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Expatriation of *Xyrichtys novacula* (Pisces: Labridae) larvae: Evidence of rapid cross-slope exchange

by Jonathan A. Hare¹ and Robert K. Cowen¹

ABSTRACT

Larvae of *Xyrichtys novacula* (Pisces: Labridae) have been collected in the Middle Atlantic Bight (MAB) hundreds of kilometers north of reported adult ranges by both the Marine Monitoring and Assessment Program (MARMAP) and by our ichthyoplankton cruises. These larvae could be from a previously unknown population north of Cape Hatteras or they could have been transported north from southern populations. In order to examine these two hypotheses both biological and physical oceanographic data were considered, including size-specific larval distribution, larval age, vertical distribution of larvae, satellite imagery of sea surface temperature, and temperature and salinity measurements. Larvae captured during our 1988 ichthyoplankton cruises ranged from 3.11 mm to 13.13 mm in length with small larvae (≤ 5 mm) found in association with the shelf break and larger larvae (> 5 mm) found distributed across the outer shelf and shelf break. Based on aging of daily otolith increments larval age was found to range from 7 to 36 days and backcalculated birthdates, derived from estimated age and date of capture, were found to be from mid-June to early August. Larvae occurred predominantly near the surface (≤ 10 m) at night and deeper (> 10 m) during the day. Concurrent hydrographic data revealed that small larvae were found in shelf water (< 35 psu) but with underlying slope water (> 35 psu) at depths of 15–30 m suggesting that small larvae were in shelf water at night but either at the boundary with or within slope water during the day. Satellite imagery from 1988 revealed a warm-core ring offshore of our 1988 sampling area. An analysis of historical warm-core ring data from Northwest Atlantic Fisheries Organization data reports in conjunction with captures of *X. novacula* during the years 1984–1987 demonstrated that the presence of warm-core rings offshore was associated with the occurrence of *X. novacula* on the MAB shelf, north of Chesapeake Bay. The feasibility of northward transport associated with the Gulf Stream and cross-slope transport associated with a warm-core ring was examined with a simple model which demonstrated that the required transport velocities were within the range of velocities presented in the literature. It is suggested that larvae are rapidly transported from south of Cape Hatteras to the MAB shelf break by advection associated with the Gulf Stream and a concomitant cross-slope flow related with the western edge of warm-core rings.

1. Introduction

Pelagic larvae of marine fish are typically dispersed away from the location of spawning due to the susceptibility of larvae to passive transport by advective forces

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(Hempel, 1979; Sale, 1980; Kendall *et al.*, 1984). The outcome of larval dispersal, however, is highly variable because a combination of advective forces (ie. currents, filaments, jets, eddies, and wind driven flow) are usually involved in the transport of larvae (e.g. O'Boyle *et al.*, 1984; Cowen, 1985; Fiedler, 1986; Chenoweth *et al.*, 1989; Crawford *et al.*, 1990). Contributing to this variability are several biological factors which may affect the susceptibility of larvae to advection. First, the location of spawning determines the initial advective forces encountered by the larvae (Shapiro *et al.*, 1988; McGurk, 1989). Second, the duration of the larval stage dictates the amount of time over which advection can occur and has been shown to be highly variable between individuals, species, genera and families (Victor, 1986a; Thresher and Brothers, 1989; Thresher *et al.*, 1989; Wellington and Victor, 1989; Cowen, 1991). Third, in a depth stratified water column, the vertical position of larvae will determine the water masses occupied and in part the advective forces encountered. Thus, the outcome of larval dispersal is dependent on three biological factors: starting point of advection, duration of susceptibility to advection, and vertical distribution of larvae, as well as the combination of advective forces experienced by the larvae.

One regularly observed example of the dispersal process is transport of various tropical fish larvae into temperate waters of the western North Atlantic (Colton, 1961; Markle *et al.*, 1980; Evseenko, 1982; Wroblewski and Cheney, 1984; Mountain *et al.*, 1989). In our own work, larvae of a tropical labrid have been captured in the Middle Atlantic Bight (MAB) during each of our 1988 ichthyoplankton cruises. These labrid larvae have also been collected as far north as eastern Georges Bank by the Marine Monitoring, Assessment, and Prediction (MARMAP) surveys. We have tentatively identified these larvae as *Xyrichtys novacula* (Pisces: Labridae) based on meristics and morphology and considering that *X. novacula* is found as far north as the Carolinas while the other two western Atlantic species of *Xyrichtys* are only found south of southern Florida (Randall, 1965). Adult *Xyrichtys* live in close association with the bottom and dive into the sand for protection, probably into specific sites (Clark, 1983). They establish territories and are broadcast spawners producing pelagic offspring (Victor, 1987; Baird, 1988). Consequently, pelagic larvae of *X. novacula* are consistently collected as far as 1000 km northeast of reported adult ranges.

The object of this study was to elucidate the combined biological and physical processes which result in the dispersal of *X. novacula* larvae into the temperate waters of the western North Atlantic. Two alternative hypotheses were considered regarding the source of these larvae: (a) the existence of an unknown spawning population north of Cape Hatteras outside of reported adult ranges, termed the "resident hypothesis," or (b) the presence of a spawning population south of Cape Hatteras with northward transport of larvae, termed the "expatriate hypothesis." The following assumptions were made in order to test these hypotheses: (1) the

distribution of larvae collected represented the outcome of dispersal; (2) the larval source was one of the two hypothesized locations; (3) the larval age at collection represented the duration of larval dispersal; and (4) the vertical catch data indicated the presence of larvae within particular depth stratified water masses. To identify the possible advective forces involved, three types of information were used: (1) temperature and salinity data measured in conjunction with larval fish collections, (2) satellite derived sea surface temperature data, and (3) descriptions from the literature of the physical oceanography from Cape Hatteras to Georges Bank.

2. Materials and methods

a. Larval collection and biology. Two data sets were examined for the presence of *X. novacula* larvae north of Cape Hatteras: MARMAP surveys from the years 1984 to 1987 and our ichthyoplankton surveys of 1988. The MARMAP surveys were conducted by the National Marine Fisheries Service (NMFS) at monthly to bimonthly intervals over the continental shelf from Cape Hatteras to Cape Sable, Nova Scotia. Oblique plankton tows were made using a 0.61 m bongo sampler fitted with 505 μm mesh net for larval fish collection. Complete sampling methodology and station locations were presented in Sibunka and Silverman (1989). Labridae larvae obtained from MARMAP surveys were examined and *X. novacula* identified, counted and measured. Preflexion larval lengths were measured as total length (TL) and post-flexion larval lengths were measured as standard length (SL). All length measurements were performed with a digitized light microscopy video image (Optical Pattern Recognition System [OPRS], Biosonics Corporation, Seattle, WA). Two length classes, ≤ 5 mm and > 5 mm, were considered for size-specific distribution analysis. Age and vertical distribution data were not available from MARMAP data due to preservation and collection techniques.

The second data set was obtained from four of our cruises conducted approximately every other week from July 6 to August 12, 1988. During each cruise, 35 to 49 stations were sampled (weather depending) along five transects from Montauk Point, New York to Little Egg Inlet, New Jersey, out to a depth of 2000 m. At each station, ichthyoplankton were collected with a 505 μm mesh, opening-closing, 1 m² Tucker Trawl sampling at three depths, 0–5 m, 5–10 m and 10–15 m, with a tow duration of five minutes at each depth. A flow meter was attached to the bridle of the Tucker Trawl to calculate the water volume sampled over all three depths. All samples were split onboard using a Folsom Plankton Splitter, with one half of the sample preserved in 5% formalin for identification and measurement and the other half preserved in 95% ethanol for aging. The formalin samples were sorted for eggs and larvae and the larvae were identified to the lowest possible taxonomic level. All *X. novacula* larvae from the formalin samples were counted and measured to the nearest 0.01 mm. Densities of two length classes, ≤ 5 mm and > 5 mm, were

calculated for size-specific distribution analysis by correcting for the sample splitting, summing all three depths and dividing by the total volume filtered.

