proportions) from experiments 1 and 2 (t=5 and t=9 h (±1 h)) and initial and final salinity profiles for experiments with young (top panel) and older (bottom panel) herring larvae. Stratified (diamonds) and homogeneous (squares) treatments are represented in all graphs.

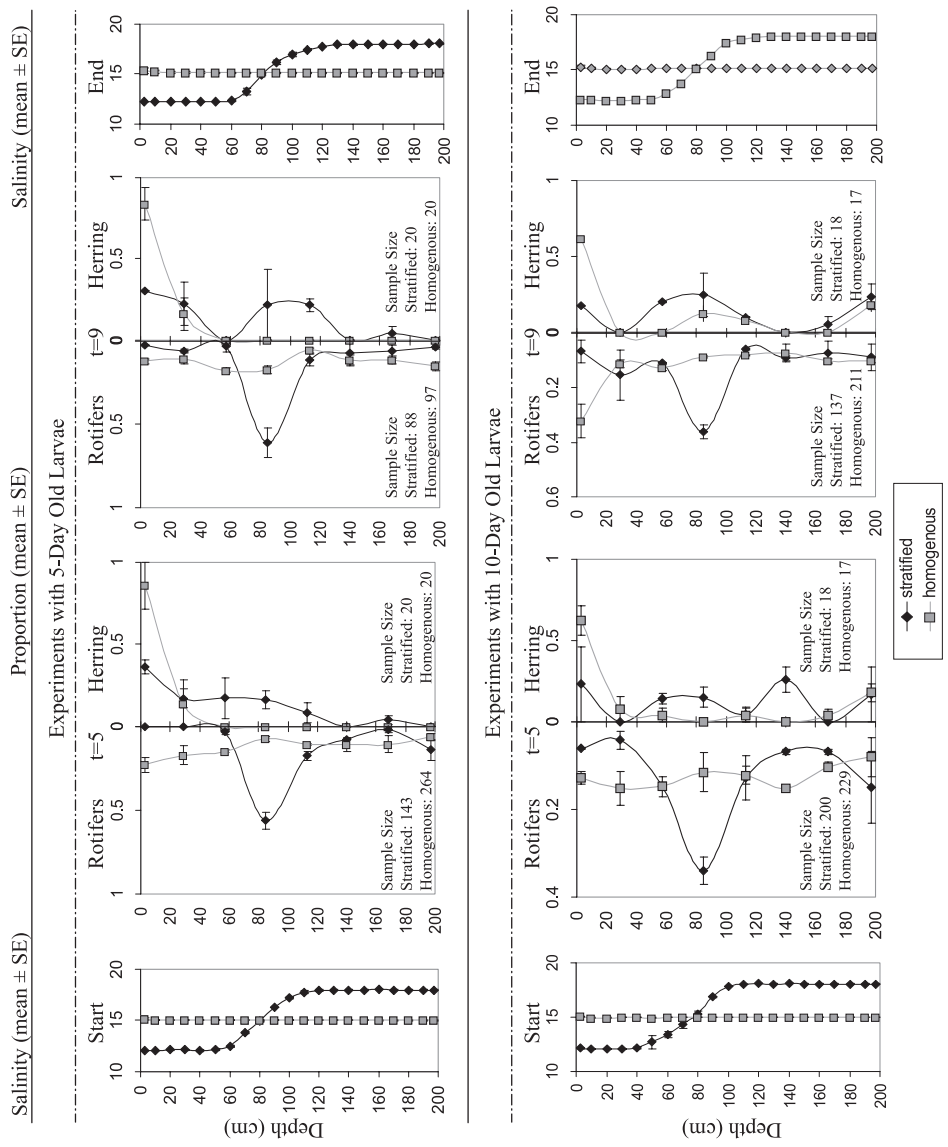

Salinity (mean ± SE)
Proportion (mean ± SE)
Salinity (mean ± SE)
Experiments with 5-Day Old Larvae
Experiments with 10-Day Old Larvae
Start
Rotifers
Herring
Rotifers
Herring
End
t=5
t=9
Depth (cm)
Sample Size
Stratified: 143
Homogenous: 264
Sample Size
Stratified: 20
Homogenous: 20
Sample Size
Stratified: 88
Homogenous: 97
Sample Size
Stratified: 20
Homogenous: 20
Sample Size
Stratified: 200
Homogenous: 229
Sample Size
Stratified: 18
Homogenous: 17
Sample Size
Stratified: 137
Homogenous: 211
Sample Size
Stratified: 18
Homogenous: 17
stratified
homogenous

