ICES Journal of Marine Science, 57: 360–371. 2000
doi:10.1006/jmsc.1999.0601, available online at http://www.idealibrary.com on IDEAL®

Explaining advection: do larval bay anchovy (*Anchoa mitchilli*) show selective tidal-stream transport?

Eric T. Schultz, Robert K. Cowen,
Kamazima M. M. Lwiza, and Angela M. Gospodarek

Schultz, E. T., Cowen, R. K., Lwiza, K. M. M., and Gospodarek, A. M. 2000. Explaining advection: do larval bay anchovy (*Anchoa mitchilli*) show selective tidal-stream transport? – ICES Journal of Marine Science, 57: 360–371.

Bay anchovy (*Anchoa mitchilli*) have been reported in several systems to display net up-estuary larval movements, against the mean flow. However, the means by which such transport occurs is poorly understood. We address how estuarine circulation and larval behaviors serve to transport larvae of the bay anchovy. In two successive summer seasons, we conducted multiple near-synoptic samples of larval distributions and water column structure along a 45-km section of the middle Hudson River estuary. The analysis focuses on patterns in the vertical distribution of larvae that may help explain transport, and the along-river distribution of different ontogenetic stages. The prediction that post-flexion larvae induce selective tidal-stream transport (STST) by vertically migrating in conjunction with tidal or diel cycles was tested via harmonic regression. Larval concentrations and average larval depths often varied with tidal stage. Maximum concentrations tended to occur at times of slack water, and larvae were often closer to the surface during slack tides as well. These patterns may be the result of tidal movements of horizontal abundance gradients, rather than vertical migrations. The prediction that larval transport is facilitated by a preference for deep water was addressed via analysis of variance, testing for depth effects on time-averaged concentration estimates. At some sites, larvae were most concentrated at intermediate depths, which would promote retention (no net horizontal movement) or slow up-river transport. However, in 1996, larvae were found most concentrated at the surface at two sites, suggesting down-river advection. With respect to along-river distribution, we tested the prediction that ontogenetic stages differed in their distribution in a manner consistent with up-river transport. In 1995, pre-flexion larvae were distributed further up river than eggs, and post-flexion larvae were slightly up river of pre-flexion larvae. Along-river distributions were perturbed in 1996 by a storm that caused high run-off and forced larvae down river. Following this event, along-river position did not vary with ontogenetic stage. The study design that combined analysis of larval depth distribution and along-river distribution enabled us to make and test predictions regarding transport processes. A portion of our depth distribution data implied stasis or weak up-river advection, and we found evidence that this was the case.

Key words: Engraulidae, estuary, larvae, migration, transport.

E. T. Schultz: Dept. of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA; R. K. Cowen: Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA; A. M. Gospodarek: Fish and Wildlife Conservation Commission, Florida Marine Research Institute, 19100 SE Federal Highway, Tequesta, FL 33469, USA; K. M. M. Lwiza: Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, USA.

Introduction

Larval and juvenile stages of many coastal marine fishes, including species of commercial importance, seasonally concentrate in estuaries. While there are many complex flow features in an estuary, net flow is seaward. How then are low-salinity areas in the middle and upper estuary populated by newly recruiting larvae? The movement of organisms in association with tidal estuarine circulation has long been of interest (e.g., Rogers, 1940). Purely passive mechanisms, such as sinking during slack tides and mixing back into the water

1054–3139/00/010360+12 $30.00/0

column during tidal flow, will promote some degree of retention (Laprise and Dodson, 1989). Larval behaviors that may regulate transport include a fixed depth preference, or vertical movements in response to one or several cues, which in turn cause changes in horizontal velocity. This latter behaviour is known as selective tidal stream transport (STST; Greer Walker *et al.*, 1978). A final possibility for organisms that can swim at rates comparable to or exceeding horizontal flows, is directed horizontal swimming. Behaviors that could serve to retain, export, or import organisms have been imputed to zooplankton (e.g., Rogers, 1940), larval benthic invertebrates (Cronin and Forward, 1979; Epifanio, 1988; Rothlisberg, 1982), adult invertebrates (Hughes, 1969), larval and juvenile fish (Boehlert and Mundy, 1988; Creutzberg *et al.*, 1978; Fortier and Leggett, 1982, 1983; Graham, 1972; Loos and Perry, 1991; McCleave and Kleckner, 1982; Miller, 1988; Rowe and Epifanio, 1994a; Weinstein *et al.*, 1980), and adult fish (Greer Walker *et al.*, 1978).

The estuarine advection of bay anchovy (*Anchoa mitchilli* [Valenciennes, 1848]) larvae is of special interest for several reasons. Firstly, the location of a larva may affect its survival. The rate of successful completion of the larval stage is low in this species, even by marine fish standards (Castro and Cowen, 1991; Houde, 1987; Leak and Houde, 1987). The abundance of predators and the availability of food resources are known to influence the success of anchovy larval cohorts (Castro and Cowen, 1991; Dorsey *et al.*, 1996; Houde *et al.*, 1994; Purcell *et al.*, 1994). Less is known about the effect of flow and other physical processes. Secondly, advection involves a considerable redistribution of biomass (Wang and Houde, 1995) and therefore may have a pronounced effect on the spatial pattern of trophic transfer in an estuary. Finally, larval anchovy advection bears on the issue of power plant impacts. Mortality rates induced by power plant operations are dependent on the species' distribution and movement patterns within the estuary. The results of efforts to model and quantify the population-wide impact of entrainment mortality (Boreman *et al.*, 1981; Polgar *et al.*, 1988) reflect a particular sensitivity to the natural fluxes of larvae, clearly pointing to the need for a better mechanistic understanding of these movements.

We present analyses of depth-specific anchovy larval abundance in the Hudson River estuary to test for simple depth preferences and STST. Additional analyses were conducted to test whether anchovy larvae are transported up river, as reported to occur over the summer months (Dovel, 1981; Schmidt, 1992).

The bay anchovy is a central living component of estuarine systems along the East Coast. Numerically, it is typically the most abundant fish (Haedrich, 1983; McHugh, 1967). In the Hudson River, it is the most important prey species for early life stages of economically important fishes such as bluefish (Juanes *et al.*, 1993).

Adult anchovies are widespread, but younger stages rely almost exclusively on inshore estuarine waters for their development (Vouglitois *et al.*, 1987). Annual patterns of movement within the Hudson were outlined by Dovel (1981). Adults spawn in more saline waters ($\geq$10 psu), from May through August. Eggs are concentrated in the river from Manhattan and down. Larvae are most abundant in regions of the river where the average salinity is low (<10 psu). Juveniles feed in the middle estuary until waters cool in the fall, then they migrate downstream and out of the river. Reinvasion of the river occurs as waters warm in the spring.

