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# The Dynamics of Bay Anchovy in the Hudson River Estuary: Process-oriented Studies and Long-term Changes

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The dynamics of bay anchovy in the Hudson River estuary:

process-oriented studies and long-term changes

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## Abstract

We review three areas of recent research on Hudson River bay anchovy. One focus has been the along-estuary movement of early life stages. A cohort analysis of samples collected in a spatiotemporally extensive monitoring program has confirmed that early-stage anchovy migrate up-estuary, at an estimated rate of 0.6 km/d. Complementary fine-scale field sampling was designed to clarify behaviors that effect the migration. This work found that early-stage anchovy can show preferences for depth and can conduct periodic vertical migration. To determine whether these behaviors were sufficient to produce up-estuary migration, larval flux and velocity were estimated. These estimates were consistent with local retention rather than concerted migration. High priority should be given to examining individual migration histories through analysis of otolith microchemistry. A second focus of research on Hudson anchovy has been on local population structure, permitting comparison to anchovy in other locations. The demography of the Hudson River anchovy appears to be unique. Anchovy that spawn in the Hudson River are larger than those spawning in the Chesapeake Bay region and are mostly two years old, whereas yearlings predominate in other estuaries. Batch fecundity was lower and egg mortality higher in Hudson River than in Chesapeake Bay. A key issue arising from these recent findings is the degree to which the Hudson anchovy pool is connected with other large anchovy pools, such as Narragansett Bay and Chesapeake Bay. A third focus of research on Hudson anchovy has been analysis of interannual variability in early-stage abundance. A >20 year time series of juvenile bay anchovy abundance shows that juvenile abundance has varied over one order of magnitude. There has been no significant change in abundance over the entire time series, but abundance

has declined 10-fold since a peak in the late 1980s. Anchovy abundance was negatively associated with the abundance of early-stage striped bass, and positively associated with the abundance of early-stage tomcod. We suggest that these associations reflect direct interactions among the species and urge further work on the ecological role of striped bass in the estuary.

## Introduction

The bay anchovy (*Anchoa mitchilli*; hereafter referred to simply as anchovy) is an abundant marine-estuarine fish of the eastern seaboard. It is a predominant member of the estuarine fish assemblage, ranging from tropical and subtropical estuaries in the Gulf of Mexico and the Atlantic coast of the southeastern US (Deegan and Thompson 1985; Castillo-Rivera et al. 1994; Snelson and Johnson 1995; Ayala Perez et al. 1998) to the temperate estuaries of the North Atlantic Bight and southern New England (Dovel 1981; Monteleone 1992; Keller et al. 1999; Dorfman 2000). Early-stage (larvae and juvenile) anchovy are often the most abundant members of the summer ichthyoplankton assemblage (Olney 1983; Setzler-Hamilton 1987; Monteleone 1992; Keller et al. 1999; Schultz et al. 2003). In northern latitudes, anchovy migrate out of estuaries to coastal waters in the autumn, returning in spring as reproduction commences (Dovel 1981; Voughlitois et al. 1987; Schmidt 1992; Wang and Houde 1995). In contrast, in the Gulf of Mexico (Hackney and de la Cruz 1981; Dokken et al. 1984) and Florida (Tremain and Adams 1995) anchovy are estuarine residents for the entire year. Anchovy are found in a wide range of habitats, including salt-marsh creeks (Rozas and Hackney 1984; Allen et al. 1995; Able et al. 2001), marsh tide pools (Crabtree and Dean 1982), marsh lakes (Griffith and Bechler 1995), eelgrass beds (Orth and Heck 1980), the surf zone (DeLancey 1989), and the open water of small to large estuaries. Anchovy are pelagic with no preference for structure; they are most abundant in unvegetated areas (Rozas and Minello 1998; Thayer et al. 1999; Rozas and Zimmerman 2000). Older studies of bay anchovy habitat use were reviewed by Morton and Moran (1989).

Anchovy are an important part of estuarine food webs. Anchovy are planktivorous; they prey on crustaceans (Johnson et al. 1990; Peebles et al. 1996; Peebles 2002) and fish eggs and larvae (Cowan and Houde 1992). There are indications of competitive interactions and resource partitioning with other zooplanktivorous fish (Ogburn-Matthews and Allen 1993; Allen et al. 1995). Anchovy are major prey of piscivorous fish such as bluefish, striped bass, and weakfish (Manooch 1973; Richards 1976; Baird and Ulanowicz 1989; Juanes et al. 1993; Hartman and Brandt 1995). Anchovy production is also important to ctenophores, which feed on eggs and small larvae (Monteleone and Duguay 1988; Govoni and Olney 1991; Purcell et al. 1994).

The anchovy has been subject to annual monitoring in the Hudson River for almost three decades. An extensive sampling program was designed to assess the effects of power plant operations on fish populations and communities (Barnthouse et al. 1988). Data on distribution and abundance of anchovy and other target species are disseminated in annual reports (e.g., ASA Analysis & Communication 2004) and in research publications (e.g., Schmidt 1992 and other papers in this volume).

Here, we review three areas of recent research on Hudson River anchovy. One focus has been on the up-estuary migration of early life stages. A second focus has been population structure and vital rates of Hudson River anchovy, in comparison to anchovy in other locations. Careful attention to interpopulation variability in these vital rates is warranted, given the ecological importance of this species. A third focus has been interannual variability in anchovy abundance. One important application of long-term monitoring program data is exploration of local factors that may influence the abundance of 'target species' in the estuary. Hypothesis-based explorations, combined with tightly-

focused research on processes, are essential to understand the Hudson River estuary's ecological dynamics.