Table 2
Summary of results from repeated measures ANOVAs for proportions of rotifers, with time as the repeated measures factor

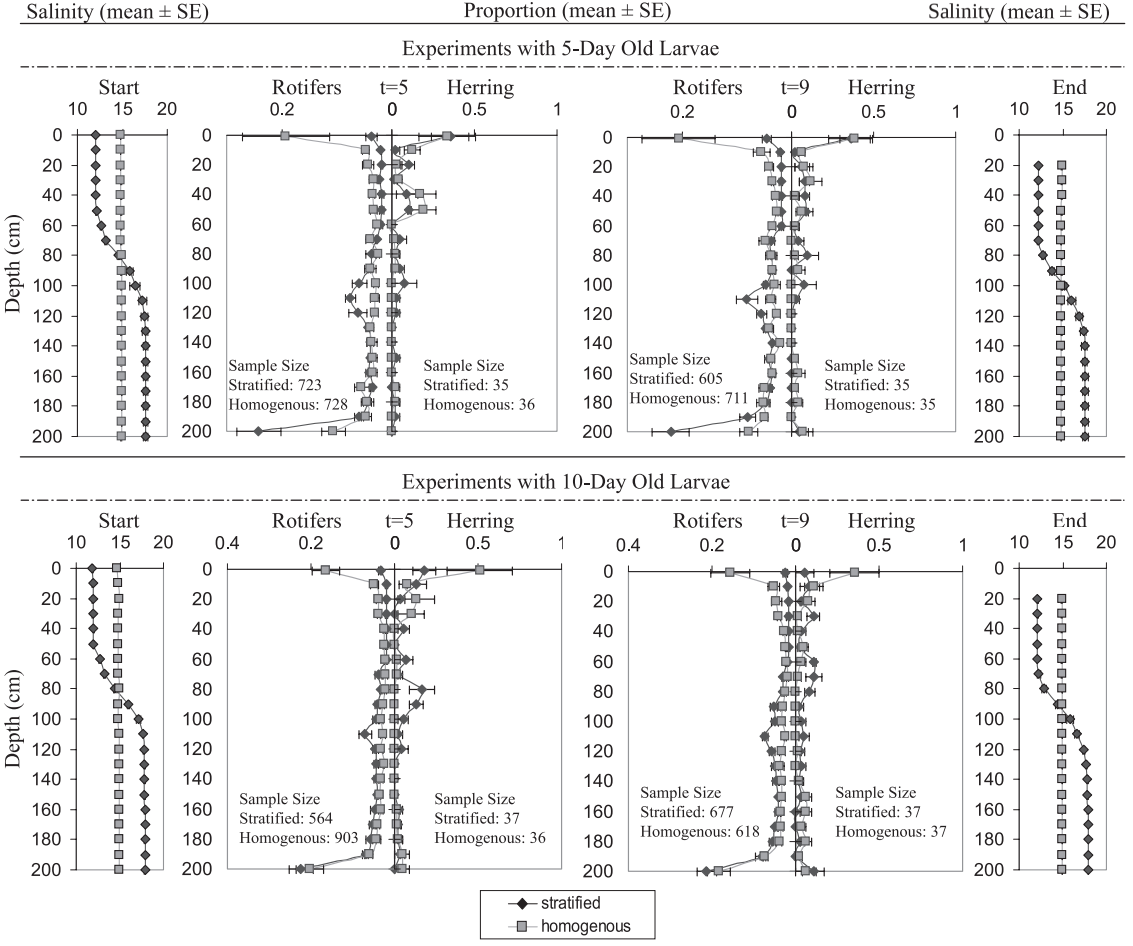
	Degrees of freedom	MS	*F* value	*P* value
Experiments 1–2 and 3–6 (setup effects)				
Time×Setup	2.927	0.00007095	0.090	0.963
Time×Setup×Trtmt	2.927	0.003248	4.117	0.007**
Time×Setup×Depth	55.607	0.001332	1.688	0.001**
Time×Setup×Trtmt×Depth	55.607	0.001428	1.810	<0.001***
Setup	1	0.01435	4.481	0.035*
Setup×Trtmt	1	0.01456	4.544	0.033*
Setup×Depth	19	0.01164	3.634	<0.001***
Setup×Trtmt×Depth	19	0.01846	5.762	<0.001***
Experiments 1–2				
Time	1.726	0.05479	2.716	0.079
Time×Trtmt	1.726	0.02851	1.413	0.248
Time×Depth	10.356	0.04953	2.456	0.011*
Time×Trtmt×Depth	10.356	0.03658	1.813	0.066
Trtmt	1	0.205	2.562	0.115
Depth	6	0.564	7.057	<0.001***
Trtmt×Depth	6	0.670	8.376	<0.001***
Experiments 3–6				
Time	2.903	0.001155	1.313	0.269
Time×Trtmt	2.903	0.002611	2.969	0.033*
Time×Depth	55.149	0.003492	3.971	<0.001***
Time×Trtmt×Depth	55.149	0.002764	3.143	<0.001***
Trtmt	1	0.03144	9.532	0.002**
Depth	19	0.07332	22.228	<0.001***
Trtmt×Depth	19	0.07408	22.458	<0.001***
Experiments 7–10				
Time	2.855	0.0006933	0.905	0.434
Time×Trtmt	2.855	0.001747	2.281	0.081
Time×Depth	54.242	0.002679	3.498	<0.001***
Time×Trtmt×Depth	54.242	0.0006085	0.794	0.885
Trtmt	1	0.00004478	0.014	0.904
Depth	19	0.03228	10.400	<0.001***
Trtmt×Depth	19	0.01642	5.291	<0.001***