Materials and methods

Sampling

The sampling procedure was constructed as a multi-way factorial design in order to determine the best predictors of larval abundance. Our sampling design includes stratification by location on the river (up river/down river), depth, tidal cycle (at daily and biweekly time scales, i.e. slack/rising and falling tide, and spring/neap tide), and light (day/night).

Our sampling field extended from Dobbs Ferry, New York, to as far north as Newburgh, New York (Fig. 1). This is roughly the region with highest concentrations of larvae, according to Dovel (1981). The actual location of sampling sites differed slightly between the first and second sampling season, because along-river salinity gradient differed among years, and salinity is an important determinant of the spatial limits to spawning of the bay anchovy. Four sites, spaced approximately 15 km apart, were sampled within the region each year. Maximum depth varied among sites (Table 1).

Cruises were scheduled at weekly intervals to coincide with spring and neap tides. We completed three cruises in 1995 and four cruises in 1996 (Table 2), in July and early August. Within a cruise, each site was occupied for a 12.5-h period, starting with the lowest site and moving in sequence to sites further upriver. The 12.5-h site occupation enabled sampling over one complete semidiurnal tidal cycle. During cruise 1996-C2, nightly port calls were necessary, and stations were occupied during the day only, over 4 days. The cruises were conducted on the R/V "Onrust", of the State University of New York, Stony Brook.

At each site, we sampled ichthyoplankton at four stages in the tidal cycle, roughly every 3 h: during maximum flood, slack water on the falling tide, maximum ebb, and slack water on the rising tide. Ichthyoplankton was collected with a 1 m^2 opening-closing Tucker trawl fitted with 333 μm mesh nets. The trawl

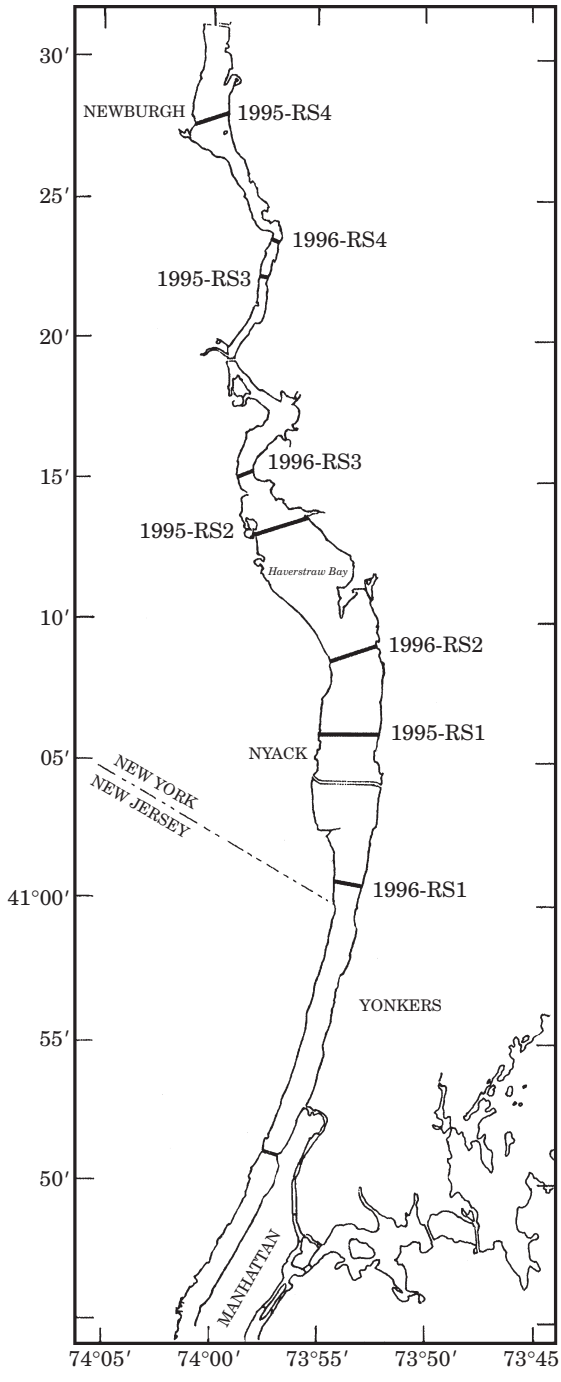

Figure 1. Sampling sites along the Hudson River in 1995 and in 1996.

was fitted with a depth sensor, a deck box connected to a customized trigger mechanism so that nets could be opened at precisely determined depths, and a flow meter to measure volume sampled. At all sites, we sampled in four 2-m depth bins (1–3, 3–5, 5–7, 7–9). Deeper water at several sites enabled us to sample additional 4-m bins (9–13, 13–17, 17–21). Each net was towed for 3 min, for a mean filtered volume of about 150 m^3. All tows were replicated (n=2).

Following net retrieval, each net was washed down, the codends were removed and samples were flushed, using river water, into 333-μm mesh sieves. The samples were then stored in 95% EtOH. Samples appearing to contain more than 400 larvae were split. Eggs were counted by taking five replicate aliquots from each sample.

At roughly 30-min intervals, we deployed an Applied Microsystems CTD at the center of the river channel, where the ichthyoplankton was sampled. Only on the 1996 cruises was the CTD deployed on the western and eastern shoals as well.

Analysis

Several patterns of larval distribution would be consistent with behaviors that transport larvae up river. One is a preference for deeper water, which shows a residual flow in an up-river direction. Another is upward vertical movement during flood tides. Maximum larval abundance in lesser depths should occur around the time of maximum flood tide. Conversely, maximum abundance in deeper water should occur around the time of maximum ebb tide. We assume that anchovy larvae do not move en masse during ebb tides to a boundary layer near the bottom, where they would not be captured by our gear. Finally, larvae may show vertical movements on a diel cycle, which have been shown to promote along-estuary transport (Hill, 1991). In this case, times of maximum larval abundance closer to the surface and in deeper water should differ by roughly 12 h.

To test these predictions, we employed harmonic regression and analysis of variance (ANOVA). Analyses were limited to post-flexion stage larvae, which are most likely to show STST. The statistical models used in these tests are listed in Appendix I. Harmonic regressions (Lorda and Saila, 1986), using sinusoidal transformations of time variables as predictors, were used to determine the times of maximum abundance at depth. The significance level and the time of maximum larval concentration are reported for significant harmonic regressions. Error mean squares and F-tests were adjusted for the fact that response variables were residuals from prior regressions. Results that were nominally significant ($p<0.05$) were subjected to a sequential Bonferroni procedure (Rice, 1989) to ensure a year-wide Type I error rate of 0.05. Larval concentrations (number of larvae in 100 m^3) were transformed by adding 1 and taking the natural logarithm. This did not completely homogenize variances, as inferred from Levene's tests, but did eliminate mean-variance correlation. For these analyses, we eliminated the data from cruise 1996-C2,

Table 1. Tidal and diel cycles in mean depth of post-flexion larvae. For each site, maximum depth during flood tide and the time-averaged larval mean depth (ZCD) are listed. For sites where significant tidal and/or diel changes in ZCD were observed, the range of variability in ZCD over the cycle, the time of maximum and minimum ZCD, and p value under the null hypothesis that there is no temporal change are presented (values adjusted for prior regression steps; i.e. seasonal detrending).