#### Analyses of young anchovy migration

A conspicuous feature of anchovy estuarine residency is the apparent up-estuary migration of early life stages. Seasonal redistribution of early-stage anchovy to upper estuary areas has been reported for the Hudson River (Dovel 1981; Schmidt 1992), tributaries of Chesapeake Bay such as the Patuxent River (Dovel 1971; Loos and Perry 1991), and Chesapeake Bay proper (Wang and Houde 1995), but has not been found in some locations (e.g. Narragansett Bay, Bourne and Govoni 1988). An instance of the apparent seasonal upriver shift in the Hudson River is provided by hydroacoustic data collected during 1997. Mobile, down-looking hydroacoustic surveys with a Simrad<sup>®</sup>, 120 kHz split-beam sonar were used to estimate the density of larval anchovy (10-22 mm TL) during spawning (June-August) and post-spawning (September) periods along the lower 122 km of the river (Tipton 2003). During the 1997 spawning season spawning was most active in the Tappan Zee region (mean river km 46) and in the East River and Arthur Kill/Kill Van Kull tributaries of the Hudson (near river km 0) (data not shown; Bassista 2000). The concentration of larval anchovy was greatest in the lower two regions, and at mean river km 69 upriver of the spawning patches (Figure 1A).

Subsequently there was a pronounced upriver shift in larval distribution; during the post-spawning period larvae were present entirely in the West Point region (river km 83; Figure 1B). The distribution of eggs, larvae and young-of-year anchovy sampled in the 1997 Longitudinal River Survey (LRS) of ichthyoplankton conducted by the Hudson

Fig 1

River utility companies (see ASA Analysis & Communication 2004 for further details on this sampling program) is broadly similar to that found in the hydroacoustic analysis.

Three general processes could produce up-estuary shifts, alone or in combination: 1) migration by larvae and juveniles (hypothesized by Dovel 1981); 2) migration by spawning adults (hypothesized by Schmidt 1992); and, 3) mortality gradients. Thus, if larvae in lower portions of the estuary are more likely to die than those in upper portions, redistribution will occur that mimics migration. MacGregor and Houde (1996) concluded that mortality gradients had a pronounced effect on redistribution of anchovy larvae from offshore to inshore areas of Chesapeake Bay. In contrast, Loos and Perry (1991) refuted the mortality hypothesis in favor of the early-stage migration hypothesis. Here, we first present analyses demonstrating that neither adult migration nor gradients in early-stage mortality are sufficient to explain the up-estuary redistribution of anchovy in the Hudson River. Then we describe efforts to determine the mechanisms of migration.

The hypothesis that early-stage anchovy migrate up-estuary has been tested with a cohort approach (Schultz et al. In review). Cohort identification involves assigning individuals to birth-date classes (Limburg 2002), which is possible in many fish species via analysis of the daily age record in otoliths (Jones 2002). The cohort analysis of anchovy migration focused on the summer and autumn portion of the 1998 LRS (ASA Analysis & Communication 2001). Briefly, the steps in this analysis were: 1) determining daily age of an LRS subsample representative of LRS dates and locations; 2) estimating birth-date for all anchovy collected in the 1998 LRS based on the strong relationship ( $R^2 = 0.82$ ; Schultz et al. In press) between size and age found in step 1, and



pooling the birth dates into weekly cohorts; 3) mapping the distribution of 11 different cohorts as they aged.

Cohorts shifted up-estuary, favoring the migration hypothesis over the alternative hypotheses of adult migration and mortality gradients (Schultz et al. In press). We summarized our data on net cohort movements as the relationship between mean river location of a cohort and its age (Fig. 2). Cohorts early in their life showed a net movement up-estuary at a mean rate of 0.6 km/d. However, once they aged to 35 to 40 d there was no further up-estuary movement. The overall relationship between cohort position and cohort age was strong ( $R = 0.58$ ,  $P = 0.0001$ ). This test demonstrated that the apparent movement of early-stage anchovy was not the result of seasonal movements of adult spawners. Another prediction we tested was that migration should entail an upriver increase and a downriver decrease in cohort regional abundance. We estimated regional standing crop (the number of individuals in a specified portion of the river), scored whether a cohort's regional standing crop decreased from one sampling period to the next, and then tested whether the probability that regional standing crop decreased varied with region. The results were clear; in downriver regions, standing crop usually decreased, while in upriver regions they usually increased (Fig. 3). This test demonstrated that the apparent movement of early-stage anchovy was not entirely the result of spatial variation in mortality.

Fig 2

Fig 3

By what means might larvae migrate up-estuary? Because net flow in a river-fed estuary is seaward, a pool of passive larvae distributed randomly in the water column would on average move down-estuary (for an empirical demonstration of passive particle movement in the Hudson estuary see Hellweger et al. 2004). Of course larvae are not

passive and could exhibit behaviors that function to promote up-estuary migration, such as: 1) directed swimming away from the sea); 2) lateral preference (e.g., Forward et al. 1999), because along-river flow can have pronounced lateral variability; 3) preference for deeper water, where in many systems there is residual up-estuary flow (e.g., Melville-Smith et al. 1981); 4) periodic vertical migration. A well-documented form of the last strategy is synchronization of vertical migration and tidal flow, termed ‘selective tidal stream transport’ (reviewed by Forward and Tankersley 2001). Vertical migration that is entrained to the day/night cycle is also common in marine organisms and can in theory affect along-estuary movement (Hill 1991).

The behavioral mechanisms underlying migration of early-stage anchovy have been recently studied in the Hudson River (Schultz et al. 2000; Schultz et al. 2003). These projects have been conducted in the field, sampling the ichthyoplankton to reveal behaviors through patterns of distribution. Sampling was precisely controlled with respect to depth and tidal stage, permitting tests of temporally-averaged depth distribution as well as tests of temporal changes in depth distribution indicating periodic vertical migration.