An age-length relationship was determined for *X. novacula* larvae utilizing otolith aging techniques (Pannella, 1971; Campana and Neilson, 1985) and assuming daily increment formation based on previous validation studies on other labrids (Victor, 1982; Cowen, 1985). The larvae used for aging ($n = 39$) represented the entire size range collected. Each larvae was measured and both sagittal otoliths were removed, cleared of tissue and placed on a glass slide in immersion oil. For each otolith, two to four separate blind counts of the increments were made along the maximum radius at $400\times$ with the aid of OPRS. The maximum otolith radius and width of each increment were also measured. The age of an individual was determined from the mean counts of both sagitta, plus two days to account for the period between spawning and first otolith ring deposition (Victor, 1986a). Preservative specific shrinkage differences (Theilacker, 1980) were examined to apply the ethanol derived age-length relationship to formalin preserved larvae. All larvae from the formalin ($n = 268$) and ethanol ($n = 268$) halves of two samples were measured and eight correction factors (+0%, +6%, +7%, +7.5%, +8%, +8.5%, +9% and +10%) applied to the lengths of the ethanol preserved larvae. The corrected ethanol lengths were tested against the formalin lengths using the Kolmogorov-Smirnov Two Sample Test (Zar, 1984) and the correction factor resulting in the least Maximum Difference was used to convert the lengths of the aged larvae to corrected lengths. The resulting age-corrected length relationship was then used to transform the lengths of all formalin larvae into estimated ages. Estimated ages were used in conjunction with the date of capture to estimate the birthdates of all formalin larvae.

Depth stratified capture data collected by the three nets of the Tucker Trawl, 0–5 m, 5–10 m, 10–15 m, were examined to determine the overall vertical distribution of *X. novacula* larvae. The depth-stratified data were also analyzed in relation to time of day for evidence of daily vertical migration and in relation to length for evidence of ontogenetic pattern in vertical distribution.

b. Physical analyses. During our 1988 ichthyoplankton cruises, salinity and temperature data were collected at every station using a Martek Mark VI Multiparameter Recorder. Measurements were made every meter from the surface to approximately 70 m, or to 10 m from the bottom, whichever depth was less. Salinity and temperature depth profiles and along-transect cross-sections were created in order to examine the hydrographic structure of the sampling area. Identified features included thermocline depth, pycnocline depth, shelf water distribution, slope water distribution and location of the shelf-slope front. The size-specific distribution of *X. novacula* was examined in relation to the observed hydrographic structure.

Satellite derived sea surface temperature images from the summer of 1988 covering the region from Cape Hatteras to Georges Bank were examined for large

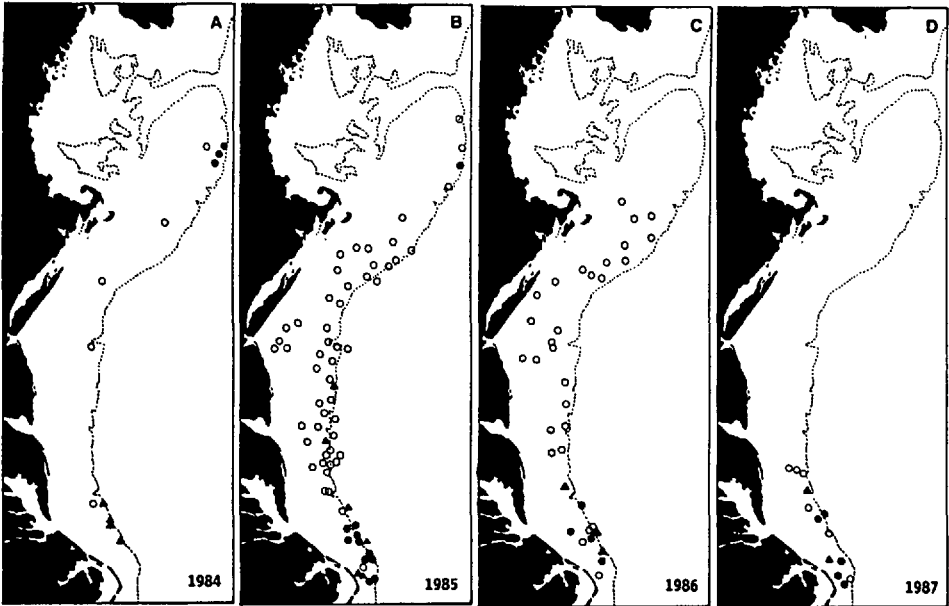


Figure 1. Distribution of *Xyrichtys novacula* larvae captured by MARMAP surveys during the years 1984–1987, (A) to (D) respectively. Filled triangles represent stations where larvae ≤ 5 mm were captured, filled circles represent stations where larvae both ≤ 5 mm and > 5 mm were captured, and open circles represent stations where larvae > 5 mm were captured. The 200 m isobath (dotted line) represents the shelf break.

scale physical features such as the location of the Gulf Stream, presence of meanders, presence of warm-core rings, and position of shelf-slope front. Historical warm-core ring data from 1984 to 1987 (Price, 1985; Price and Barton, 1986, 1987; Barton and Sano, 1988) were examined to determine whether a relationship existed between *X. novacula* larvae captured north of Cape Hatteras by MARMAP and the presence of warm-core rings in the slope water. The MARMAP stations where *X. novacula* larvae were captured were assigned to one of the six zones which the warm-core ring reports use to subdivide the region from Cape Hatteras to Georges Bank. For each capture station the presence (1) or absence (0) of a warm-core ring was recorded and the resulting binary code was tested for randomness using a sign test (Wilkinson, 1987).

3. Results

a. Biological analyses. The MARMAP survey data demonstrated considerable inter-annual variation in the along-shelf distribution of larval *X. novacula*, yet little variation in the pattern of across-shelf distribution. A total of 400 *X. novacula* larvae were captured by MARMAP north of Cape Hatteras in numbers ranging from 42 in 1984 to 160 in 1985. In 1984 (Fig. 1A) the distribution of larvae was dichotomous,

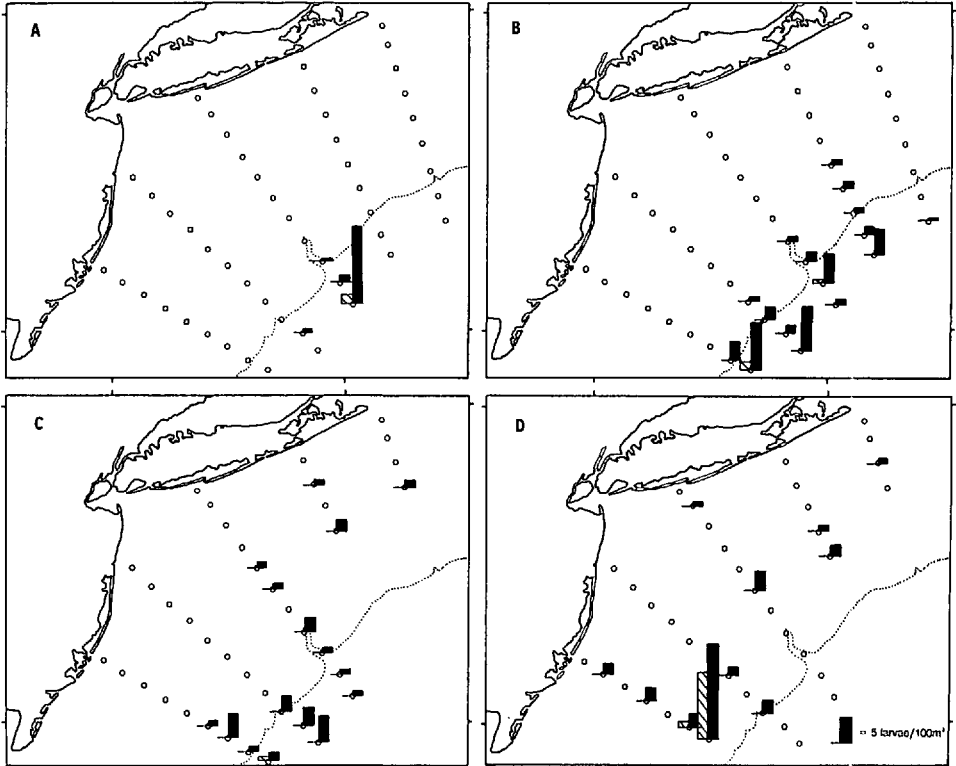


Figure 2. Distribution and density of *Xyrichtys novacula* larvae captured during 1988 summer ichthyoplankton cruises: (A) DEL-3-88, July 6–9, (B) DEL-4-88, July 16–22, (C) DEL-5-88, July 29–August 2, and (D) DEL-6-88, August 8–12. Hatched bars represent the density of larvae ≤ 5 mm in length and solid bars represent the density of larvae > 5 mm in length. A key to the height of the bars is in the lower right hand corner. The 200 m isobath (dotted line) represents the shelf break.

with most captured either south of Chesapeake Bay or on Georges Bank, and only a few larvae found between the two areas. The distributions in 1985 (Fig. 1B) and 1986 (Fig. 1C) ranged throughout the MAB from Cape Hatteras to Georges Bank. In contrast, the distribution in 1987 was limited to south of Delaware Bay (Fig. 1D). Considering all years, small larvae (≤ 5 mm) were collected predominantly along the shelf break. Larger larvae (> 5 mm), however, were not restricted to the shelf break and were distributed across the outer continental shelf.