			Tidal effects				Diel effects			
Site	Depth	ZCD	Range	T_{max}	T_{min}	p	Range	T_{max}	T_{min}	p
1995-RS1	12	5.0	0.35	11.4	5.2	0.04				
1995-RS2	13	5.0	0.60	0.6, 5.6	9.2	0.03	0.66	0	12	0.009
1995-RS3	25	9.5	2.3	9.4	0.6, 5.6	0.02				
1995-RS4	13	5.1	0.33	4.4	10.6	0.0001				
1996-RS1	15	4.5								
1996-RS2	12	5.1								
1996-RS3	16	6.7	0.54	9.2	3.0	0.02				
1996-RS4	19	3.5	2.0	3.0	9.2	0.04	2.2	6	18	0.02

Table 2. Schedule of cruises in 1995 and 1996.

Cruise	Begin date	Begin time	End date	Tide
1995-C1	7/12	1016	7/14	Spring
1995-C2	7/19	0442	7/21	Neap
1995-C3	7/26	0955	7/28	Spring
1995-C4	8/2	0220	8/2	Neap
1996-C1	7/9	1841	7/11	Neap
1996-C2	7/16	1054	7/19	Spring
1996-C3	7/23	1626	7/25	Neap
1996-C4	7/30	0944	8/1	Spring

because larvae were absent from most of the sampling region (see below).

An ANOVA model was then used to test for depth preferences, independently of the temporal predictors. We also performed harmonic regressions on mean larval depth (depth center-of-distribution, ZCD) to test for temporal changes in overall depth distribution (see Appendix I). We report the mean ZCD and any significant tidal or diel cycles in ZCD. Because we did not sample the deepest part of the water column, our estimate of ZCD is an underestimate.

Finally, we addressed the factors influencing horizontal (along-river) distribution for all early ontogenetic stages (eggs, pre-flexion, and post-flexion larvae). We quantified mean concentration at a site on a given date by averaging ln-transformed concentration over replicate tows, depths, and tides. If larvae were in fact advected along the river, then horizontal (along-river) distribution should vary with ontogenetic stage, such that the more developed stages should be found further up river. To test this, we estimated a summary variable of horizontal distribution, the along-river center of distribution (YCD, see Appendix II). Replicate estimates of YCD were calculated for each cruise, and were subjected to ANOVA to test the effects of ontogenetic stage and cruise on the horizontal distribution of early-stage anchovy. We also examined the along-river distribution of salinity, using CTD data, to test whether temporal changes in larval distribution were concordant with temporal changes in salt. To this end, we selected all CTD deployments conducted at maximum flood tide, and averaged salinity over the water column for each site occupation.

Results

Tidal and diel cycles

Tidal components had a significant influence on the concentration of post-flexion larvae in most site-depth combinations in both years (Fig. 2A,B). No pattern of changes in time of maximum concentration with site or depth is evident.

In 1995, 12 of the 19 site-depth combinations yielded a significant (nominal $p<0.05$) harmonic regression of tidal components (Fig. 2A). A sequential Bonferroni procedure indicated that the six regressions with nominal $p<0.01$ were significant at the year-wide error rate of 0.05. Half of the significant regressions were from one site, 1995-RS3. Larval concentration at this site tended to be highest during the second half of the tidal clock, especially at or shortly after slack water on the rising tide (9 h). Maximum larval concentrations in the remaining significant regressions occurred in the first half of the tidal clock, during falling water.

In 1996, 12 of the 18 site-depth combinations yielded a significant harmonic regression of tidal components (Fig. 2B), of which the seven regressions with nominal $p<0.01$ were significant at the year-wide error rate of 0.05. Most of these were from sites 1996-RS3 and 1996-RS4. Larval concentration at these sites tended to be highest around the slack water on the rising tide (3 h).

Diel fluctuations in larval abundance were generally weaker than tidal patterns. In 1995, only one of the

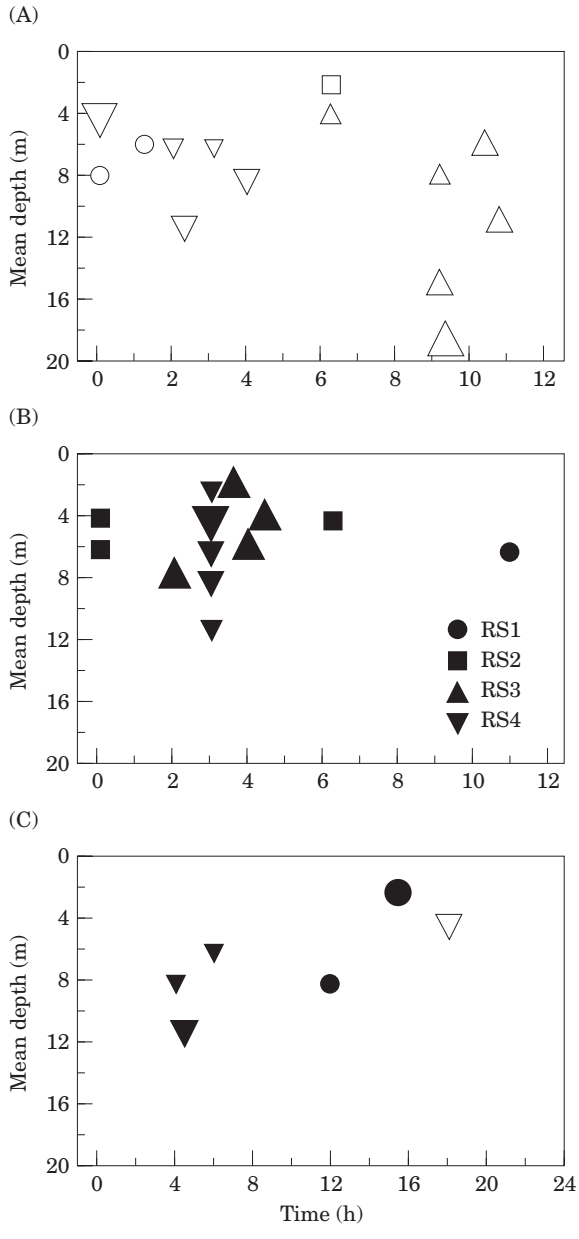

Figure 2. Temporal changes in post-flexion larvae. Time of maximum concentration plotted against depth, by site (RS1–RS4), for depth-site combinations that yielded a significant harmonic regression of temporal components only (small symbols: $0.01<p<0.05$; intermediate: $0.001<p<0.01$; large: $p<0.001$; symbol shape represents site; open symbols: 1995; closed symbols: 1996). (A) tidal components (12.4 h tidal clock), 1995. (B) tidal components, 1996. At site RS2 at 4 m depth, a significant 6.2 h harmonic was found, yielding a double peak in concentration. (C) Diel components (24 h clock), 1995 and 1996.