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

2.4. Data analysis

To account for possible bias in our video sampling of rotifers, the relationship between rotifer density resulting from the video observations and the valve samples were compared

Fig. 2. Representative rotifer and herring distributions (as proportions) from experiments 3 through 6 (t=5 and t=9 h (±1 h)) and initial and final salinity profiles for experiments with young (top panel) and older (bottom panel) herring larvae. Stratified (diamonds) and homogeneous (squares) treatments are represented in all graphs.


Salinity (mean ± SE)
Proportion (mean ± SE)
Salinity (mean ± SE)
Experiments with 5-Day Old Larvae
Start
Rotifers t=5 Herring
Rotifers t=9 Herring
End
Depth (cm)
Sample Size Stratified: 723 Homogenous: 728
Sample Size Stratified: 35 Homogenous: 36
Sample Size Stratified: 605 Homogenous: 711
Sample Size Stratified: 35 Homogenous: 35
Experiments with 10-Day Old Larvae
Sample Size Stratified: 564 Homogenous: 903
Sample Size Stratified: 37 Homogenous: 36
Sample Size Stratified: 677 Homogenous: 618
Sample Size Stratified: 37 Homogenous: 37
stratified
homogenous

(using data pooled from a subset of five of the experiments) for each tank using a regression run in SPSS® version 10.0. Cook's D statistics were calculated to arrive at robust parameter estimates using SAS® statistical analysis software system for windows, version 8, and outliers were removed based on the conservative measure that any point with a Cook's D value greater than $4/n$ was removed (Fry, 1993). The resulting regression lines, one for each tank, were used to convert the density of rotifers counted from the video at each depth to the number of rotifers (number ml^{-1}) present at each depth, and these density values were used in all further statistical analyses. Resulting data on the vertical distribution of rotifers and larval herring were used to calculate proportions of water column total rotifers and herring occurring in each 10 cm depth bin, and these were transformed using the standard arcsine square root transformation for proportions (Zar, 1999) for all subsequent statistical analyses.

Regressions comparing the abundance of larval herring to that of rotifers at a number of depths were also run in SPSS® version 10.0.