During our cruises in 1988, small *X. novacula* larvae (≤ 5 mm) also appeared to be associated with the shelf break. *X. novacula* larvae were quite abundant and collected in all four cruises in numbers ranging from 138 on the first and third cruise to 276 on the fourth cruise. During the first cruise, both small and large (> 5 mm) larvae were only found offshore of Hudson Canyon (Fig. 2A). The distribution of *X. novacula* larvae during the second cruise encompassed an area northeast and

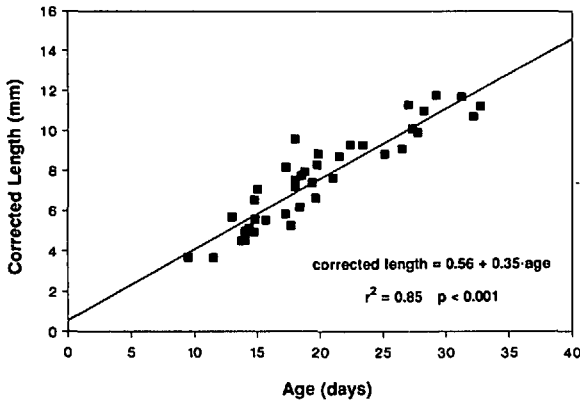


Figure 3. Age-corrected length relationship for *Xyrichtys novacula* larvae ($n = 39$) captured in the Middle Atlantic Bight during the summer of 1988.

southwest of the capture locations in the previous cruise, and in general remained associated with the shelf break (Fig. 2B). During the third cruise, small larvae were once again captured along the shelf break, however, larger larvae were found on the shelf (Fig. 2C). A majority of the larvae captured during the last cruise were on the shelf but small larvae were predominantly collected within 20 km of the shelf break (Fig. 2D).

The age corrected-length relationship (Fig. 3) was significant ($p < 0.001$), as was the relationship between age and otolith radius ($\text{radius} = -11.150 + 3.582 \text{ age}$, $r^2 = 0.949$, $p < 0.001$) and the relationship between otolith radius and corrected-length ($\text{corrected-length} = 1.535 + 0.100 \text{ radius}$, $r^2 = 0.905$, $p < 0.001$). There was a trend of decreasing increment width after increment 25 but that decrease was not significant (Two-Tailed t -Test, $p > 0.05$). In the comparison of corrected ethanol and formalin lengths, the conversion factor of +8.5% applied to the ethanol lengths resulted in the smallest Maximum Difference (K-S Two Sample Test, MD = 0.060). Based on the age corrected-length relationship, larval ages ranged from 8 to 36 days with a median of 17.8 days (Fig. 4). Larvae ≤ 5 mm were therefore, approximately ≤ 12.5 days old. Backcalculated birthdates of all larvae from all cruises demonstrated that spawning occurred over the period of June 19 to August 2 (Fig. 5), with an apparent continual influx of young larvae during the six weeks of sampling.

Analysis of the depth stratified capture data demonstrated that *X. novacula* larvae were most abundant in the 10–15 m depth range ($n = 638$; 76%). Since 10–15 m was the deepest depth sampled, it was possible that larvae were also distributed deeper than 15 m. However, an analysis of the depth distribution with respect to time indicated that at night a majority of larvae were captured in the upper 10 m of the water column (Fig. 6). Therefore, *X. novacula* larvae occur predominantly in the 10–15 m range and deeper during the day but at night they occur predominantly in the upper 10 m of the water column. This interpretation of the depth-stratified data

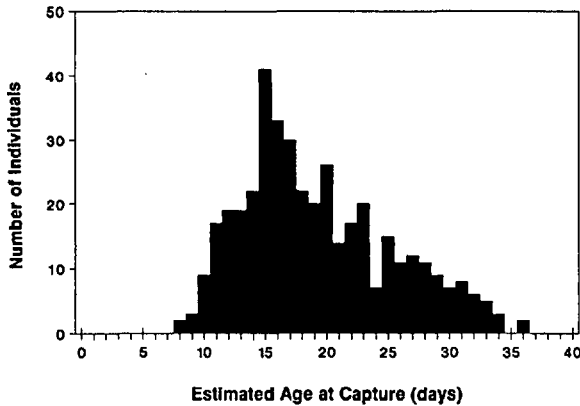


Figure 4. Estimated age at capture for all *Xyrichtys novacula* larvae preserved in formalin ($n = 412$) which were collected during the summer of 1988.

is supported by the fact that *X. novacula* larvae were collected only in the upper 30 m of the water column (Hare and Cowen, unpublished data) during an ichthyoplankton survey off of southern New Jersey in 1982 using a Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) sampling eight discrete depth intervals: 100–80 m, 80–60 m, 60–50 m, 50–40 m, 40–30 m, 30–20 m, 20–10 m and 10–0 m (LeBlanc, 1986).

b. Physical analysis. The temperature and salinity data revealed physical structure in the sampling region (Fig. 7) consistent with other studies (Gordon *et al.*, 1976; Burrage and Garvine, 1988; Houghton *et al.*, 1988). The seasonal thermocline was well developed and generally became deeper offshore. Cold bottom water, or the “cold pool” (Ketchum and Corwin, 1964), and a subsurface shelf-slope temperature front were clearly evident. A layer of low salinity water (30–34 psu) was found stretching from the coast to distances of 100 nautical miles (185 km) offshore. Underneath and offshore of the fresh coastal water was higher salinity shelf and slope water. The salinity maximum was observed associated with the pycnocline as also reported by Gordon and Aikman (1981). All small *X. novacula* larvae (≤ 5 mm) were captured in waters with salinities of 30 to 33.5 psu (Fig. 8), however, at all these stations but one, salinity exceeded 35 psu at depths between 17 to 30 m (Fig. 8). Considering the vertical distribution data, this hydrographic structure indicates that at night, small *X. novacula* larvae are in low salinity water (< 35 psu) but during the day they are within or at the boundary of the underlying high salinity water (> 35 psu).

Sea surface temperature satellite imagery from the summer of 1988 showed two warm-core rings in the slope water: Ring 88-C south of Cape Cod and Long Island, and Ring 88-E to the east of 88-C and south of Georges Bank and Cape Cod (Fig. 9). During the period of our four cruises (July 6–August 12, 1988), Ring 88-C drifted

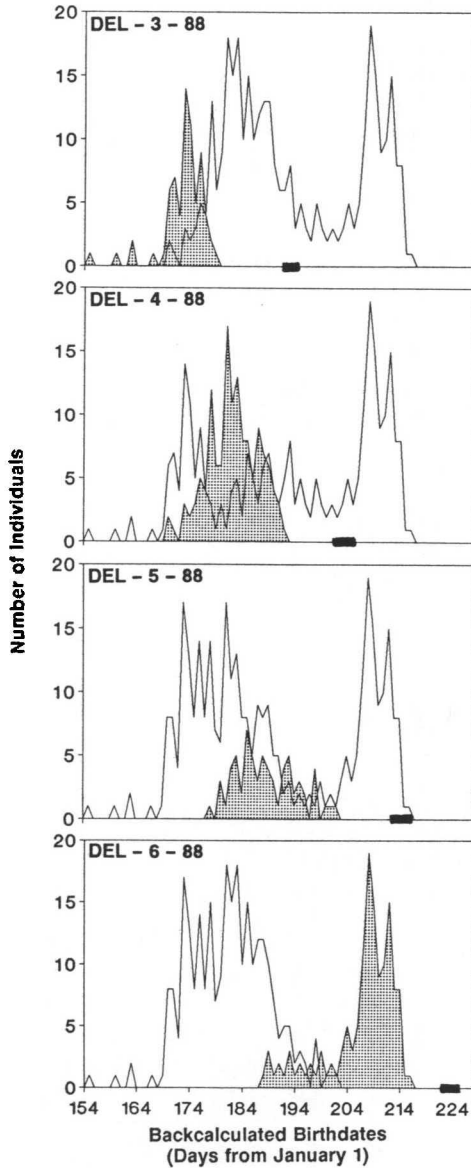


Figure 5. Backcalculated birthdates of *Xyrichtys novacula* larvae collected during the summer of 1988. Each panel shows the birthdates of larvae captured during one of the four cruises (shaded) and the birthdates of larvae captured during the other three cruises (line). The rectangle on the x-axis of each panel denotes the dates over which the specific cruise occurred.