Temporally-averaged depth distributions of early-stage anchovy have often been nonuniform but have not been consistent. In some circumstances anchovy exhibited preference for greater depth (see also Loos and Perry 1991; Schultz et al. 2003). During one three-day period of sampling in neap tide conditions at Croton Point (Fig 4B) anchovy were two to four times more concentrated at depth in the channel than at the surface. Yet under spring tide conditions a week earlier at the same site no depth preference was evident (Fig. 4A). The difference in vertical stratification between these

Fig 4

periods may be attributable to changes in vertical mixing: larval preference for greater depth was evident during neap tide but may have been overwhelmed by increased turbulence associated with more vigorous tidal flows during spring tide. Another sampling effort attempted to assess vertical stratification of anchovy at multiple sites and average over longer periods to smooth over neap-spring variability (Schultz et al. 2000). Vertical stratification was often significant but no consistent pattern emerged: at some sites anchovy were most concentrated at middle depths, at other sites the most anchovy were found in the shallowest water, and at yet other sites the greatest concentrations were in the shallows and at depth.

Anchovy also appear to exhibit vertical migration in some situations (Schultz et al. 2003). Harmonic regression (Lorda and Saila 1986) was used to test for periodic change in abundance and mean depth of anchovy in synchrony with predominant tidal cycles (i.e. the M2 tide, 12.4 h, and the M4 tide, 6.2 h) and/or the diel cycle (24 h). Periodic changes in mean abundance (Fig. 5) were consistent with diel migration into the water column at night. However small larvae during spring tide displayed no periodic changes in abundance or depth distribution. Other studies have also found that early-stage anchovy migrate vertically in a diel cycle, but while in one case anchovy were shallowest at night (Bourne and Govoni 1988), in another anchovy were deepest at night (Loos and Perry 1991).

Fig 5

Further work on depth preferences and vertical migrations is needed. There is as yet no coherent picture of how young anchovy are distributed in the water column. An important issue that has not been adequately addressed is the need for a complete depth profile, including a sample just above the bottom. The mid-water collecting gear used in

previous studies (Schultz et al. 2000; Schultz et al. 2003) was kept above the bottom to avoid fouling. Depth distributions such as that shown in Fig. 4B suggest that such collecting methods may be missing the highest concentrations of young anchovy at times.

The patterns of depth preference and vertical migration observed off Croton Point (Schultz et al. 2003) were consistent with retention in an area rather than concerted migration upriver. Estimates of transport rate were derived by combining the data on early-stage anchovy distribution with contemporaneous data on flow collected with a 600 kHz Acoustic Doppler Current Profiler (RD Instruments, San Diego CA). We estimated flux and transport velocity (Dittel et al. 1991; Rowe and Epifanio 1994; Jager and Mulder 1999) of early-stage anchovy during spring and neap tides. These analyses indicate weak movement that was predominantly downriver (Lwiza and Schultz, unpubl. data). During spring tide, small and large early-stage anchovy were moving downriver at roughly 0.05 km/d. During neap tide, small anchovy were moving downriver at about one-third that rate, while large early-stage anchovy were virtually motionless. This result is quite inconsistent with the upstream migration scenario suggested by larval survey data (Dovel 1981; Tipton 2003) and our cohort analysis. A likely explanation for this discrepancy is that flux and transport calculations were biased; no data were available on anchovy concentrations in the deepest part of the water column where net flow tends to be up-estuary.

We conclude this section with further thoughts on approaches to analyzing the estuarine redistribution of young fish. The research to date on early-stage anchovy has been conducted on two spatiotemporal scales, with fine-scale analyses of larval distributions and fluxes and broad-scale analyses of net transport. Both approaches can

yield estimates of migration rate. We advocate such complementary multi-scale research programs (Table 1). For instance, the cohort-level analysis yields insight into the broad patterns of redistribution but not the mechanism of migration. None of the methods so far employed to assess anchovy migration in the Hudson River can address individual variability. Fortunately there are methods for retrospective analysis of movement via assays for tracers of environmental conditions. Analysis of strontium-calcium ratios in fish otoliths has yielded important insights into estuarine migration (Limburg 1995; Secor and Piccoli 1996; Jessop et al. 2002). The microchemistry technique was recently applied to quantify the timing and rate of young anchovy migration in Chesapeake Bay (Kimura et al. 2000). Kimura et al.'s (2000) analyses indicated that anchovy juveniles did indeed migrate up-estuary. The microchemical signal of migration did not appear until individuals were relatively large (25 mm and larger), in contrast to the cohort analysis of Hudson River anchovy indicating that net migration occurs only among smaller individuals. There are several possible reasons for this discrepancy, including the possibility that it arises from differences between estuaries in flow patterns and larval behavior. Clearly conducting parallel cohort-level and individual-level analyses of migration in Chesapeake Bay and/or the Hudson River would be enlightening.

#### Demography and vital rates of the Hudson River anchovy

Extensive sampling of adult anchovy permits demographic comparisons between anchovy in the Hudson River and other locations. Anchovy size structure varies geographically. In the Hudson River in July 1997, yearling-and-older (mature) anchovy averaged about 70 mm fork length (Fig. 6A). A similar size structure was observed in Narragansett Bay in July 1997 (Fig. 6B). In contrast, mature anchovy in July in

Chesapeake Bay were mostly about 50 mm fork length (Newberger and Houde 1995). There is also variability in age structure among estuaries. In Narragansett Bay (Fig. 6B; Lapolla 2001) and Chesapeake Bay (Newberger and Houde 1995) most of the mature anchovy were yearlings, but the mature anchovy in the Hudson River were predominantly age-2 and older (Fig. 6A). Some reproductive parameters vary across estuaries (Table 2). In particular, batch fecundity was lower and egg mortality higher in Hudson River than in Chesapeake Bay. There also may be differences between Hudson River and Chesapeake spawning frequency and sex ratios: in comparison to the results of some Chesapeake studies Hudson River anchovy spawn more frequently, in more equitable sex ratios. Such differences in reproductive parameters may be related to the greater size and age of the Hudson River adults, environmental differences, or to geographic genetic variation.