Repeated measures ANOVAs were run in SPSS® version 10.0 using a type III sums of squares and an alpha level of p=0.05. The Greenhouse–Geiser correction was used for any deviations from the assumption of sphericity (resulting in adjusted degrees of freedom, which are sometimes not whole numbers). The sample design was fixed, such that the variables in each group of experiments were the same. Data were separated for analysis such that experiments 1 and 2 were grouped, experiments 3 through 6 were grouped, and experiments 7 through 10 were grouped (Table 1). In the case of experiments 1 and 2, this was due to unique sampling techniques (visual assessments only). In the cases of experiments 3 through 6 and experiments 7 through 10, this was due to different experimental design (treatments) and significant differences in resulting rotifer distributions between experiments 3 through 6 and 7 through 10 (Table 2). A separate ANOVA was run for each group of experiments on both rotifer and herring distributions. In all cases, time was included as the repeated measure, and between subjects factors included herring age, treatment, and depth bin. In order to meet the assumption of independence the bottom-most depth bin was not included, as the proportion of organisms in this depth bin could be determined by the sum of the proportions of organisms in all other depth bins within a given tank, thus only 19 of each tank's twenty 10-cm depth bins were included for analysis.

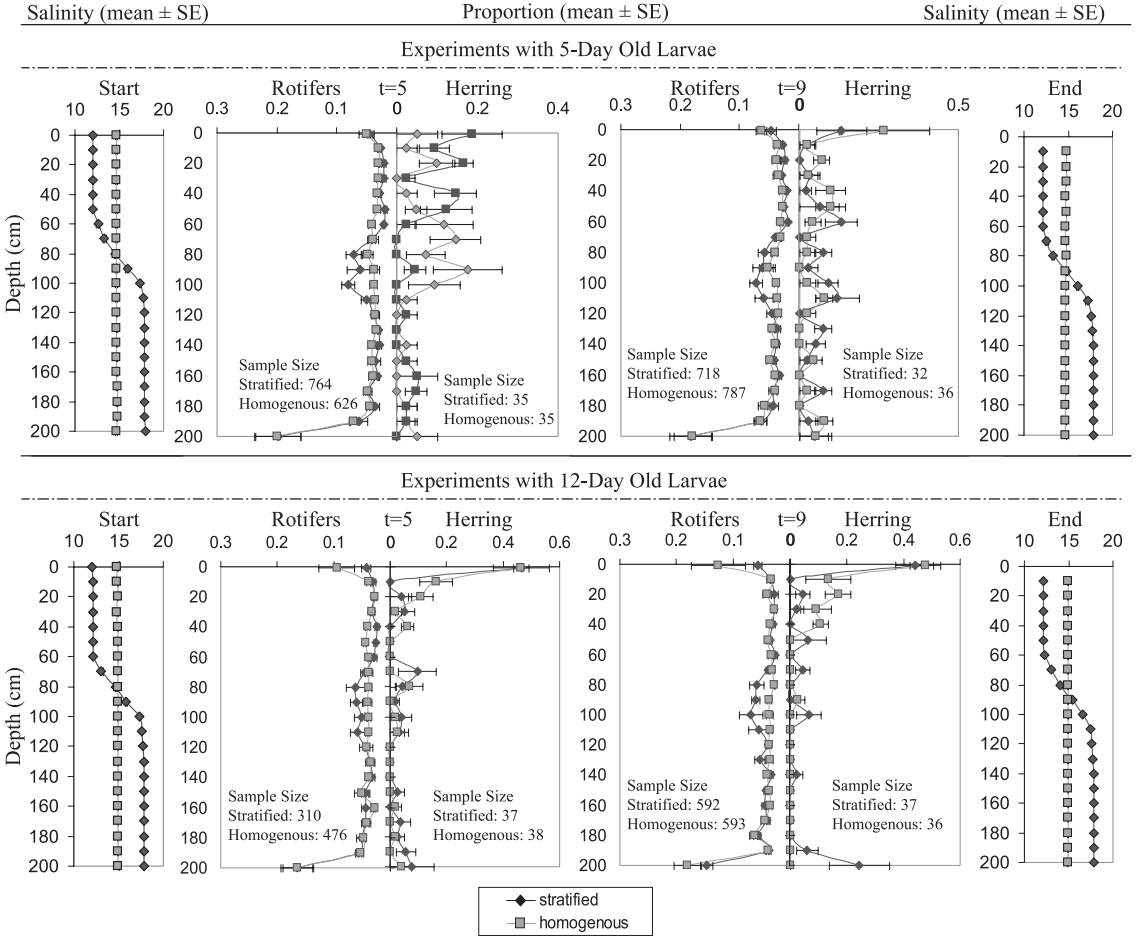
It should be noted that all figures presented include only a representative subset of the data that was included in the statistical analyses.