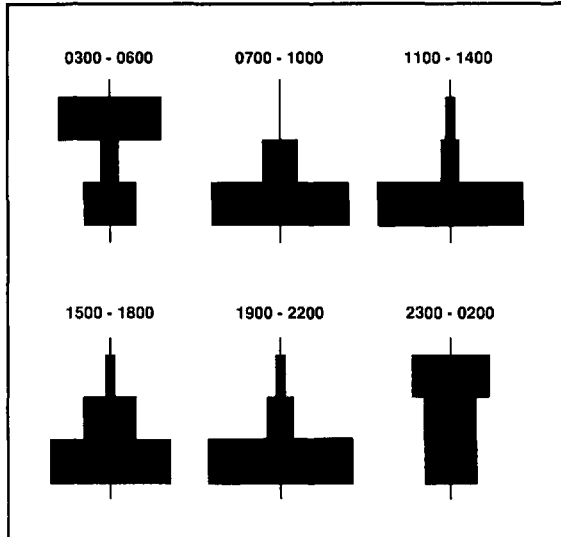


Figure 6. Percentage of total catch of *Xyrichys novacula* larvae captured in each depth strata sampled (0–5 m, 5–10 m, and 10–15 m) in relation to time of day. For each four hour time period, the 0–5 m catch is represented by the top bar, the 5–10 m catch by the middle bar, and the 10–15 m catch by the bottom bar.

southwest along the offshore boundary of our sampling area (Sano and Fairfield, 1989), demonstrating the presence of a warm-core ring offshore for all *X. novacula* captures on the shelf during 1988. For the MARMAP surveys, the presence or absence of warm-core rings in the slope water at the time of *X. novacula* captures on the shelf from Cape Hatteras to Georges Bank was not significantly different from a random sequence (Table 1). However, if the presence of a warm-core ring in an adjacent zone was also considered as a ring being present, then the presence of *X. novacula* larvae compared with the presence or absence of warm-core rings was significantly different from random (Table 1). In addition, if Zone 8, Cape Hatteras to Chesapeake Bay, was considered separately from zones 3–7, Chesapeake Bay to Georges Bank, the relationships between larvae and rings in both instances were significantly different from random (Table 1). *X. novacula* were found on the shelf from Chesapeake Bay to Cape Hatteras predominantly when there was not a ring offshore. North of Chesapeake Bay, however, larvae were only found on the shelf when there were rings offshore (Table 1). The presence of warm-core rings therefore, appears to be associated with the presence of *X. novacula* larvae on the shelf north of Chesapeake Bay.

4. Physical oceanography of the region

The physical oceanography of the region from Cape Hatteras to Georges Bank is dominated by three water masses: the Gulf Stream, slope water, and shelf water. The

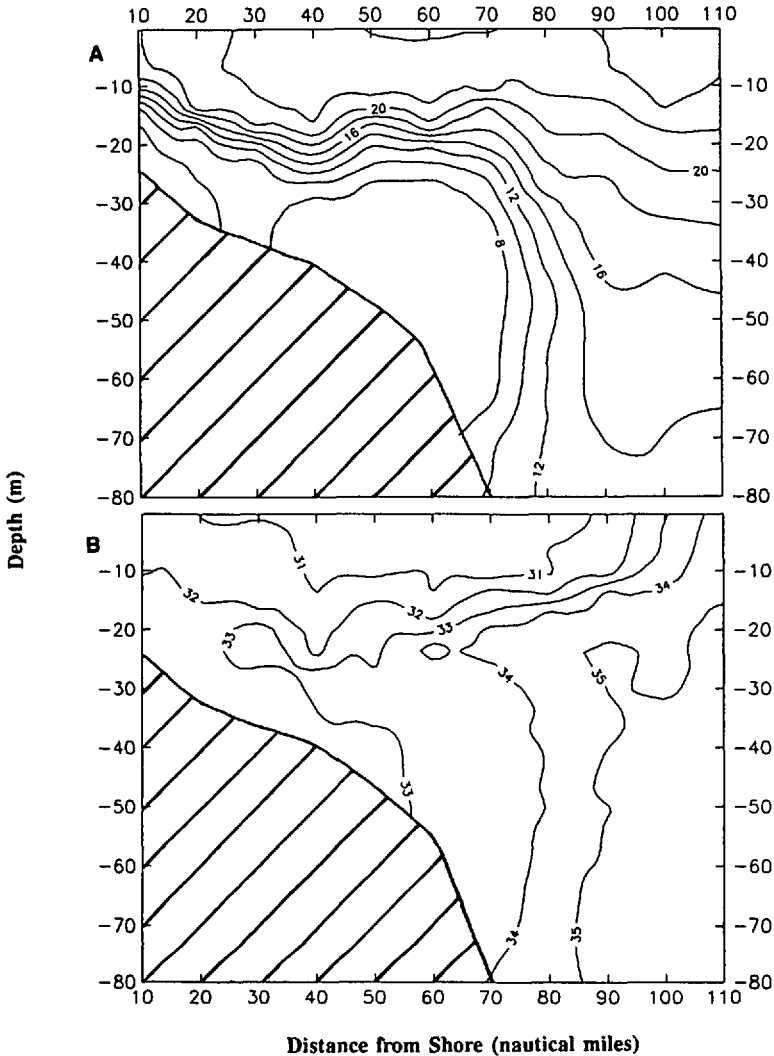


Figure 7. Cross section of (A) temperature ($^{\circ}\text{C}$) and (B) salinity (psu) measured along transect 2 ($39^{\circ} 59' \text{N}$, $73^{\circ} 50' \text{W}$ to $38^{\circ} 52' \text{N}$, $72^{\circ} 13' \text{W}$), during the second cruise DEL-4-88, July 18–19, 1988.

Gulf Stream flows northward along the coast of the southern United States and separates from the continental shelf at about 36°N , slightly north of Cape Hatteras ($35^{\circ}15' \text{N}$; Brown *et al.*, 1986; Auer, 1987). Average current velocities at the surface of the main axis are $100\text{--}200 \text{ cm s}^{-1}$ (Pierce and Joyce, 1988; Leaman *et al.*, 1989; Joyce *et al.*, 1990). Meanders in the Gulf Stream downstream of Cape Hatteras change the local direction of flow (Hansen, 1970; Halliwell and Mooers, 1979) and sometimes pinch off, forming warm-core rings in the slope water north of the Gulf Stream (Hansen, 1970; Saunders, 1971; Gotthardt and Potocsky, 1974). Warm-core rings

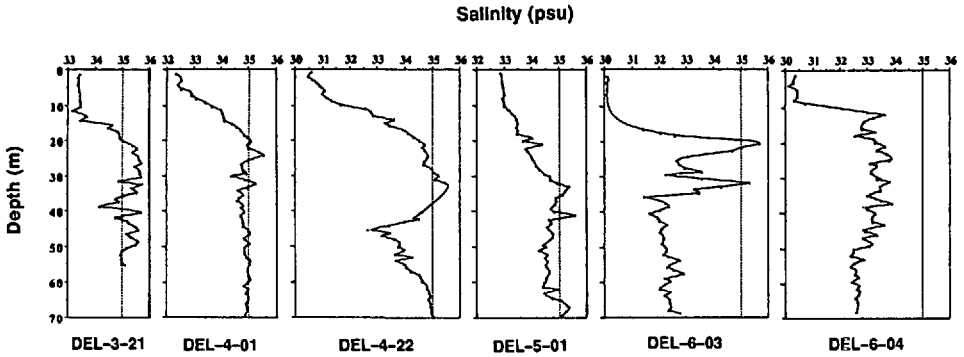


Figure 8. Salinity (psu)-depth (m) profiles for stations where small *Xyrichtys novacula* larvae (≤ 5 mm) were captured during the summer of 1988. Slope water (> 35 psu) is denoted by the vertical dotted line. Specific cruise and stations number are beneath each profile.

drift southwest at velocities averaging 6 ± 4 (SD) cm s^{-1} (Zheng *et al.*, 1984) and rotate anticyclonically at tangential velocities averaging 58.1 ± 28.7 (SD) cm s^{-1} (Zheng *et al.*, 1984).