Table 2

The demographic differences among estuaries are remarkable, yet difficult to interpret. Lapolla (2001) suggested that the large size of yearling anchovy in Narragansett Bay reflects faster growth of fish in northern populations (see also Castro and Cowen 1991) and relatively little mixing with Chesapeake Bay. However, Hudson River anchovy are comparable in size-at-age to Chesapeake Bay (cf. Fig 6 and Newberger and Houde 1995). The absence of yearling spawners in the Hudson River could be the result of delayed maturation or an age-specific exchange with other locations, such that Hudson River origin fish spawn as yearlings elsewhere and only older fish use the Hudson River estuary. The best resolution of these issues would involve a comprehensive sampling program of adults during the spawning season from multiple

major estuaries, to clarify geographic patterns in size at age, age structure, and genetic population structure.

#### Year-class strength: long-term indices and their predictors

A time series of juvenile bay anchovy abundance in the Hudson Estuary was collected through the utility monitoring program (Central Hudson Gas and Electric Corp. et al. 1999; ASA Analysis & Communication 2004). No index was developed for anchovy eggs, yolk-sac larvae, or adults in the Hudson River because of inappropriate gear (yolk-sac larvae, adults) or sampling interval mismatched to stage duration (eggs, yolk-sac larvae). An index for post-yolksac larvae (PYSL) was derived from catches in the Longitudinal River Survey (LRS; Central Hudson Gas and Electric Corp. et al. 1999); however, the earlier portions of this time series may be of limited value because the spatial coverage of the LRS did not include the lowest region of the estuary (Battery) until 1988. The juvenile index, representing the annual mean abundance of juveniles for an eight-week period from mid-August to early October, is derived from catches in the Fall Shoals Survey (FSS). The series of juvenile indices from 1979 to 2002 was published in the 2002 year class report (ASA Analysis & Communication 2004).

Juvenile abundance varied over one order of magnitude in the 23-year time series (Fig. 7A). Maximal abundance was recorded at 34.1 individuals/100 m<sup>3</sup> in 1988, while lowest abundance was 3.7 individuals/100 m<sup>3</sup> in 2000. There was no significant change in abundance over the entire time series (bivariate regression of log-transformed abundance against year,  $P = 0.10$ ), and there was no evident temporal autocorrelation in the time series (detrended time series, test for effects of one- and two-year lagged abundance  $P = 0.35$  and  $0.88$  respectively).

Fig 7

What factors contributed to fluctuations in abundance of juvenile anchovy within this time period? Among the possible ecological relationships of importance, work has focused on three potentially interacting fish species: striped bass (*Morone saxatilis*, a potential competitor and predator), Atlantic tomcod (*Microgadus tomcod*, a potential competitor), and bluefish (*Pomatomus saltatrix*, a predator). Young striped bass abundance was estimated via two indices, of post yolk-sac larvae (from the LRS, as mean abundance in a seven-week period around the period of peak abundance) and juveniles (from the Beach Seine Survey (BSS), as average number in a 100 ft haul from mid-August to early October). Other indices of early-stage striped bass (for eggs and yolk-sac larvae) may be less reliable because the duration of these stages is short relative to the one-week sampling interval of the LRS (Central Hudson Gas and Electric Corp. et al. 1999). Bluefish abundance was indexed from the BSS as average number of juveniles in a 100 ft haul from mid-August to early October. Tomcod abundance was indexed from the LRS as mean abundance of PYSL and juveniles in the LRS in May.

Analysis of the relationships among the indices supports the hypothesis that striped bass abundance is affecting anchovy abundance but does not support the hypothesis of tomcod-anchovy competition. Over the entire time series, striped bass PYSL was negatively correlated with anchovy abundance and tomcod juveniles were positively correlated with anchovy abundance; the strength of the relationships depends on whether the abundance indices are transformed (Table 3A). A multiple regression indicated that both striped bass and tomcod were independently associated with anchovy abundance (all indices log-transformed;  $P = 0.05$  for striped bass,  $P = 0.007$  for tomcod). We repeated the analyses for the latter portion of the time series (1988-2002) because: 1)

Table 3



the increased spatial coverage of the LRS in those years should yield more reliable estimates of striped bass and tomcod PYSL abundance; 2) striped bass abundance in all stages has been consistently higher in recent years. The negative association between striped bass and anchovy was pronounced in the last 14 years, and the positive association between tomcod and anchovy persisted (Table 3B; multiple regression of log-transformed indices,  $P < 0.0001$  for striped bass,  $P = 0.01$  for tomcod). In the first 9 years of the time series the abundance of tomcod was the only significant predictor of anchovy abundance ( $r = 0.72$ ,  $P = 0.03$ ).

Abiotic factors that may influence anchovy abundance were also tested for the 1988-2002 time series. The amount of freshwater flow, which has demonstrable effects on Hudson River fish community structure (Hurst et al. 2004) and has been observed to influence the distribution of early-stage bay anchovy (Schultz et al. 2000), was quantified as USGS flow at Poughkeepsie

([http://ny.water.usgs.gov/projects/dialer\\_plots/Hudson\\_R\\_at\\_Poughkeepsie\\_Freshwater\\_Discharge.htm](http://ny.water.usgs.gov/projects/dialer_plots/Hudson_R_at_Poughkeepsie_Freshwater_Discharge.htm)). We also tested for the effect of temperature; mean regional temperatures for every sampling week of the LRS (drawn from each Year Class Report, May - September) were condensed into mean monthly temperatures for the estuary from Poughkeepsie to the Battery. The anchovy juvenile index was not correlated with any monthly mean flow or temperature, nor was it correlated with seasonal average (May-September) flow or temperature (results not shown). We tested combined biotic and abiotic factors via a stepwise regression. In addition to the negative effect of PYSL striped bass abundance ( $P < 0.0001$ ), the flow during August also entered the model as a

significant regressor with a negative slope ( $P = 0.04$ ). Given the number of regressors that were tested, it seems likely that this is a spuriously significant result.