3. Results

3.1. Rotifers

In all analyses there was a significant treatment and depth interaction. The rotifer distributions in experiments 1 and 2 (which included stratified and homogeneous treat-

Fig. 3. Representative rotifer and herring distributions (as proportions) from experiments 7 through 10 (t=5 and t=9 h (±1 h)) and initial and final salinity profiles for experiments with young (top panel) and older (bottom panel) herring larvae. Stratified (diamonds) and homogeneous (squares) treatments are represented in all graphs.


Salinity (mean ± SE)
Proportion (mean ± SE)
Salinity (mean ± SE)
Experiments with 5-Day Old Larvae
Start
Rotifers
t=5
Herring
Rotifers
t=9
Herring
End
Depth (cm)
Sample Size
Stratified: 764
Homogenous: 626
Sample Size
Stratified: 35
Homogenous: 35
Sample Size
Stratified: 718
Homogenous: 787
Sample Size
Stratified: 32
Homogenous: 36
Experiments with 12-Day Old Larvae
Sample Size
Stratified: 310
Homogenous: 476
Sample Size
Stratified: 37
Homogenous: 38
Sample Size
Stratified: 592
Homogenous: 593
Sample Size
Stratified: 37
Homogenous: 36
stratified
homogenous

ments) were mostly as would be predicted based on experimental setup. There were more rotifers in the surface and near the bottom in the homogeneous tanks, and more rotifers at mid-depth in the stratified tanks (Fig. 1, Table 2). Rotifer distributions in experiments 3 through 6 (which also included stratified and homogeneous treatments, but automated video sampling) were similar to those in experiments 1 and 2. Again, there were significant differences in rotifer distributions between treatments, with a higher abundance of rotifers at the surface in the homogeneous tanks, and a higher abundance at mid-depth in the stratified tanks (however, it should be noted that this mid-depth peak in rotifer abundance was slightly deeper than that in experiments 1 and 2 [Fig. 2, Table 2]).

Unexpectedly, experiments 7 through 10 (in which we attempted to create a physically stratified (but biologically homogeneous) treatment, along with a homogeneous treatment) also had significant differences in rotifer distributions between treatments. There were slightly more rotifers at the surface in the homogeneous tanks, and more rotifers at the mid-depths in the physically stratified tanks (Fig. 3, Table 2).

There were significant time and depth interactions in all analyses, such that there were more rotifers at the surface, and fewer rotifers at mid-depths over time (Table 2).

3.2. Larval herring

The vertical distribution of larval herring was significantly different between treatments in all analyses (significant treatment×depth interaction). In comparing homogeneous and stratified treatments from experiments 1 and 2, herring were more abundant near the surface in the homogeneous tanks and more abundant at mid-depths in the stratified tanks (Fig. 1, Table 3). Similar results occurred in experiments 3 through 6 as well, where there were more herring toward the surface in the homogeneous tanks, and more herring at mid-depths in the stratified tanks than in the homogenous tanks (Fig. 2, Table 3). In experiments 1 and 2 and experiments 3 through 6, 5-day-old and 10–12-day-old larvae behaved similarly (i.e., there were no significant age effects; Table 3; Figs. 1 and 2).

Finally, the herring distribution in experiments 7 through 10 (which were set up to include a physically stratified (but biologically homogeneous) treatment and a homogeneous treatment) was the only instance in which distributions varied depending upon treatment and also larval age. In the case of the younger larvae, there were more at surface depths and towards the bottom in the homogeneous treatment, and more at mid-depths in the physically stratified treatment, however there was a great deal of variance between experiments. In the case of the older larvae again there were more herring at the surface in the homogeneous treatments, however there was not a higher abundance of larvae toward the bottom. But, as with the younger larvae there was a higher abundance of older larvae at mid-depth in the physically stratified tanks than in the homogenous tanks (Fig. 3, Table 3).

In experiments 1 and 2, and 3 through 6 there were significant differences in herring distributions due to the interaction between age and depth, however there was no clear pattern (Figs. 1 and 3, Table 3). In addition, the interaction between time and depth was only significant for experiments 3 through 6, but here too there was no clear pattern (Table 3).