The water inshore of the Gulf Stream and offshore of the continental shelf with salinities of 35–36 psu is termed slope water (Csanady and Hamilton, 1988). The slope water close to the Gulf Stream, flows in the same direction at velocities of

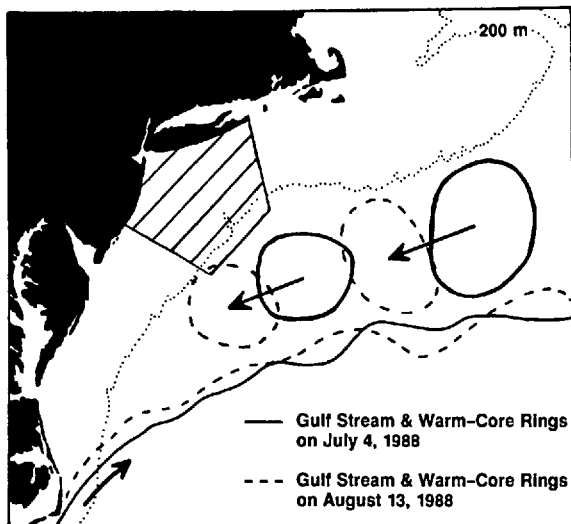


Figure 9. Sketch of sea surface temperature satellite images from July 4, 1988 (two days prior to the first cruise) and August 13, 1988 (one day after the fourth cruise). The western wall of the Gulf Stream and two warm-core rings (88-C to the west and 88-E to the east) are illustrated. Between July 4 and August 13, the western boundary of the Gulf Stream moved north and both rings drifted to the southwest. Our sampling region is denoted by the hatched area south of Long Island and east of New Jersey.

Table 1. Number of stations where *Xyrichtys novacula* larvae were captured by MARMAP during the years 1984–1987 in three regions: Cape Hatteras to Georges Bank, Chesapeake Bay to Georges Bank, and Cape Hatteras to Chesapeake Bay. For each region two sign tests were performed on the presence or absence of warm-core rings: within the zone of capture (Test I) and within zone of capture and adjacent zones (Test II). The results of the sign tests determine whether the distribution of *X. novacula* larvae in relation to warm-core rings is significantly different from random: $p < 0.001$ (**), $p < 0.05$ (*), and not significant (ns).

	Warm-Core Ring	Cape Hatteras to Georges Bank (All Zones)	Chesapeake Bay to Georges Bank (Zones 3–7)	Cape Hatteras to Chesapeake Bay Zone 8
	Present in Capture Zone	66	62	4
Test I	Absent in Capture Zone	64	23	41
	significance	ns	**	**
	Present in Capture or Adjacent Zone	100	85	15
Test II	Absent from Capture and Adjacent Zones	30	0	30
	significance	**	**	*

0–100 cm s⁻¹ (Churchill *et al.*, 1989; Joyce *et al.*, 1990; Lillibridge *et al.*, 1990). The remaining slope water on average flows toward the southwest at velocities of 5–15 cm s⁻¹ (Parker, 1976; Csanady and Hamilton, 1988; Pierce and Joyce, 1988). Csanady and Hamilton (1988) have suggested that two gyres are present in the slope water creating cross slope flow, but that these gyres would be interrupted by the presence of a warm-core ring.

The water inshore of the Gulf Stream on the continental shelf with salinities less than 35 psu is termed shelf water (Csanady and Hamilton, 1988) and generally flows to the southwest at velocities of 5–15 cm s⁻¹ (Bumpus, 1973; Beardsley *et al.*, 1976). Reversals to the northeast have been observed at locations from Delaware Bay to Georges Bank, attaining velocities of 5–15 cm s⁻¹ (Beardsley *et al.*, 1985; Butman and Beardsley, 1987; Epifanio *et al.*, 1989). Both the southwest flowing shelf and slope water are entrained by the northeast flowing Gulf Stream north of Cape Hatteras in the area offshore of Chesapeake Bay (Ford *et al.*, 1952; Fisher, 1972; Churchill *et al.*, 1989; Lillibridge *et al.*, 1990).

5. Discussion

Before considering the hypotheses for the location of spawning and examining the processes responsible for the observed larval distributions, it is necessary to critically assess the validity of the biological data, primarily the otolith data. Although daily

increment formation has not been validated in *X. novacula*, it has been validated in other species within the family Labridae (Victor, 1982; Cowen, 1985) and in other species within the suborder Labroidei (Thresher *et al.*, 1989; Wellington and Victor, 1989; Schultz, 1990). Therefore, the assumption of daily increment formation in *X. novacula* is reasonable. Another potential concern is that some larval fish have been shown to slow their growth upon reaching a certain size related to the attainment of settlement competency (Victor, 1986b; Cowen, 1991). Slower somatic growth should be recorded in the otolith as a decrease in increment width, assuming otolith growth is coupled with somatic growth (Campana and Neilson, 1985). As stated in the results, there was a significant correlation between otolith radius and corrected-length, validating the assumption of coupled otolith and somatic growth. The pattern of increment width did show a decrease from increment number 25 and greater but this decrease was not significant when compared to the width of increment numbers less than 25. It does not appear that *X. novacula* larvae in our samples slowed their growth in response to attaining competency. Thus, we feel the otolith data presented here is valid and correctly represents the age and growth of *X. novacula* larvae.

There are several "scenarios" which explain the observed larval distributions relative to the two possible sources of *X. novacula* larvae. The presence of small larvae at the shelf break and their absence on the shelf would require either a slope population with onshore larval transport, a shelf break population with upward movement of larvae, a shelf population with offshore larval transport at depth, or an origin outside the MAB. The first three possibilities represent different scenarios of the resident hypothesis and the last represents the expatriate hypothesis. Megafaunal studies of the MAB shelf break and slope utilizing trawl and photographic methods (Markle and Musick, 1974; Haedrich *et al.*, 1975; Hecker, 1990) have not reported any species of the genus *Xyrichtys*. Additionally, *X. novacula* south of Cape Hatteras are regularly collected but only at depths less than 60 m (Wenner *et al.*, 1979a, 1979b, 1980). Both sets of evidence suggest that there are no deep water populations of *X. novacula* in the MAB. In addition, the Groundfish Survey conducted by NMFS, Northeast Fisheries Center, which samples the continental shelf and upper slope from south of Cape Hatteras to Georges Bank, has captured *X. novacula* only south of Cape Hatteras (Don Flescher, pers. com.). The data gathered to date indicate that there are no *X. novacula* populations resident on the shelf, shelf break or slope of the MAB.

The other hypothesis is that *X. novacula* larvae collected in the MAB are expatriates from southern populations. Small larvae were found associated with the shelf break, the offshore edge of both our sampling and the MARMAP surveys, suggesting an offshore source. These small larvae were captured in shelf water overlying slope water. Given their diel movement from surface water (< 10 m) to deeper water (10–15 m or greater) and their occurrence only in the upper 30 m of the water column (Hare and Cowen, unpublished data), these small larvae were encoun-

tering both shelf and slope water. An offshore source and evidence for small larvae occupying slope water, implies that the source of *X. novacula* to the shelf was slope water.

Three potential mechanisms can be evaluated by which larvae are advected from Cape Hatteras to the MAB shelf break. The first mechanism is northward transport along the shelf associated with a shelf current reversal. A reversal of 15 cm s^{-1} , the upper range of velocities observed (Beardsley *et al.*, 1985; Butman and Beardsley, 1987; Epifanio *et al.*, 1989), would require 30 days to advect larvae from Cape Hatteras to MAB capture locations (400 km) and 77 days to advect larvae to capture locations on Georges Bank (1000 km). Since a majority of larvae captured in the MAB were less than 20 days old and current reversals with periods greater than 30 days have not been observed (Beardsley *et al.*, 1985; Butman and Beardsley, 1987; Epifanio *et al.*, 1989), shelf current reversals are not a possible northward transport mechanism.

The second possible mechanism is northward transport in association with the Gulf Stream, then incorporation into a warm-core ring upon formation and release from the ring at various points along the shelf break. In 1988 Warm Core Ring 88-C formed at the end of March (Sano and Fairfield, 1989), 60 days prior to the first birthdates captured and 120 days prior to the birthdates of small larvae captured during the last cruise (Fig. 6). In addition new birthdates were captured during each 1988 cruise indicating a continual supply of larvae which could not be provided from an isolated ring. Therefore, incorporation of larvae into a ring during its formation does not explain the occurrence of *X. novacula* larvae in the MAB.