What are the mechanisms driving the negative association between anchovy and striped bass, and the positive association between anchovy and tomcod? Based on the non-significance of abiotic factors, we suggest that the associations are not the result of independent responses to the same environmental drivers. Direct interactions among these species are more likely. One possibility that explains both associations is that striped bass have a dominant negative influence on both anchovy and tomcod. Further analysis of the ecological role of striped bass should be fruitful as the species continues to recover from overexploitation.

#### Summary and prospects for further work

Recent process-oriented studies of bay anchovy in the Hudson River include research into the redistribution or migration of early life stages. We have learned that young anchovy do indeed migrate into the estuary, and we are working towards agreement among different methods of estimating migration rate. Future studies of the migration process will need to assess interannual variability in migration patterns and should include an individual-level approach via otolith microchemistry. The function of the migration is poorly understood; what benefit might there be for individuals who move up-estuary? Are these individuals substantially more successful in growth and/or survival than those that remain in coastal waters? Is there a continuous and substantial exchange of early-stage anchovy between the estuary and coastal waters or do these pools of anchovy remain distinct?

The demography of the Hudson River anchovy may be unique, even among the higher-latitude locations; certainly the anchovy in higher-latitude estuaries have a distinctly different size structure than others to the south. How these differences arise is not known. A key question in this regard is: to what extent is the Hudson anchovy pool connected with other pools in the area (e.g., Narragansett Bay) and elsewhere in the range (e.g., Chesapeake Bay)?

The accumulation of long-term monitoring data offers a rare opportunity to see how processes play out over successive year classes. Analysis of the anchovy data has shown that (unsurprisingly) there is interannual variability in juvenile abundance. Anchovy abundance has declined 10-fold since a peak in the late 1980s, but no overall change in abundance is evident over the entire time series. The analysis further suggested that one cause for the decline has been a rebound in striped bass abundance. It is not clear whether this negative interaction is competitive or predatory. There was a positive association between anchovy and tomcod, contrary to the expectation of a competitive negative association. A missing element in the analysis of ecological relationships is gelatinous zooplankton. Jellies are known to be important predators elsewhere and are certainly abundant in the lower reaches of the estuary during the summer (ETS, pers. obs.). The lack of temperature and flow effects on the estuarine population of juvenile anchovy may be attributable to connections with coastal waters. Perhaps local perturbations disappear because their effect is spread out well beyond the estuary, as young anchovy in the river move out to the coastal waters and vice versa. Revealing the various connections between the Hudson Estuary anchovies, those in other

local waters, and those of other major estuaries, is clearly an important and challenging task for the future.

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Table 1. Comparison of empirical methods of transport/migration analysis. For each method we list the scale of the analysis, precision of migration estimates, whether the method provides any direct information on the mechanism by which the transport occurs, and whether the method provides any information on individual variability in transport history. The fine-scale analyses of larval distribution represented by Schultz et al. (2003), and of larval flux (Lwiza, unpubl.) are combined into one row.

Method	Spatiotemporal Scale	Precision	Mechanistic	Individual variability
Behavior/Flux	Fine	Moderate	yes	no
Microchemistry	Fine	High	no	yes
Survey	Broad	Low	no	no
Cohort	Broad	Moderate	no	no

Table 2. Demographic comparisons between bay anchovy in the Hudson River and Chesapeake Bay.

Variable	Hudson	Chesapeake
Spawning frequency (%/d)	73 – 89% <sup>a</sup>	67 - 100% <sup>b</sup> ; 54 – 78% <sup>b</sup>
Fecundity (eggs/g)	506 ± 17.3 (SE) <sup>a</sup>	687 ± 55 (SE) <sup>b</sup> ; 740 – 803 <sup>c</sup>
Egg mortality (%/d)	72 - 99% (mean 93%) <sup>a</sup>	73 - 78% <sup>d</sup>
Sex ratio (%)	50% <sup>a</sup>	>50% <sup>e</sup> ; 45% - 57% <sup>c</sup>

<sup>a</sup> Bassista and Hartman (In press)

<sup>b</sup> Zastrow et al. (1991), June and July

<sup>c</sup> Luo and Musick (1991), July and August

<sup>d</sup> Dorsey et al. (1996)

<sup>e</sup> Newberger (1989)



Table 3. Interannual variation in anchovy abundance: correlation of juvenile bay anchovy abundance with abundance of potential predators and competitors. The correlations are tested for untransformed and log-transformed indices, and over two intervals.

Factor	<i>Untransformed</i>		<i>Log-transformed</i>	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
A) 1979-2002				
Striped bass PYSL	-0.52	0.0091	-0.39	0.062
Striped bass juveniles	-0.051	0.81	0.14	0.51
Bluefish juveniles	-0.17	0.43	0.05	0.81
Tomcod PYSL/ juveniles	0.48	0.018	0.53	0.0075
B) 1988-2002				
Striped bass PYSL	-0.70	0.0034	-0.84	< 0.0001
Striped bass juveniles	-0.081	0.77	0.24	0.38
Bluefish juveniles	-0.20	0.50	0.014	0.96
Tomcod PYSL/ juveniles	0.42	0.12	0.46	0.087

## Figure captions

- Fig. 1. Along-river distribution of early-stage anchovy and salinity for two different time periods in 1997. Concentration of anchovy (mean  $\pm$  standard error) that were 10-22 mm (total length) and salinity are plotted against location as the mean along-river distance of eight regions used for the Longitudinal River Survey (LRS). Concentration of anchovy was determined in hydroacoustic surveys; salinity was determined from the mean of two CTD deployments per LRS region. Letters above the bars signify assignment to groups that are not statistically distinguishable by Tukey's Studentized Range Test on LS means. Note that the scales for anchovy densities differ between the two panels. A) During the spawning season, June – early August. B) After the spawning season, September. From Tipton (2003).
- Fig. 2. Net cohort transport of early-stage bay anchovy. Ten cohorts were sampled multiple times at biweekly intervals in 1998. The mean river location of each cohort is plotted against the age of the cohort. Identity of each cohort is indicated by symbol, as represented in the legend. From Schultz et al. (In press).
- Fig. 3. Along-river shifts in cohort distributions, as indicated by changes in regional standing crop. Ten cohorts were sampled multiple times at biweekly intervals in 1998 (see Fig. 2). Changes in regional standing crop from one sample to the next are summarized as the proportion of intervals that cohorts decreased in regional standing crop against location, as the mean along-river distance of eight regions used for the LRS. From Schultz et al. (In press).