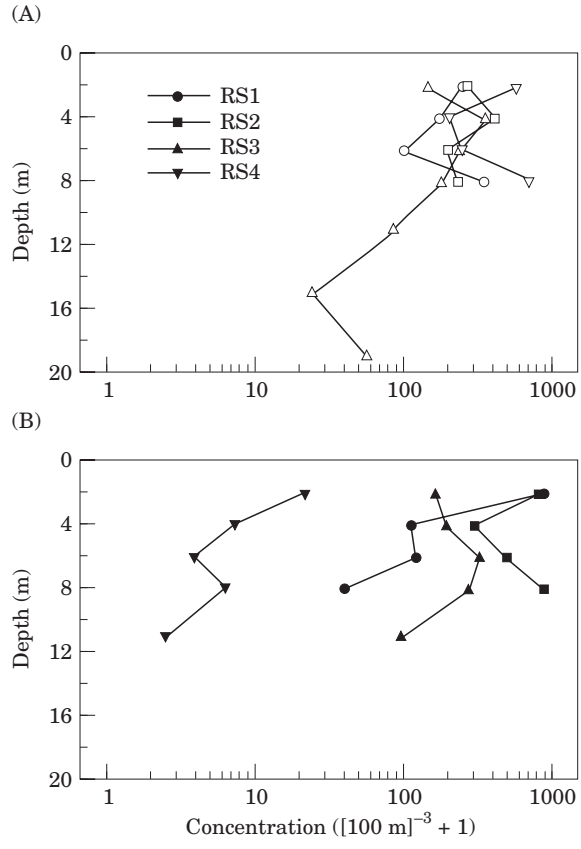

Figure 3. Depth distribution of post-flexion larvae. Mean larval concentration plotted against depth, by site (RS1–RS4). Mean concentrations were calculated by removing temporal components and adding residual to initial concentration (Appendix I). The sum was back-transformed, corrected for the resulting bias (Newman, 1993). Symbol shape represents site; open symbols: 1995; closed symbols: 1996. (A) 1995. (B) 1996.

19 site-depth combinations was significant (Fig. 2C). In 1996, five out of 18 were significant. All results were significant at the year-wide error rate of 0.05. Most of the significant results are from the most up-river site each year, and in most cases concentrations were highest during daylight hours. Otherwise, no pattern is evident.

Changes with depth

The depth distribution of post-flexion larvae varied with river site (Fig. 3A,B). In each year, the full ANOVA model (equation I.8) contained significant depth*site interactions. The depth effect was therefore evaluated separately for each site, by year.

In 1995, larvae at sites 1995-RS2 and 1995-RS3 were most concentrated at 4 m (Fig. 3A). At the other two sites, high concentrations occurred at the surface and at 8 m. The effect of depth on concentration was not significant at 1995-RS2 but was highly significant at other sites. The time-averaged center of distribution (ZCD) was approximately at mid-depth at all sites (Table 1).

In 1996, larvae were most concentrated in the shallowest depth bin (sites 1996-RS1, 1996-RS4; Fig. 3B), at mid-depth (1996-RS3), or at 2 m and 8 m (1996-RS2). The effect of depth was significant ($p=0.0001$) at all sites. Time-averaged ZCD was at mid-depth at all but the most up-river site (Table 1).

The ZCD of post-flexion larvae often changed with tidal stage (Table 1). Harmonic regression analysis indicated that tide had a significant influence at all 1995 sites and two 1996 sites. Three of these regressions (1995-RS3, 1995-RS4, 1996-RS3) were significant at the year-wide rate of 0.05, suggesting more pronounced tidal effects at up-river than down-river sites. The change in ZCD predicted by the harmonic regressions was typically small (0.33–2.3 m). Deepest ZCDs were observed near the time of both rising water slack tide (9–12 h on the tidal clock) and falling water slack tide (3–6 h). A diel shift in ZCD was also found at two year-site combinations (Table 1), suggesting a deeper distribution at night or around dawn.

Along-river patterns

In 1995, the distribution of salt in the sampling field was relatively stable with only a slight increase over the 3-week study period (Fig. 4A): depth-averaged salinity varied from 9–10 psu at the down-river end to 1–2 psu at the up-river end. In contrast, the distribution changed considerably in 1996 (Fig. 4B). A tropical storm passed through the region shortly after cruise 1996-C1. During cruise 1996-C2, river discharge was high and salinity was quite low over the entire sampling field. The system rapidly returned to the pre-storm condition, such that by cruise 1996-C3 salinity at all sites was the same as or higher than it had been on the first cruise.

The abundance of eggs and larvae varied along the river, and from cruise to cruise. The concentration of eggs usually declined up river (Fig. 5A,B). By cruise 1995-C3, spawning had evidently ceased down river, but was apparently continuing at a low rate up river. In 1996, eggs were absent during cruise 1996-C2, following the storm. During cruise 1996-C3, eggs were found further up river than they were during cruise 1996-C1, paralleling changes in salinity.

Pre-flexion larvae were more evenly distributed along the river than eggs; they were generally less concentrated than eggs down river and more so up river (Fig. 5C,D). Temporal changes in concentration of larvae followed that of eggs. During cruise 1995-C3, the concentration was low, reflecting the low concentration of eggs. Following the 1996 storm, they were found only at 1996-RS1, then the concentration recovered up river over the next 2 weeks.

Post-flexion larvae were even more uniformly distributed than pre-flexion larvae from site to site and

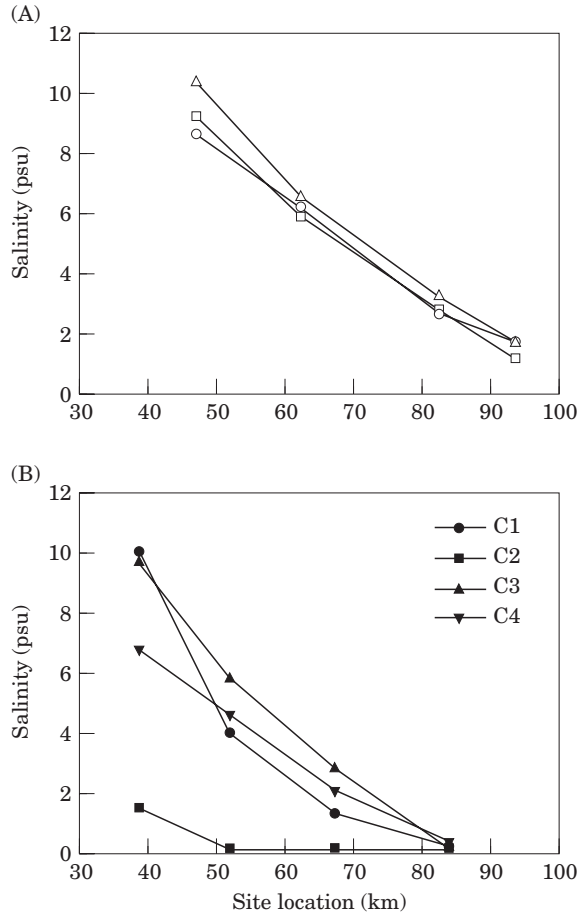

Figure 4. Along-river distribution of salt. Location (km upstream from river mouth) is plotted against depth- and tide-averaged salinity, by cruise (C1–C4). Symbol shape represents cruise; open symbols: 1995; closed symbols: 1996. (A) 1995. (B) 1996.