The third possible mechanism is northward transport in association with the Gulf Stream and a concomitant cross-slope flow. Csanady and Hamilton (1988) suggested that a cross slope flow could exist in relation to gyre development in the slope water, but such flow would be lost in the presence of a warm-core ring. It has been demonstrated that for all captures of *X. novacula* north of Chesapeake Bay there was a warm-core ring in the slope water. This would suggest that cross-slope transport associated with a slope gyre is not possible, however, it is possible that cross-slope transport is provided by warm-core rings.

A model was developed to examine the feasibility of Gulf Stream transport with concomitant cross-slope flow associated with a warm-core ring. The feasibility model determined the velocities necessary to transport larvae from Cape Hatteras to MAB capture locations within times equivalent to the ages of captured larvae. The basic equation was

$$\text{age} = D_{GS}/V_{GS} + D_{CS}/V_{CS}$$

where D_{GS} is the distance travelled in the Gulf Stream, D_{CS} is the distance travelled cross slope, V_{GS} is velocity while traveling D_{GS} , and V_{CS} is velocity while travelling D_{CS} . The distances were determined from satellite images dated July 4 and August 13

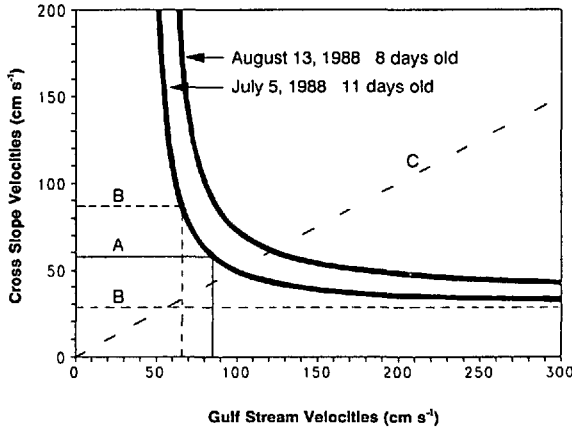


Figure 10. Solutions to the feasibility model (heavy lines) solved for the youngest larvae captured during the first and the last cruise, 11 and 8 days respectively. The horizontal portion of line A represents the mean tangential velocity of a warm-core ring and the horizontal portion of line B represent ± 1 SD, as presented by Zheng *et al.* (1984). The corresponding vertical portions of line A and B show the required concomitant velocity associated with the Gulf Stream necessary to transport the youngest larvae to their capture locations. Line C shows the cross-slope velocity of a streamer formed from Gulf Stream water moving at a given velocity, as theorized by Nof (1988).

assuming that Gulf Stream associated transport occurred at the western boundary of the Gulf Stream and cross slope transport was associated with the western side of the warm-core ring. The distances used were 430 km in the Gulf Stream and 260 km cross-slope for July 4 and 360 km in the Gulf Stream and 240 km cross-slope for August 13. The ages used in the model were that of the youngest larvae captured during the first (July 6–9) and fourth cruise (August 8–12), 11 and 8 days respectively. The solution of the equation resulted in the combinations of Gulf Stream velocities and cross-slope velocities which would have transported larvae over the total transport distance within the appropriate time (Fig. 10).

The feasibility model demonstrates that cross-slope transport associated with the western side of warm-core rings is physically possible. Considering the range of warm-core ring tangential velocities presented by Zheng *et al.* (1984; 29.4–86.8 cm s^{-1}), in order to transport the youngest larvae to capture locations the model required Gulf Stream velocities of 80–300 cm s^{-1} (Fig. 10, lines A & B). For those larvae aged 12.5 days old, age of 5 mm larvae, the range of necessary velocities was 40–130 cm s^{-1} . These calculations assume that cross-slope transport occurred within the ring itself. However, another possibility is that a ring impinged on the Gulf Stream or associated slope water flow causing a portion of that flow to propagate around the ring forming a “streamer” (Joyce *et al.*, 1984; Evans *et al.*, 1985). Theoretical work done by Nof (1986, 1988) has suggested that the propagation speed of a streamer around a ring is not related to the ring’s tangential velocity or radius

but is equal to one half the speed of the initial Gulf Stream flow which formed the streamer. Given the theoretical velocities of streamers, the feasibility model predicted for the youngest larvae captured during the first cruise, velocities of 100 cm s^{-1} in the Gulf Stream and 50 cm s^{-1} cross slope (Fig. 10, line C). For the youngest larvae captured in the fourth cruise the model predicted Gulf Stream flows of 130 cm s^{-1} and cross slope flows of 65 cm s^{-1} (Fig. 10, line C). Both the cross slope velocities presented in Zheng *et al.* (1984) and the theoretical streamer velocities derived by Nof (1986, 1988) indicated that the youngest larvae would have been in the Gulf Stream itself (velocities $> 100 \text{ cm s}^{-1}$) but older larvae could have been transported either in the Gulf Stream or in the associated slope water flow (velocities $< 100 \text{ cm s}^{-1}$).

The apparent relationship between *X. novacula* larvae on the shelf and warm-core rings offshore and the physical feasibility of cross-slope transport via warm-core rings suggests that rings are responsible for the cross-slope component of *X. novacula* expatriation. From the data presented several points can be made regarding cross-slope transport associated with warm-core rings. First, transport northward associated with the Gulf Stream and cross-slope transport associated with warm-core rings must occur rapidly; the youngest fish captured were 8 days old while the median age was 17.8 days. Second, cross slope transport provided by warm-core rings may occur continuously over the period of weeks as evidenced by the continuous capture of new birthdates during 1988 (Fig. 6). Third, cross-slope transport has occurred consistently every year from 1984 to 1988 and in addition, our ichthyoplankton surveys of 1989, 1990 and 1991 in the MAB have also captured *X. novacula* (Cowen and Hare, unpublished data). Although this mechanism operates every year, the spatial occurrence of ring-Gulf Stream interactions exhibits a large degree of interannual variability (Fig. 1). Fourth, south of Chesapeake Bay warm-core rings are not the predominant cross-slope transport mechanism which is evident from the non-random occurrence of *X. novacula* on the shelf when rings were not present offshore (Table 1). South of Chesapeake Bay the distance between the Gulf Stream and the shelf break is small (0–100 km) and most warm core ring are absorbed by the Gulf Stream northeast of Chesapeake Bay (Brown *et al.*, 1986; Auer, 1987). Cross-slope transport south of Chesapeake Bay might be provided by several different mechanisms including impingement of the Gulf Stream on the shelf, cyclonic shear along the Gulf Stream-slope water boundary (Lillibridge *et al.*, 1990), eddies at the shelf-slope boundary (Garvine *et al.*, 1988; Garvine *et al.*, 1989) or cyclonic eddies in slope water (Kennelly *et al.*, 1985; Churchill *et al.*, 1986).

Warm-core rings have previously been hypothesized to transport tropical fish larvae (Wroblewski and Cheney, 1984) and oceanic zooplankton (Cox and Weibe, 1979) into temperate waters of the North Atlantic. In this study, we present evidence which not only supports this hypothesis, but also provides an explanation of the transport processes involved. *Xyrichtys* adults are found south of Cape Hatteras to a

depth of 60 m (Wenner *et al.*, 1979a, 1979b, 1980; Don Flescher pers. com.). Their offspring are incorporated into Gulf Stream associated flows, either in entrained shelf and slope water or in the Gulf Stream itself. From these Gulf Stream associated flows, the larvae are transported northeast along the path of the Gulf Stream until an interaction with a warm-core ring occurs. This interaction might involve the collision of a ring with either the Gulf Stream or associated slope flow and result in a narrow band of Gulf Stream or slope water, i.e. a streamer, to flow around the western side of the ring (Joyce *et al.*, 1984; Evans *et al.*, 1985; Nof, 1986, 1988). The ring-Gulf Stream interaction may be analogous to the formation of shelf streamers generated when a ring interacts with the shelf-slope front and advects shelf water southward across the slope (Halliwell *et al.*, 1979; Evans *et al.*, 1985). However, rather than resulting in the advection of larvae from the shelf as in the case of shelf streamers (Flierl and Wroblewski, 1985; Myers and Drinkwater, 1989), the interaction between ring and Gulf Stream results in the advection of *X. novacula* larvae to the shelf-slope front. Once near the shelf-slope front, *X. novacula* larvae enter shelf water either through vertical migration from underlying slope water, physical mixing across the shelf-slope front, or a combination of both. We have demonstrated that *X. novacula* larvae move vertically and these movements would take larvae from the surface to the upper boundary of impinging slope water and perhaps deeper. Several cross-frontal mixing processes have been described which may be involved in the exchange of young *X. novacula* from slope to shelf waters including the impingement of slope water along the pycnocline (Fig. 7) with subsequent exchange through small-scale turbulence and double diffusion (Voorhis *et al.*, 1976; Houghton *et al.*, 1988) and contortion of the shelf-slope front by eddies (Morgan and Bishop, 1977; Churchill *et al.*, 1986, Garvine *et al.*, 1988, Garvine *et al.*, 1989).