Fig. 4. Lateral and vertical distribution of early-stage anchovy at Croton Point, late July 1998. Log-transformed larval concentration (mean  $\pm$  standard error) is plotted for multiple depths in the river channel and for the uppermost 2 m over the east and west shoals. For clarity the depth values for east and west shoal stations have been slightly offset from 2 m and only one side of the error bar is displayed for some points. Small larvae are  $\leq 11$  mm standard length and large larvae and juveniles are  $\geq 13$  mm SL. The legend applies to both panels. A) Cruise 1, during spring tide conditions. B) Cruise 2, during neap tide conditions. From Schultz et al. (2003).

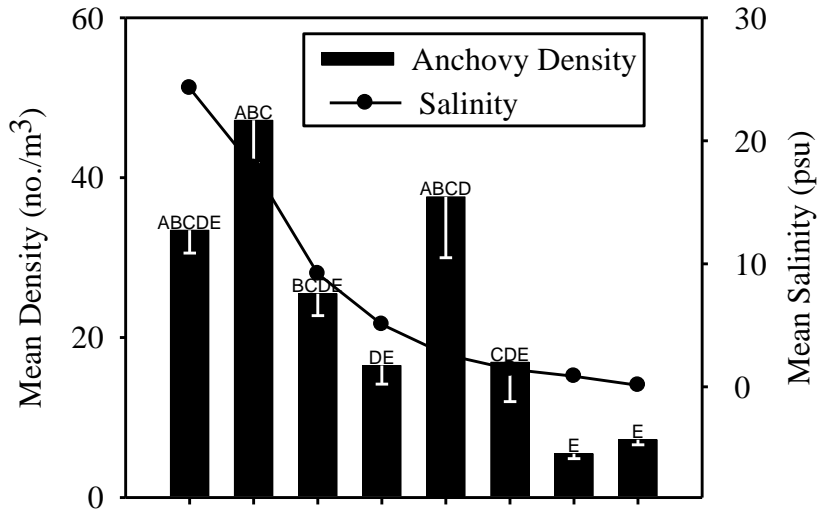
Fig. 5. Temporal variability in abundance of early-stage anchovy at Croton Point, late July 1998. The symbols represent observed values of depth-averaged concentration (log-transformed) against the time the sample was collected. The lines represent the fitted relationship based on harmonic regression. Results for small ( $\leq 11$  mm) and large ( $\geq 13$  mm) are presented separately; for clarity the values for small larvae have been shifted up one increment on the y-axis and the values for large larvae have been shifted down one increment. The time series for cruise 1, during spring tide conditions, are to the left, and the time series for cruise 2 (neap tide conditions) are to the right. From Schultz et al. (2003).

Fig. 6. Size and age structure of two northern populations of the bay anchovy in July 1997. Bars in the size-frequency histograms are subdivided to represent different age classes, as shown in the legend. A) Hudson River, from Bassista and Hartman (In press). B) Narragansett Bay, from Lapolla (2001).

Fig. 7. Long-term record of early-stage bay anchovy abundance in the Hudson River. A) The year-class index for juvenile anchovy for 1979 - 2001. Error bars represent  $\pm 2$  standard errors. B) A long-term inverse relationship between bay anchovy abundance and striped bass abundance, 1979-2001. The index of abundance for juvenile bay anchovy is plotted against the index for post-yolk sac striped bass larvae. The first 9 years of data are plotted in a different symbol from the subsequent 14 years.