cruise to cruise (Fig. 5E,F). In 1995, the concentration of post-flexion larvae declined slightly over the 3 weeks. Up river, post-flexion larvae were relatively abundant, in contrast to eggs and pre-flexion larvae. The influence of the 1996 storm on post-flexion larvae was similar to the effects on the earlier life stages: larvae were most concentrated down river on cruise 1996-C2, but thereafter increased at up-river sites while declining down river. Post-flexion larvae were less concentrated up river at 1996-RS4, during all cruises.

The prediction that larvae were being advected up river was tested using the summary variable of horizontal distribution (YCD). The effect of ontogenetic stage was initially tested in a two-way ANOVA, with cruise as the other class variable. In each year, stage differences varied with cruise (stage X cruise interaction; 1995: $p=0.06$; 1996: $p=0.0001$). Because of the significant

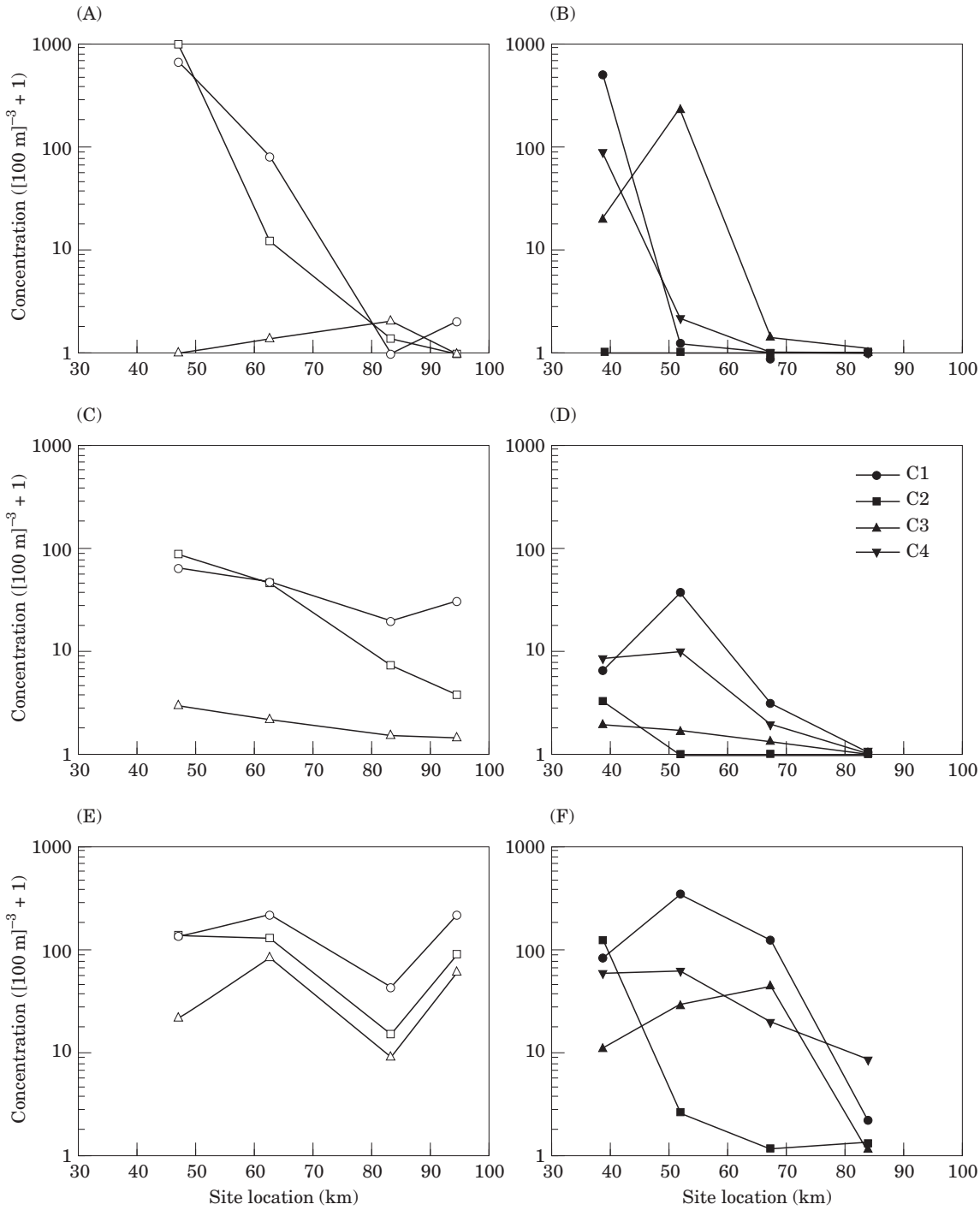

Figure 5. Along-river distribution of eggs and larvae. Location (km upstream from river mouth) is plotted against depth-averaged concentration, by cruise (C1–C4). Back-transformed concentration was corrected for bias (Newman, 1993). Symbol shape represents cruise as indicated in legend; open symbols: 1995; closed symbols: 1996. (A) Eggs, 1995. (B) Eggs, 1996. (C) Pre-flexion larvae, 1995. (D) Pre-flexion larvae, 1996. (E) Post-flexion larvae, 1995. (F) Post-flexion larvae, 1996.

Table 3. Differences among ontogenetic stage in along-river center of distribution (YCD, square-root transformed, in km), tested against stage as a classification effect in one-way ANOVAs. Significant effects are tested further via post-hoc Tukey's studentized range comparison (different letters among stages indicate significant differences).

Cruise	Egg	Pre-flexion	Post-flexion
1995-C1	55.4a	69.4b	70.8c
1995-C2	51.8a	63.4b	69.1c
1995-C3	76.0a	64.7b	71.2ab
1996-C1	39.1a	50.3b	54.3b
1996-C2	a	a	a
1996-C3	a	a	a
1996-C4	a	a	a

interactions, we analyzed the stage effect with a set of one-way ANOVAs, one for each cruise.