As tracers of transport mechanisms, *X. novacula* larvae have enabled the elucidation of several important exchange processes. Cross-frontal exchange (i.e. across the shelf-slope front) of biological constituents may be facilitated by active crossing of the frontal feature via vertical or horizontal movements. Cross-slope exchange by the interaction of warm-core rings with Gulf Stream associated flows causes surface water (<100 m) moving in association with the Gulf Stream to be deposited at the shelf-slope front. The cross-slope exchange can be continuous over the period of weeks and occurs consistently every year, however, the along-shelf location of exchange is variable. This suggests that warm-core rings regularly interact with the Gulf Stream after their formation anywhere from Georges Bank to Chesapeake Bay. Precise information gained from larval otolith analysis has demonstrated the rapid time scale (days to weeks) within which exchange of water from south of Cape Hatteras to the MAB shelf break must occur. The possibility of such rapid, continuous and consistent exchange needs to be considered in future oceanographic studies of the Gulf Stream-slope water-MAB shelf water system.

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REFERENCES

- Auer, S. J. 1987. Five-year climatological survey of the Gulf Stream system and its associated rings. *J. Geophys. Res.*, *92*, 11709–11726.
- Baird, T. R. 1988. Abdominal windows in straighttailed razorfish, *Xyrichtys martinicensis*: an unusual female sex character in a polygynous fish. *Copeia*, 1988, 496–499.
- Barton, K. W. and M. H. Sano. 1988. Anticyclonic warm core rings off the northeastern United States during 1987. NAFO SCR Document No. 88/07, Serial No. N1442, 20 pp.
- Beardsley, R. C., W. C. Boicourt and D. V. Hansen. 1976. Physical oceanography of the Middle Atlantic Bight. *Amer. Soc. Limnol. Oceanogr. Spec. Symp.*, *2*, 20–33.
- Beardsley, R. C., D. C. Chapman, K. H. Brink, S. R. Ramp and R. Schlitz. 1985. The Nantucket Shoals Flux Experiment (NSFE79). Part I: A basic description of the current and temperature variability. *J. Phys. Oceanogr.*, *15*, 713–748.
- Brown, O. B., P. C. Cornillon, S. R. Emmerson and H. M. Carle. 1986. Gulf Stream warm rings: a statistical study of their behavior. *Deep-Sea Res.*, *33*, 1459–1473.
- Bumpus, D. F. 1973. A description of the circulation on the continental shelf of the east coast of the United States. *Prog. Oceanogr.*, *6*, 111–157.
- Burrage, D. M. and R. W. Garvine. 1988. Summertime hydrography at the shelfbreak front in the Middle Atlantic Bight. *J. Phys. Oceanogr.*, *18*, 1309–1319.
- Butman, B. and R. C. Beardsley. 1987. Long-term observations on the southern flank of Georges Bank. Part I: A description of the seasonal cycle of currents, temperature, stratification, and wind stress. *J. Phys. Oceanogr.*, *17*, 367–384.
- Campana, S. E. and J. D. Neilson. 1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.*, *42*, 1014–1032.
- Chenoweth, S. B., D. A. Libby, R. L. Stephenson and M. J. Power. 1989. Origin and dispersion of larval herring (*Clupea harengus*) in coastal waters of eastern Maine and southwestern New Brunswick. *Can. J. Fish. Aquat. Sci.*, *46*, 624–632.
- Churchill, J. H., P. C. Cornillon and P. Hamilton. 1989. Velocity and hydrographic structure of subsurface shelf water at the Gulf Stream's edge. *J. Geophys. Res.*, *94*, 10791–10800.
- Churchill, J. H., P. C. Cornillon and G. W. Milkowski. 1986. A cyclonic eddy and shelf-slope

- water exchange associated with a Gulf Stream warm-core ring. *J. Geophys. Res.*, *91*, 9615–9623.
- Clark, E. 1983. Sand-diving behavior and territoriality of the Red Sea razorfish, *Xyrichtys pentadactylus*. *Bull. Inst. Oceanogr. Fish.*, *9*, 81–98.
- Colton, J. B. 1961. The distribution of eyed flounder and lanternfish larvae in the Georges Bank area. *Copeia*, 1961, 274–279.
- Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. *J. Mar. Res.*, *43*, 719–742.
- 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Mar. Ecol. Prog. Ser.*, *69*, 9–15.
- Cox, J. and P. H. Wiebe. 1979. Origins of oceanic plankton in the Middle Atlantic Bight. *Estuar. Coast. Mar. Sci.*, *9*, 509–527.
- Crawford, W. R., A. V. Tyler and R. E. Thomson. 1990. A possible eddy retention mechanism for ichthyoplankton in Hecate Strait. *Can. J. Fish. Aquat. Sci.*, *47*, 1356–1363.
- Csanady, G. T. and P. Hamilton. 1988. Circulation of slopewater. *Cont. Shelf Res.*, *8*, 565–624.
- Epifanio, C. E., A. K. Masse and R. W. Garvine. 1989. Transport of crab larvae by surface currents off Delaware Bay, USA. *Mar. Ecol. Prog. Ser.*, *54*, 35–41.
- Evans, R. H., K. S. Baker, O. B. Brown and R. C. Smith. 1985. Chronology of warm-core ring 82B. *J. Geophys. Res.*, *90*, 8803–8811.
- Evseenko, S. A. 1982. Ichthyoplankton of slope and Gulf Stream waters off Nova Scotia in late autumn 1974. *J. Northw. Atl. Fish. Sci.*, *3*, 127–139.
- Fiedler, P. C. 1986. Offshore entrainment of anchovy by a displacement eddy. *Calif. Coop. Oceanic Fish. Invest. Rep.*, *27*, 144–152.
- Fisher, A. 1972. Entrainment of shelf water by the Gulf Stream northeast of Cape Hatteras. *J. Geophys. Res.*, *77*, 3248–3255.
- Fliertl, G. R. and J. S. Wroblewski. 1985. The possible influence of warm core Gulf Stream rings upon shelf water larval fish distributions. *Fish. Bull.*, *83*, 313–330.
- Ford, W. L., J. R. Longard and R. E. Evans. 1952. On the nature, occurrence and origin of cold low salinity water along the edge of the Gulf Stream. *J. Mar. Res.*, *11*, 282–293.
- Garvine, R. W., K.-C. Wong and G. G. Gawarkiewicz. 1989. Quantitative properties of shelfbreak eddies. *J. Geophys. Res.*, *94*, 14475–14483.
- Garvine, R. W., K.-C. Wong, G. G. Gawarkiewicz, R. K. McCarthy, R. W. Houghton and F. Aikman. 1988. The morphology of shelfbreak eddies. *J. Geophys. Res.*, *93*, 15593–15607.
- Gordon, A. L. and F. Aikman. 1981. Salinity maximum in the pycnocline of the Middle Atlantic Bight. *Limnol. Oceanogr.*, *26*, 123–130.
- Gordon, A. L., A. F. Amos and R. D. Gerard. 1976. New York Bight water stratification—October 1974. *Amer. Soc. Limnol. Oceanogr. Spec. Symp.*, *2*, 45–57.
- Gotthardt, G. A. and G. J. Potocsky. 1974. Life cycle of a Gulf Stream anticyclonic eddy observed from several oceanographic platforms. *J. Phys. Oceanogr.*, *4*, 131–134.
- Haedrich, R. L., G. T. Rowe and P. T. Polloni. 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J. Mar. Res.*, *33*, 191–212.
- Halliwell, G. R. and N. K. Mooers. 1979. The space-time structure and variability of the shelf water-slope water and Gulf Stream surface temperature fronts and associated warm-core eddies. *J. Geophys. Res.*, *84*, 7707–7725.
- Hansen, D. V. 1970. Gulf Stream meanders between Cape Hatteras and the Grand Banks. *Deep-Sea Res.*, *17*, 495–511.