fig. 1

A) Spawning Period 1997



B) Post-spawning Period 1997

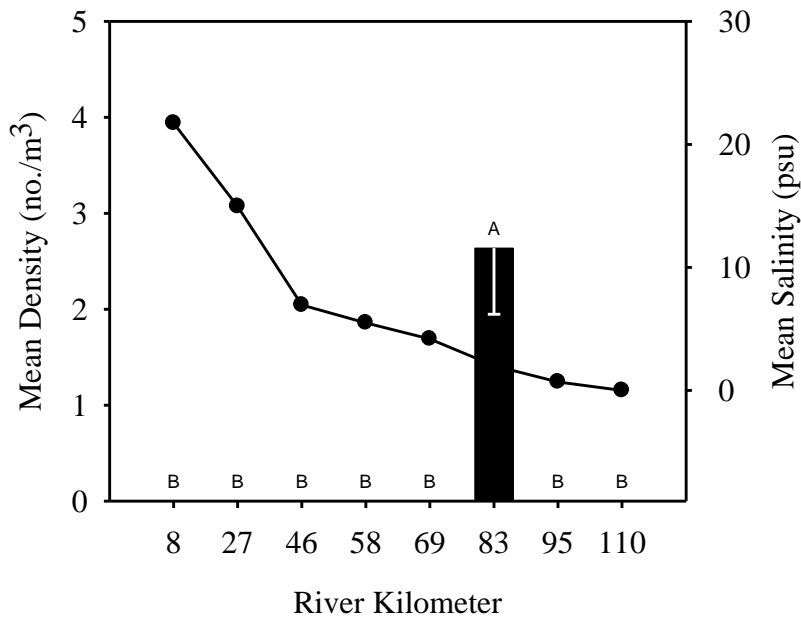


Fig. 2

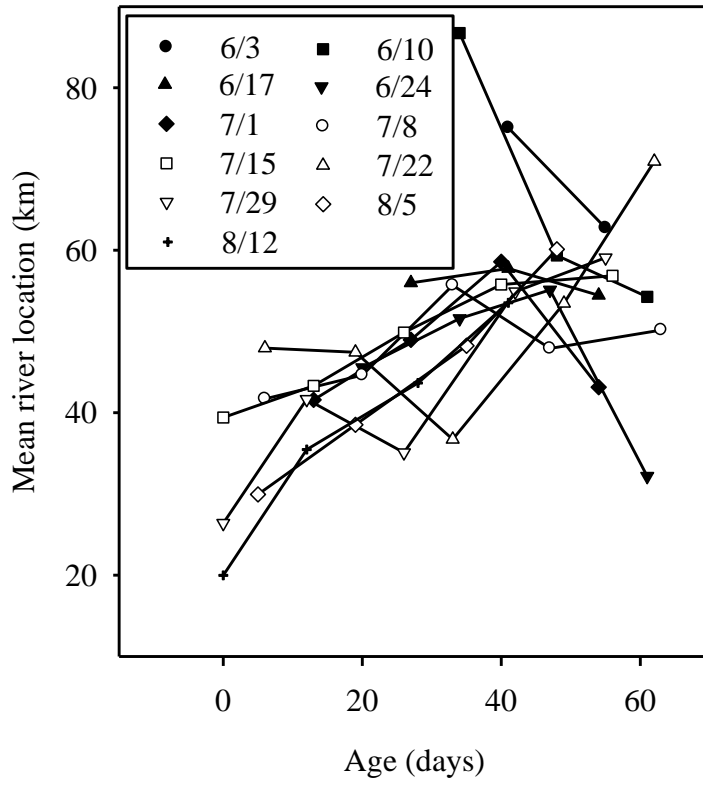


Fig. 3

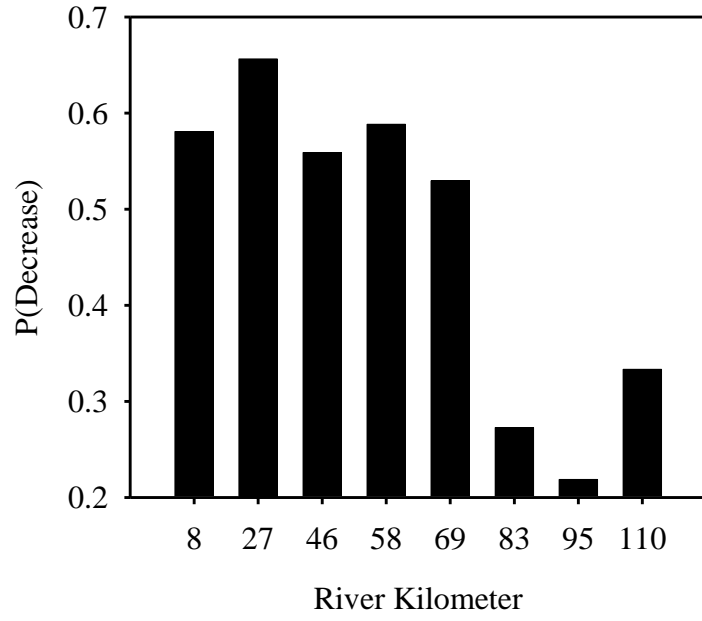
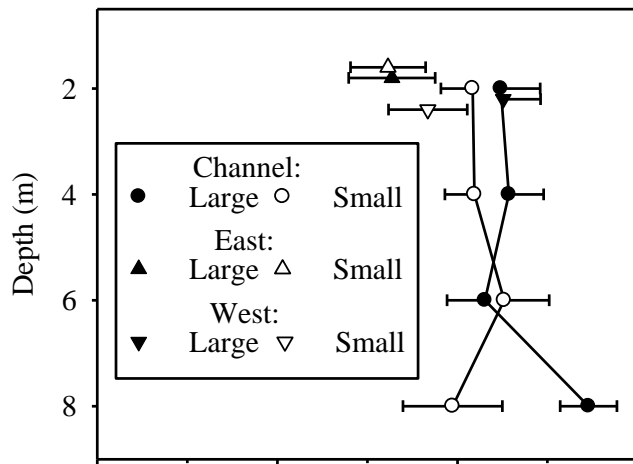