To summarize our results, all analyses indicated remarkably similar rotifer and herring distributions, but with markedly different distributions between treatments. The larval herring distributions in experiments 3 through 6 and experiments 7 through 10 included

Table 3
Summary of results from repeated measures ANOVAs for the proportions of herring, with time as the repeated measures factor

	Degrees of freedom	MS	*F* value	*P* value
Experiments 1–2				
Time×Trtmt	5.381	0.007847	0.155	0.983
Time×Depth	32.286	0.06303	1.247	0.189
Time×Age	5.381	0.02050	0.406	0.857
Time×Trtmt×Depth	1.317	0.04079	0.807	0.759
Time×Trtmt×Age	5.381	0.005396	0.107	0.993
Time×Depth×Age	32.286	0.06474	1.281	0.163
Time×Trtmt×Depth×Age	32.286	0.04634	0.917	0.600
Depth	6	3.428	38.715	<0.001***
Trtmt×Depth	6	2.060	23.267	<0.001***
Trtmt×Age	1	0.01411	0.163	0.690
Depth×Age	6	0.293	3.307	0.014*
Trtmt×Depth×Age	6	0.07129	0.805	0.574
Experiments 3–6				
Time×Trtmt	8.278	0.003806	0.161	0.996
Time×Depth	157.277	0.03329	1.410	0.001**
Time×Age	8.278	0.003558	0.151	0.997
Time×Trtmt×Depth	157.277	0.02419	1.025	0.405
Time×Trtmt×Age	8.278	0.002705	0.115	0.999
Time×Depth×Age	157.277	0.02484	1.052	0.320
Time×Trtmt×Depth×Age	157.277	0.02785	1.179	0.070
Depth	19	1.650	16.704	<0.001***
Trtmt×Depth	19	0.257	2.601	<0.001***
Trtmt×Age	1	0.02459	0.249	0.618
Depth×Age	19	0.127	1.282	0.196
Trtmt×Depth×Age	19	0.08195	0.830	0.670
Experiments 7–10				
Time×Trtmt	8.564	0.004555	0.198	0.993
Time×Depth	162.719	0.02524	1.098	0.196
Time×Age	8.564	0.008762	0.381	0.939
Time×Trtmt×Depth	162.719	0.02669	1.161	0.087
Time×Trtmt×Age	8.564	0.004365	0.190	0.994
Time×Depth×Age	162.719	0.02577	1.121	0.148
Time×Trtmt×Depth×Age	162.719	0.02630	1.144	0.110
Depth	19	1.436	29.898	<0.001***
Trtmt×Depth	19	0.275	5.717	<0.001***
Trtmt×Age	1	0.03201	0.666	0.415
Depth×Age	19	0.667	13.884	<0.001***
Trtmt×Depth×Age	19	0.08158	1.698	0.037*

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

peaks in abundance at the surface in all treatments, as well as peaks in the stratified treatments within the mid-salinity zone. In experiments 1 and 2 the only rotifer peak was in the stratified tanks centered within the mid-salinity layer, and peaks in herring

abundance occurred at the surface in both treatments, and in the mid-salinity zone in the physically and biologically stratified treatment. In experiments 3 through 6, and experiments 7 through 10 the highest proportions of rotifers in both the stratified and homogeneous tanks were at the bottom, but when comparing treatments there were more rotifers at the surface in the homogeneous tanks, and toward the middle of the tank in the stratified tanks. However, in experiments 3 through 6 the middle rotifer peak in the stratified tanks was mostly just below the mid-salinity layer, while in experiments 7 through 10 it was centered within the mid-salinity layer.

4. Discussion

The vertical distribution of herring larvae was not affected by larval age, within the range of ages tested here. This is not surprising when considering the feeding behaviors, sinking and swimming rates, and behavioral responses to physical factors by larvae of these ages. First, although larval feeding behaviors and rates of swimming and sinking vary with size (Batty, 1987), larvae of these ages tend to be of similar length and have similar swimming velocities (Rosenthal and Hemple, 1970). In addition, although 5-day-old larvae still have a yolk-sac, they do feed exogenously (Blaxter, 1962; Rosenthal and Hemple, 1970; Alderdice and Velson, 1971) and so both of these ages of larvae are likely to be similarly affected by prey distributions.