In some cruises, successive ontogenetic stages were distributed further up river as predicted. In all 1995 cruises and the first 1996 cruise, the stages significantly differed in along-river distribution (Table 3). Following the storm in 1996, however, there was no difference in the mean position among stages. When ontogenetic differences were significant, these were as predicted in three cases, with post-flexion larvae distributed the farthest up river. Eggs were farthest up river in cruise 1995-C3, when spawning had ceased at the lowest river sites.

Discussion

Our analyses are initial steps in the study of whether bay anchovy larvae undergo up-river transport in the Hudson River estuary, and by what mechanism such transport may occur. The study of larval vertical distributions was designed to shed light on behaviors that might facilitate up-river transport. The analysis of along-river distributions provides a preliminary look at whether up-river transport did in fact occur. This approach should in principle enable us to make predictions regarding transport processes, and test these predictions against observed changes in along-river distributions. The results of the present study are encouraging; a portion of our depth distribution data implied stasis or weak up-river advection, and we found evidence that this was the case.

Larval concentration often varied with tidal stage, particularly at up-river sites (Fig. 2). Concentration was most often maximized at two times on the tidal clock, slack water on the rising tide (1996) and slack water on the falling tide (1995). These are times when depth-averaged salinity is lowest and highest, respectively. The prediction that larvae would be most concentrated at lesser depths at maximum flood, and deeper water at maximum ebb, was not confirmed.

Many of the significant tidal effects observed were probably the result of tidal shifts in along-river abundance gradients. Regional gradients would cause local tidal fluctuations, as water that is relatively rich in larvae moves into and out of the river site being sampled. The series of significant tidal effects at 1995-RS3 (Fig. 2A) is one example. Post-flexion larvae were relatively sparse at this site (Fig. 5E). Within the resolution of our sampling design, it appears that post-flexion larval abundance increased more rapidly upstream of this site than downstream. If so, then the tidal stage of lowest salinity (about 9 h on the tidal clock) would be when the site would be highest up the larval concentration gradient. Conversely, in 1996, larvae were most sparse at the site farthest upriver (Fig. 5F), with a gradient of increasing larval concentration downstream to 1996-RS2 (except during cruise 1996-C3). As expected in this case, larval concentration at both of the up-river sites increased as water levels rose and salinity increased, and was highest at slack water during the rising tide. It appears that the tidal effects on larval concentration can largely be explained via cyclic along-river movement of gradients in larval concentration.

Analysis of larval depth distributions was designed to test for STST, or for depth preferences that promote up-river transport. Post-flexion larvae were typically non-randomly distributed with depth, and the depth distributions varied among sites (Fig. 3). At some mid-river sites, larvae tended to be most concentrated at 4–6 m, or were uniformly distributed with depth. This pattern implies retention or weak up-river advection. At other sites, the distribution of post-flexion larvae seemed to be split between the surface and the bottom. It is not possible to predict the consequences for transport of this distribution pattern; analysis of larval size distributions may clarify whether the surface pool and deep pool of larvae were drawn from the same source. Finally, a third pattern we found was a clear concentration of larvae at the surface, implying advection down river at these sites.

As required for STST, depth distribution often changed with time. Harmonic regression of mean depth (ZCD) often indicated slight cyclic change in the vertical position of larvae, primarily due to tidal influences (Table 1). Larvae tended to be closer to the surface during slack water on the falling tide, or during slack water on the rising tide. These changes are not those predicted by STST, and are not clearly indicative of up-river or down-river advection, but suggest relatively fixed positions (i.e. retention). A more complete evaluation of the predicted rate and direction of transport from observed patterns of larval concentration with time and depth is beyond the scope of this paper.

It should be noted that a process other than vertical movements of larvae could drive the apparent tidal shifts in larval depth. If vertical distributions of larvae

vary along the river, then vertical distributions will locally vary with tidal stage as well. For example, in 1995 there was a pronounced decrease in larval concentration below 8 m at 1995-RS3 (Fig. 3). This may represent a regional scarcity of larvae at depth in the region between 1995-RS2 and 1995-RS4. If so, then this could drive the observed tidal changes in vertical distribution at 1995-RS2: when there is water from up river at the site, there is a low number of larvae at depth and a shallow mean larval depth. Finer-scale along-river sampling would be needed to confirm this explanation.

Other investigators have found evidence for cyclic changes in the distribution of anchovy larvae, particularly on a diel cycle. Bourne and Govoni (1988), working in Narragansett Bay, and Loos and Perry (1991), working in the Patuxent River, both described day/night shifts in larval distributions. They found opposite patterns; the former found that larvae move up at night, while the latter found movement to deeper waters at night.

Our study design differs from most prior investigations of vertical larval movements and STST in that our samples were spatially dispersed. Many studies of STST (e.g., Graham, 1972; McCleave and Kleckner, 1982; Weinstein *et al.*, 1980) collect samples continuously or frequently at one or two stations. Recent applications of this approach, employing sophisticated time-series analysis, have demonstrated that sacrificing spatial dispersion for the sake of temporal continuity has important advantages (Fortier and Leggett, 1982, 1983; Rowe and Epifanio, 1994b). A drawback is that it can be difficult to distinguish tidal movements of static horizontal gradients from vertical migrations. The potential for this confounding was illustrated clearly in our results. Modeling will be required to show the extent to which the former effect may mask vertical migrations.

The prediction that successive ontogenetic stages should be found progressively farther up river was generally confirmed (Table 3), suggesting that larvae are advected up river after hatching. Other features of the along-river analysis include a sudden cessation of spawning down river in 1995, and a sharp perturbation to the distribution of salt, eggs and larvae caused by a storm in 1996.

Differences in YCD were found among all three ontogenetic stages. The difference between post- and pre-flexion larvae tended to be smaller in magnitude than that between eggs and pre-flexion larvae. Pre-flexion larvae are regarded as less capable of concerted vertical migrations, and probably are advected up river via a tendency to be concentrated in deeper water with up-river flow. Post-flexion larvae should be capable of vertical migrations, but as discussed above do not show STST. The analyses of vertical and horizontal distribution patterns both suggest that post-flexion larvae were retained in a relatively fixed position, or showed weak up-river transport. An alternative interpretation of the along-river patterns is that they reflect temporal changes in the location of spawning: younger stages were located down river of older stages because adults were spawning further down river over time. We provisionally reject this possibility because it is inconsistent with known patterns of spawning, wherein adults tend to spawn further up river as the season progresses. Another interpretation is that the along-river patterns reflect a gradient of mortality: later stage larvae were more likely to be found up river because survival rates were higher there. This cannot be tested directly with existing data.

The effect of the 1996 storm on the distribution of salt and larvae is an interesting feature of our results. After the storm, most of the study area was riverine rather than estuarine, with virtually no salt-water intrusion and no landward flow. Larvae, and spawning adults, had moved downstream, and eggs were absent. Over the following 2 weeks, eggs reappeared at the down-river sites (Fig. 5B), and the distribution of pre- and post-flexion larvae rapidly recovered to pre-storm conditions (Fig. 5D,F). Similar temporal changes in salinity (Fig. 4B) indicate that larvae passively flowed back into this section of the river along with the salt. The event homogenized anchovy distribution with respect to stage, and may have affected vertical distributions (note the differences between 1995 and 1996 vertical distributions).