Fig. 4

## A) Cruise 1, spring tide



## B) Cruise 2, neap tide

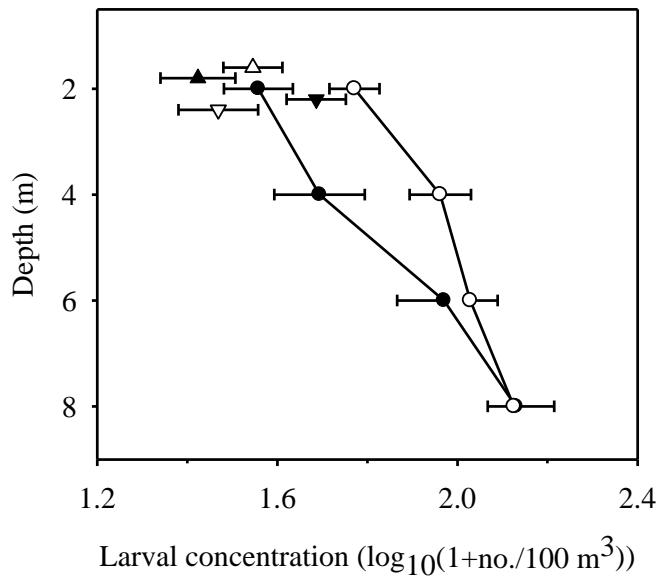




Fig. 5

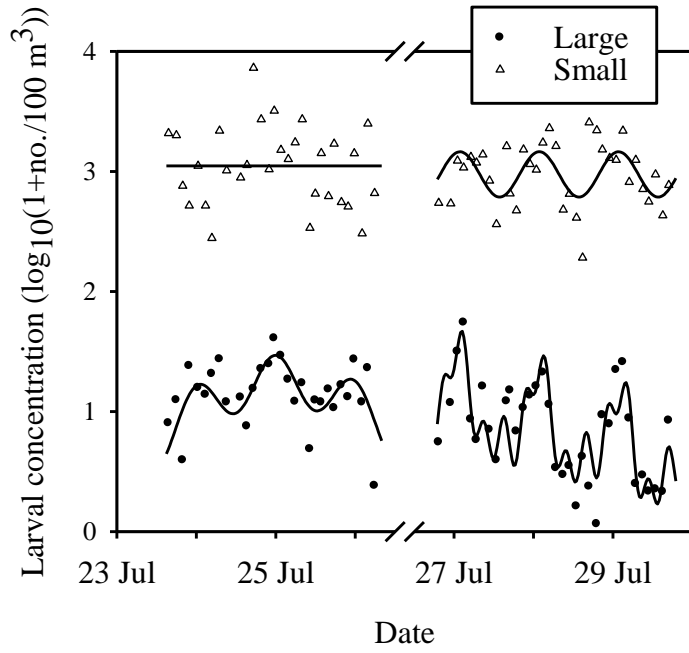
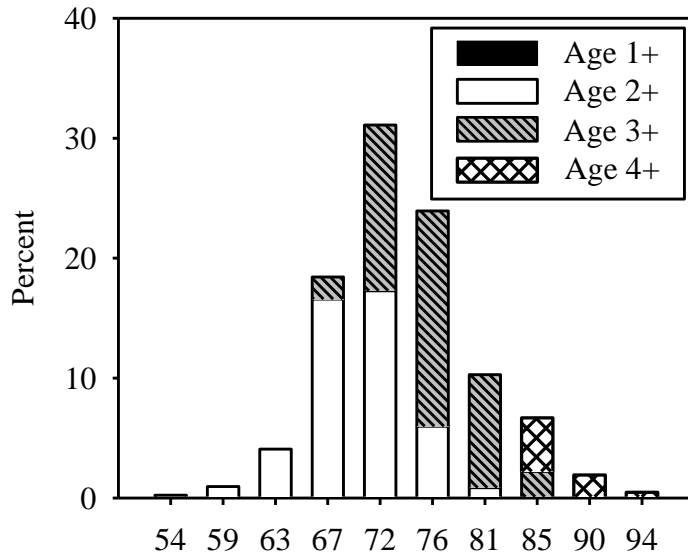


Fig. 6

A) Hudson River, July 1997



B) Narragansett Bay, July 1997

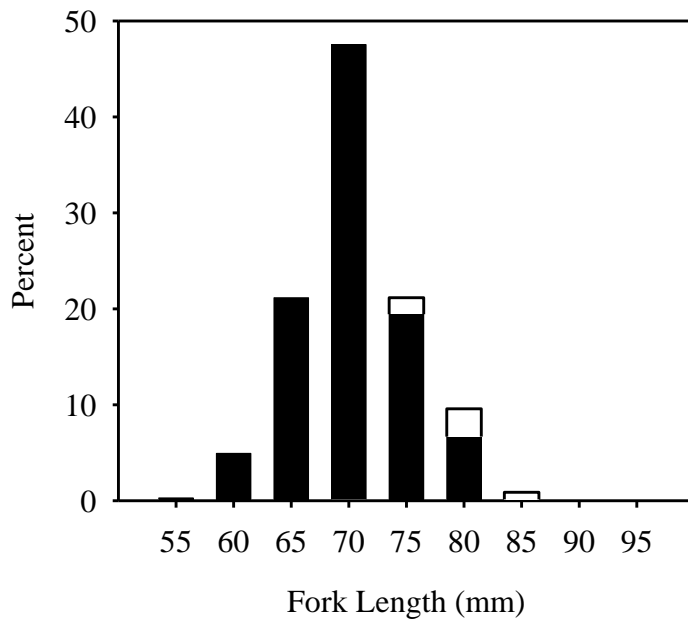
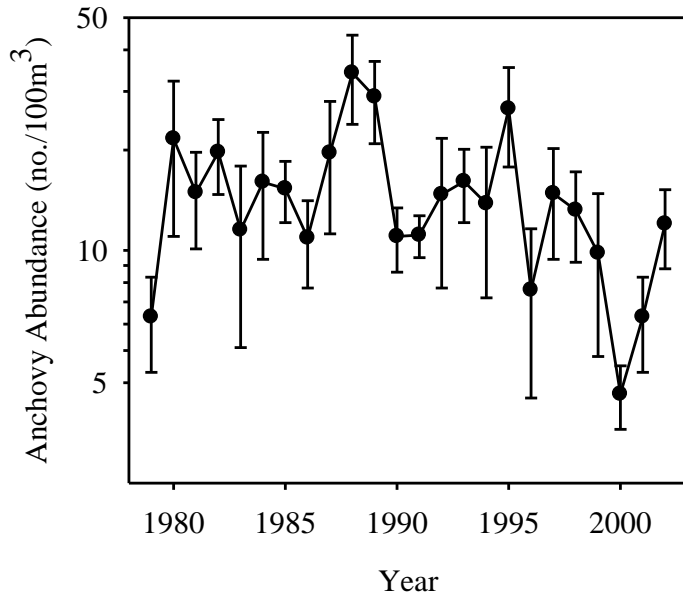


Fig. 7

A)



B)