Second, larvae of these ages have been shown to have similar behavioral responses to physical factors. In the case of salinity discontinuities, the distributions of newly hatched and 3–6-day-old larval herring were similar (Lougee et al., 2002), and so one might expect that larvae as old as 10 days would respond to changes in salinity in a similar manner. In the case of light, the many studies of the behavioral responses of herring larvae contradict each other, but none indicate that larvae of these two ages react differently to light. However, some studies indicate that larvae of these ages are positively phototactic (Grainger, 1980; Munk et al., 1989; Heath et al., 1991), others report that during daylight larval herring descend to depth (Blaxter, 1973; Seliverstov, 1974), while still others report mixed results (Sjoblom and Parmanne, 1978).

The vertical distribution of larval herring in our experiments was strongly affected by light. In experiments 3 through 6 and experiments 7 through 10 the highest proportions of herring in both treatments were within the surface depth bin. Positive phototaxis was demonstrated by other studies (Grainger, 1980; Munk et al., 1989; Heath et al., 1991). However, many other studies investigating the behavioral responses of herring larvae to light are contradictory, as noted above. One explanation for why larval herring move toward the light source is that it may directly enhance survival by increasing their rate of successful feeding. Munk et al. (1989) speculated that the daytime vertical distribution of larval herring is determined by a compromise between optimal light and prey conditions for feeding. It could be that in our experiments the high light intensity and the prey concentrations at the surface of the tanks provided optimal feeding conditions. This hypothesis may also provide an explanation as to why there was a low proportion of larval herring in the bottom-most depth bin in all tanks, where the highest rotifer proportions were often found. That is, despite high prey concentrations, feeding at this depth may be

inefficient due to low light intensities that correspond to only approximately 1.4% of natural surface light intensities.

Although aggregation at the well-lit surface may benefit larvae directly by increasing their rate of successful feeding, the indirect ecological consequences of having the majority of herring larvae at the very surface are likely to be severe. First, UV-B radiation is strongest at the surface and so larvae found at the surface are at the greatest risk of attaining UV-B damage, which may lead to mortality (Speekmann et al., 2000, and references therein). Second, larval herring at shallow depths coinciding with higher light levels may be at an increased risk of predation, as they are likely to be highly visible to visual predators including fishes and birds. These shallow depths might include the upper half of the euphotic zone, corresponding (as mentioned above) to depths of up to 2.5 m in San Francisco Estuary and the surface centimeters in our experimental tanks. Third, depending on prevalent circulation patterns, larval herring at the surface may experience a higher risk of advection out of their preferred habitat. That is, herring larvae live in environments (e.g., estuaries) where advective transport is often vertically heterogeneous, typically with a net nontidal seaward flow in the surface waters, and a net landward flow at depth (Cloern and Nichols, 1985; Pickard and Emery, 1990). Although this flow regime would likely lead to an advective loss out of the estuary of larval herring that were aggregated at the surface, this may not be the case for all clupeoids in all habitats. For example, Nelson et al. (1977) suggested that larval menhaden remain in the upper mixed layer and are dependent upon the onshore transport of this layer from offshore spawning grounds into estuarine nursery grounds. Regrettably, manipulation of UV radiation, predators, and horizontal water movement was beyond the scope of our study.

The vertical distribution of herring larvae in our experiments was also strongly affected by thin layers of prey and salinity. It is likely that the vertical distribution of larval herring is related to those of their prey, as similar distributions of larval herring and their prey (rotifers) were observed. The ability of larval fish to find and exploit prey patches is of particular importance for their survival, as it has been shown that in the absence of concentrated prey patches larval survival is food limited (Munk and Kiorboe, 1985; Heath, 1989; Letcher and Rice, 1997). Thus, the coincidence of high abundances of larval herring with high abundances of prey is to be expected.

There was one occasion when the peak in herring abundance in the mid-salinity layer did not coincide with a peak in prey abundance, suggesting that the vertical distribution of larval herring is determined, at least in part, by the salinity (density) within the water column. One possible explanation for this is that individual larval herring were moving down into the area of high prey density located just below the mid-salinity layer and then returning to rest just above the prey patch, although this investigation did not include the monitoring of individuals and so we can only speculate about this. A second explanation as to why the larval herring were aggregated in the mid-salinity layer despite a lack of prey in this zone is that the vertical distribution of larval herring is directly affected by salinity itself.