Several previous workers showed evidence for up-river transport of early-stage bay anchovies. Dovel (1981) and Schmidt (1992) both found that distribution contours of anchovy larvae shifted up river, over a time scale of weeks, in the Hudson River. Both authors also report the distribution of eggs during their sample periods; larvae clearly were distributed up river of eggs in each data set. Loos and Perry (1991), working in the Patuxent River, Maryland, also concluded that up-river transport was likely. They found large larvae accumulating in up-river stations, where smaller larvae had not been present in appreciable numbers earlier.

The present analysis of along-river distribution, in which early-stage anchovies are divided into crude ontogenetic stages, furnishes a rough, preliminary view of net transport. More precise measurements of net transport will be possible once the study population has been divided into hatch-date cohorts. We collected larvae up to 25 mm in size, which are almost 40 days old. Therefore, it could be possible to describe the change in distribution of a cohort, operationally defined as a subset of the population hatched in a limited time period (e.g., 0.5 weeks) for 5 weeks or more. In actuality, the 1995 data set was limited to a 2-week interval, and the 1996 series was ''perturbed'' by the run-off event, which

presents an interesting opportunity to examine the effect of high-flow episodes but truncates the time interval of typical flow in the study field.

Acknowledgements

We thank the legion of volunteers, too numerous to identify individually, who helped us in collecting the data. Suzanne Dorsey, Brian Steves, and Ly Williams and the captain and crew of the R/V "Onrust" (Bret Zielinski, Mark Wiggins, Felix Edwards) provided essential operations support. Special thanks for help with instrumentation to Steven Morgan, Tom Wilson, and the late David Lucyk, and also to Ernesto Lorda for helping with the analysis. Initial discussions with John Boreman and John Waldman provided impetus for the project. This research was funded by the Hudson River Foundation (#012/95A).

References

Boehlert, G. W., and Mundy, B. C. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. American Fisheries Society Symposium, 3: 51–67.

Boreman, J., Goodyear, C. P., and Christensen, S. W. 1981. An empirical methodology for estimating entrainment losses at power plants sited on estuaries. Transactions of the American Fisheries Society, 110: 253–260.

Bourne, D. W., and Govoni, J. J. 1988. Distribution of fish eggs and larvae and patterns of water circulation in Narragansett Bay, 1972–1973. American Fisheries Society Symposium, 3: 132–148.

Castro, L. R., and Cowen, R. K. 1991. Environmental factors affecting the early life history of bay anchovy, *Anchoa mitchilli*, in Great South Bay. Marine Ecology Progress Series, 76: 235–247.

Creutzberg, F., Eltink, A. T. G. W., and van Noort, G. J. 1978. The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. *In* Physiology and Behavior of Marine Organisms, pp. 243–251. Ed. by D. S. McLusky, and A. J. Berry. Pergamon Press, Oxford.

Cronin, T. W., and Forward, R. B. Jr. 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science, 205: 1020–1022.

Dorsey, S. E., Houde, E. D., and Gamble, J. C. 1996. Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay. Fishery Bulletin, 94: 257–267.

Dovel, W. L. 1981. Ichthyoplankton of the Lower Hudson estuary, New York. New York Fish and Game Journal, 28: 21–39.

Epifanio, C. E. 1988. Transport of invertebrate larvae between estuaries and the continental shelf. American Fisheries Society Symposium, 3: 104–114.

Fortier, L., and Leggett, W. C. 1982. Fickian transport and the dispersal of fish larvae in estuaries. Canadian Journal of Fisheries and Aquatic Sciences, 39: 1150–1163.

Fortier, L., and Leggett, W. C. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1543–1555.

Graham, J. J. 1972. Retention of larval herring within the Sheepscot estuary of Maine. Fishery Bulletin, 70: 299–305.

Greer Walker, M., Harden Jones, F. R., and Arnold, G. P. 1978. The movements of plaice (*Pleuronectes platessa* L.) tracked in the open sea. Journal du Conseil International pour l'Exploration de la Mer, 38: 58–86.

Haedrich, R. L. 1983. Estuarine fishes. *In* Ecosystems of the World: Estuaries and Enclosed Seas, pp. 183–207. Ed. by B. H. Ketchum. Elsevier, Amsterdam.

Hill, A. E. 1991. A mechanism for horizontal zooplankton transport by vertical migration in tidal currents. Marine Biology, 111: 485–492.

Houde, E. D. 1987. Early life dynamics and recruitment variability. American Fisheries Society Symposium, 2: 17–29.

Houde, E. D., Gamble, J. C., Dorsey, S. E., and Cowan, J. H. Jr. 1994. Drifting mesocosms: the influence of gelatinous zooplankton on mortality of bay anchovy, *Anchoa mitchilli*, eggs and yolk-sac larvae. ICES Journal of Marine Science, 51: 383–394.

Hughes, D. A. 1969. Responses to salinity change as a tidal transport mechanism of pink shrimp, *Penaeus duorarum*. Biological Bulletin of the Marine Biological Laboratory, Woods Hole, 136: 43–53.

Juanes, F., Marks, R. E., McKown, K. A., and Conover, D. O. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River estuary. Transactions of the American Fisheries Society, 122: 348–356.

Laprise, R., and Dodson, J. J. 1989. Ontogeny and importance of tidal vertical migrations in the retention of larval smelt *Osmerus mordax* in a well-mixed estuary. Marine Ecology Progress Series, 55: 101–111.

Leak, J. C., and Houde, E. D. 1987. Cohort growth and survival of bay anchovy *Anchoa mitchilli* larvae in Biscayne Bay, Florida. Marine Ecology Progress Series, 37: 109–122.

Loos, J. J., and Perry, E. S. 1991. Larval migration and mortality rates of bay anchovy in the Patuxent River. *In* Larval Fish Recruitment and Research in the Americas, pp. 65–76. Ed. by R. D. Hoyt. NOAA Technical Report NMFS 95.

Lorda, E., and Saila, S. B. 1986. A statistical technique for analysis of environmental data containing periodic variance components. Ecological Modelling, 32: 59–69.

McCleave, J. D., and Kleckner, R. C. 1982. Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). Journal du Conseil International pour l'Exploration de la Mer, 40: 262–271.

McHugh, J. L. 1967. Estuarine Nekton. *In* Estuaries, pp. 581–620. Ed. by G. H. Lauff. AAAS, Publication 83, Washington, DC.

McLellan, H. J. 1965. Elements of Physical Oceanography. Pergamon Press, Oxford.

Miller, J. M. 1988. Physical processes and the mechanisms of coastal migrations of immature marine fishes. American Fisheries Society Symposium, 3: 68–76.

Newman, M. C. 1993. Regression analysis of log-transformed data: statistical bias and its correction. Environmental Toxicology and Chemistry, 12: 1129–1133.

Polgar, T. T., Turner, M. A., and Summers, J. K. 1988. Effect of power plant entrainment on the population dynamics of the bay anchovy (*Anchoa mitchilli*). Ecological Modelling, 41: 201–218.

Purcell, J. E., Nemazie, D. A., Dorsey, S. E., Houde, E. D., and Gamble, J. C. 1994. Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Marine Ecology Progress Series, 114: 47–58.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution, 43: 223–225.

Rogers, H. M. 1940. Occurrence and retention of plankton within the estuary. Journal of the Fisheries Research Board of Canada, 5: 164–171.

Rothlisberg, P. C. 1982. Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia. Fishery Bulletin, 80: 541–554.

Rowe, P. M., and Epifanio, C. E. 1994a. Flux and transport of larval weakfish in Delaware Bay, USA. Marine Ecology Progress Series, 110: 115–120.

Rowe, P. M., and Epifanio, C. E. 1994b. Tidal stream transport of weakfish larvae in Delaware Bay, USA. Marine Ecology Progress Series, 110: 105–114.

Schmidt, R. E. 1992. Temporal and spatial distribution of bay anchovy eggs through adults in the Hudson River. *In* Estuarine Research in the 1980's, pp. 228–241. Ed. by C. L. Smith. State University of New York Press, Albany, NY.

Vouglitois, J. J., Able, K. W., Kurtz, R. J., and Tighe, K. A. 1987. Life history and population dynamics of the bay anchovy in New Jersey. Transactions of the American Fisheries Society, 116: 141–153.

Wang, S.-B., and Houde, E. D. 1995. Distribution, relative abundance, biomass and production of bay anchovy *Anchoa mitchilli* in the Chesapeake Bay. Marine Ecology Progress Series, 121: 27–38.

Weinstein, M. P., Weiss, S. L., Hodson, R. G., and Gerry, L. R. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fishery Bulletin, 78: 419–436.

Appendix I. Analysis of vertical larval distribution

Harmonic regression was used to resolve two temporal effects on abundance, the M2 tidal (McLellan, 1965) and diel cycles. The data were analyzed by site-depth combination. First the data were seasonally detrended as

$$Y_t = \alpha_0 + \beta_1 t + \beta_2 t^2, \tag{I.1}$$

where t is the number of hours from the first tow conducted during that year at that site and depth. If a significant seasonal effect was found, we removed it by calculating the residual:

$$R_{1t} = Y_t - \hat{Y}_t, \tag{I.2}$$

where $\hat{Y}_t$ was the predicted value from regression model I.1. If no significant seasonal effect was found, R_{1t} was set equal to the mean larval concentration at that site and depth for the year.

We then subjected larval concentration to harmonic regression of tidal effects. The time of each tow was scaled to the 12.4 h tidal clock (with maximum flood tide at 0) and then transformed to linearize sinusoidal fluctuations in abundance. Stepwise regression of concentration against these predictors identified significant tidally cyclic patterns. We included predictors corresponding to harmonics of the M2 tidal cycle (i.e. 6.2-h cycles), because we expected some influence on larval concentration of high turbulence at maximum flood and maximum ebb tides. The regression model evaluated was:

$$R_{1t'} = \beta_1[\cos(c*t')] + \beta_2[\sin(c*t')] + \beta_3[\cos(c/2*t')] + \beta_4[\sin(c/2*t')], \tag{I.3}$$

where t′ is the time of the tow within the tidal cycle, and $c = 2\pi/12.4$. This model was run without an intercept, because the mean residual is by definition 0. If significant tidal effects were found, then their influence was removed for subsequent analysis by calculating the residual

$$R_{2t'} = R_{1t'} - \hat{R}_{1t'}, \tag{I.4}$$

where $\hat{R}_{1t'}$ is the predicted value from equation I.3. If the regression model I.3 was not significant, $R_{2t'}$ was set equal to $R_{1t'}$.

Residuals from the tidal harmonic regression were then passed to a corresponding regression for resolution of diel effects. The regression model for diel periodicity was:

$$R_{2t''} = \beta_1[\cos(d*t'')] + \beta_2[\sin(d*t'')], \tag{I.5}$$

where t″ is the time of the tow, transformed to 24-h clock time, and $d = 2\pi/24$. If significant diel effects were found, then their influence was removed for subsequent analysis by calculating the residual

$$R_{3t''} = R_{2t''} - \hat{R}_{1t''}, \tag{I.6}$$

where $\hat{R}_{1t''}$ is the predicted value from Equation (I.5). If the regression model I.5 was not significant, $R_{3t''}$ was set equal to $R_{2t''}$.

To test for depth preferences at each site, the harmonic regressions were followed by tests of depth and river site. As above, each site-depth combination was seasonally detrended and then subjected to a harmonic regression in which the tidal and diel components were combined

$$R_{1t'} = \beta_1[\cos(c*t')] + \beta_2[\sin(c*t')] + \beta_3[\cos(c/2*t')] + \beta_4[\sin(c/2*t')] + \beta_5[\cos(d*t'')] + \beta_6[\sin(d*t'')]. \tag{I.7}$$

The residual $R_{2t'}$ was then added to α_0 (Equation (I.1)), or the mean concentration if no significant seasonal component was found, to yield an estimate of concentration from which the periodic and seasonal effects had been removed. All observations were pooled within year and tested in a two-way ANOVA:

$$(R_{2t'} + \alpha_0) = \gamma_1(\text{depth}) + \gamma_2(\text{site}) + \gamma_3(\text{depth}*\text{site}) \tag{I.8}$$

To test for temporal changes in average larval depth, we calculated ZCD for each replicate set of samples:

$$ZCD=\Sigma(P_i*Z_i), \quad \text{(I.9)}$$

where

$$P_i=(C_i*H_i)/\Sigma(C_i*H_i), \quad \text{(I.10)}$$

i=1 to n, n is the number of depth strata, C_i is the (ln-transformed) concentration of larvae in the ith depth stratum, H_i is the width of the ith depth stratum, and Z_i is the mean depth of the ith depth stratum. Estimates of ZCD were subjected to harmonic regression of tidal and diel effects (as in Equations (I.3) and (I.5)), by site.

Appendix II. Analysis of along-river larval distribution

The YCD was based on depth- and tide-averaged abundance:

$$YCD=\Sigma(P_i*X_i), \text{ where} \quad \text{(II.1)}$$

$$P_i=C_i\ \Sigma C_i, \quad \text{(II.2)}$$

i=1 to n, n is the number of river sites, C_i is the (ln-transformed) concentration of larvae, averaged over depth and tide, and X_i is the distance along the river axis from the river mouth, in km.