The hypothesis that larval herring distributions are due, at least in part, to a response to salinity is supported by findings that larvae aggregate at haloclines (e.g., Lougee et al., 2002). Orientation of larval fish to salinity discontinuities, rather than prey patches directly, is likely to be a successful strategy in finding prey patches for many reasons. First, biological thin layers have frequently been found to coincide with pycnoclines (Nielsen and Bjornsen,

1990; Bjornsen and Nielsen, 1991; Tiselius et al., 1994; Hanson and Donaghay, 1998; Dekshenieks et al., 2001; Rines et al., 2002), and therefore, due to the influence of salinity on density, salinity gradients could be used as cues to locate thin layers of prey. Second, it may be "easier" for larval fish to orient themselves according to salinities, rather than prey patches directly. Visually locating prey patches would not be a very successful method over larger scales as young larval herring have underdeveloped visual capabilities which are hindered by low light intensities (Blaxter, 1968). In addition, although there is some evidence that larval herring might use chemical cues to locate prey (Dempsey, 1978; Batty, 1987) it is unlikely that these cues would be effective over larger scales, as factors such as turbulence are likely to dissipate chemical cues. Thus, although vision and chemosenses are both likely to be effective tools for prey location at closer ranges, reactions to salinity changes are likely to be more effective for locating prey patches on larger scales.

These findings are similar to those of Batty (1994), who conducted experiments similar to these, but investigated the impact of a thermocline on the vertical distribution of larval herring in the absence of light and prey. He found that larval herring aggregate near the thermocline, despite an absence of prey, and concluded that one advantage of this behavior may be that thermoclines often coincide with high prey densities. As both salinity discontinuities and thermoclines create pycnoclines, it is possible that the vertical distribution of larval herring is due to density differences, rather than to a change in salinity or temperature specifically. The orientation of larvae to such a pycnocline may be active, due to a behavioral reaction to the pycnocline, or may be passive, dependent upon swimming and sinking rates, and/or dependent upon time spent swimming versus sinking, either of which may be a function of the density of the surrounding water. Further studies monitoring the behaviors of individual larvae are needed to investigate this possibility.

Our study provides evidence that the vertical distribution of larval herring is indeed affected by the presence of thin layers, and that these different vertical distributions may result from responses of the larvae to salinity differences, rather than just to prey patches. Thus, thin layers specifically, rather than prey patchiness generally, seem to affect the vertical distribution of larval herring. In a homogeneous distribution of prey, larval herring tend to be concentrated in the surface layers, whereas in the presence of thin layers at mid-depth a significant proportion tends to be found deeper, within the layer. By influencing vertical distribution in this manner, thin layers may increase survivorship directly and/or indirectly. First, thin layers may directly increase survivorship by enhancing feeding and growth of larval herring. Thin layers include patches of high prey density, which are necessary for larval fish survival (Munk and Kiorboe, 1985; Heath, 1989; Letcher and Rice, 1997), and, perhaps more importantly, they include complex biophysical coupling, which provides cues that larval fish can use to sense areas that are likely to include prey patches without having to sense the prey directly. In addition, the deeper distribution caused by subsurface thin layers may increase larval survivorship indirectly by reducing predation by visual predators (e.g., especially if these occur toward the bottom or below the euphotic zone), reducing mortality from UV radiation, and/or reducing the chances of advection out of estuaries by seaward flowing surface waters.

In summary, we found that during daylight the vertical distribution of larval herring is affected by the presence of thin layers of salinity and prey, such that the majority of larval herring were found toward the surface, nearest the light source, but that there were

secondary peaks in abundance at mid-depth in the thin layer tanks. In addition, our results indicate that the cues by which larval herring locate prey patches may include physical cues, such as salinity, that often coincide with prey patches. This change in vertical distribution might be expected to enhance survival via increased food availability, predator avoidance, and/or advective losses. Further studies should include investigations on how organisms orient within thin layers, with particular emphasis on the environmental cues and individual behaviors that lead to thin layer aggregation, as well as investigations on the physiological effects of thin layers on planktonic organisms.

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