- Hecker, B. 1990. Variation in megafaunal assemblages on the continental margin south of New England. *Deep-Sea Res.*, 37, 37–57.
- Hempel, G. 1979. *Early Life History of Marine Fish: The Egg Stage*. University of Washington Press, Seattle, 70 pp.
- Houghton, R. W., F. Aikman and H. W. Ou. 1988. Shelf-slope frontal structure and cross-shelf exchange at the New England shelf-break. *Cont. Shelf Res.*, 8, 687–710.
- Joyce, T. R., Backus, K. Baker, P. Blackwelder, O. Brown, T. Cowles, R. Evans, G. Fryxell, D. Mountain, D. Olson, R. Schlitz, R. Schmitt, P. Smith, R. Smith, and P. Wiebe. 1984. Rapid evolution of a warm-core ring. *Nature*, 308, 837–840.
- Joyce, T. M., K. A. Kelly, D. M. Schubert and M. J. Caruso. 1990. Shipboard and altimetric studies of rapid Gulf Stream variability between Cape Cod and Bermuda. *Deep-Sea Res.*, 37, 897–910.
- Kendall, A. W., E. H. Ahlstrom and H. G. Moser. 1984. Early life history stages of fishes and their classification, in *Ontogeny and Systematics of Fishes*, H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall and S. L. Richardson, eds., Allen Press, Lawrence, Kansas, 11–22.
- Kennelly, M. A., R. H. Evans and T. M. Joyce. 1985. Small-scale cyclones on the periphery of a Gulf Stream warm-core ring. *J. Geophys. Res.*, 90, 8845–8857.
- Ketchum, B. H. and N. Corwin. 1964. The persistence of “winter” water on the continental shelf south of Long Island, New York. *Limnol. Oceanogr.*, 4, 467–475.
- Leaman, K. D., E. Johns and T. Rossby. 1989. The average distribution of volume transport and potential vorticity with temperature at three sections across the Gulf Stream. *J. Phys. Oceanogr.*, 19, 36–51.
- LeBlanc, P. R. 1986. Distribution and abundance of larval and juvenile fishes in shelf water entrained by warm-core ring 82-B and contiguous water masses. M.Sc. Thesis, Southeastern Massachusetts University, 143 pp.
- Lillibridge, J. L., G. Hitchcock, T. Rossby, E. Lessard, M. Mork and L. Golmen. 1990. Entrainment and mixing of shelf/slope waters in the near surface Gulf Stream. *J. Geophys. Res.*, 95, 13065–13087.
- Markle, D. F. and J. A. Musick. 1974. Benthic-slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. *Mar. Biol.*, 26, 225–233.
- Markle, D. F., W. B. Scott and A. C. Kohler. 1980. New and rare records of Canadian fishes and the influence of hydrography on resident and nonresident Scotian Shelf ichthyofauna. *Can. J. Fish. Aquat. Sci.*, 37, 49–65.
- McGurk, M. D. 1989. Advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasii* in Bamfield Inlet, British Columbia. *Mar. Ecol. Prog. Ser.*, 51, 1–18.
- Morgan, C. W. and J. M. Bishop. 1977. An example of Gulf Stream eddy-induced water exchange in the Mid-Atlantic Bight. *J. Phys. Oceanogr.*, 7, 472–479.
- Mountain, D. G., M. Pastuszak and D. A. Busch. 1989. Slope water intrusion to the Great South Channel during autumn, 1977–1985. *J. of Northw. Atl. Fish. Sci.*, 9, 97–102.
- Myers, R. A. and K. Drinkwater. 1989. The influence of Gulf Stream warm core rings on recruitment of fish in the northwest Atlantic. *J. Mar. Res.*, 47, 635–656.
- Nof, D. 1986. The collision between the Gulf Stream and warm-core rings. *Deep-Sea Res.*, 33, 359–378.
- 1988. The propagation of “streamers” along the periphery of warm-core rings. *Deep-Sea Res.*, 35, 1483–1498.
- O’Boyle, R. N., M. Sinclair, R. J. Conover, K. H. Mann and A. C. Kohler. 1984. Temporal and

- spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological, and physiographic features. *Rapp. P.-v. des Reun. Cons. Int. Explor. Mer*, 183, 27–40.
- Pannella, G. 1971. Fish otoliths: daily growth layers and periodical patterns. *Science*, 173, 1124–1127.
- Parker, C. E. 1976. Some effects of lateral shifts of the Gulf Stream on the circulation northeast of Cape Hatteras. *Deep-Sea Res.*, 23, 795–803.
- Pierce, S. D. and T. M. Joyce. 1988. Gulf stream velocity structure through inversion of hydrographic and acoustic doppler data. *J. Geophys. Res.*, 93, 2227–2236.
- Price, C. A. 1985. Anticyclonic warm core rings off the northeastern United States during 1984. NAFO SCR Document No. 85/19, Serial No. N960, 12 pp.
- Price, C. A. and K. W. Barton. 1986. Anticyclonic warm core rings off the northeastern United States during 1985. NAFO SCR Document No. 86/77, Serial No. N1197, 17 pp.
- 1987. Anticyclonic warm core rings off the northeastern United States during 1986. NAFO SCR Document No. 87/14, Serial No. N1294, 19 pp.
- Randall, J. E. 1965. A review of the razorfish genus *Hemipteronotus* (Labridae) of the Atlantic Ocean. *Copeia*, 1965, 487–501.
- Sale, P. F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biology Ann. Rev.*, 18, 367–421.
- Sano, M. H. and C. P. Fairfield. 1989. Anticyclonic warm core rings off the northeastern United States during 1988. NAFO SCR Document No. 89/67, Serial No. N1644, 19 pp.
- Saunders, P. M. 1971. Anticyclonic eddies formed from the shoreward meanders of the Gulf Stream. *Deep-Sea Res.*, 18, 1207–1219.
- Schultz, E. T. 1990. Daily otolith increments and the early life history of a viviparous fish, *Micrometrus minimus* (Embiotocidae). *Copeia*, 1990, 59–67.
- Shapiro, D. Y., D. A. Hensley and R. S. Appledorn. 1988. Pelagic spawning and egg transport in coral-reef fishes: a skeptical overview. *Environ. Biol. Fish.*, 22, 3–14.
- Sibunka, J. D. and M. J. Silverman. 1989. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1984–1987). Atlas Number 3, Summary of Operations, NOAA Technical Memorandum NMFS-F/NEC-68, 197 pp.
- Theilacker, G. H. 1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. *Fish. Bull.*, 78, 685–692.
- Thresher, R. E. and E. B. Brothers. 1989. Evidence of intra- and inter-oceanic regional differences in the early life history of reef associated fishes. *Mar. Ecol. Prog. Ser.*, 57, 187–205.
- Thresher, R. E., P. L. Colin and L. J. Bell. 1989. Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). *Copeia*, 1989, 420–434.
- Victor, B. C. 1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. *Mar. Biol.*, 71, 203–208.
- 1986a. Duration of the pelagic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Mar. Biol.*, 90, 317–326.
- 1986b. Delayed metamorphosis with reduced larval growth in a coral reef fish, *Thalassoma bifasciatum*. *Can. J. Fish. Aquat. Sci.*, 43, 1208–1213.
- 1987. The mating system of the Caribbean rosy razorfish, *Xyrichtys martinicensis*. *Bull. Mar. Science*, 40, 152–160.
- Voorhis, A. D., D. C. Webb and R. C. Millard. 1976. Current structure and mixing in the shelf/slope water front south of New England. *J. Geophys. Res.*, 81, 3695–3708.

- Wellington, G. M. and B. C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Mar. Biol.*, *101*, 557–567.
- Wenner, C., C. Barans, B. Stender and F. Berry. 1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. South Carolina Marine Resources Center, Technical Report No. 41, 62 pp.
- 1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV. Winter-early spring, 1975. South Carolina Marine Resources Center, Technical Report No. 45, 57 pp.
- 1980. Results of MARMAP otter trawl investigations in the South Atlantic Bight. V. Summer, 1975. South Carolina Marine Resources Center, Technical Report No. 44, 59 pp.
- Wilkinson, L. 1987. SYSTAT: The System for Statistics. SYSTAT Inc., Evanston.
- Wroblewski, J. S. and J. Cheney. 1984. Ichthyoplankton associated with a warm core ring off the Scotian Shelf. *Can. J. Fish. Aquat. Sci.*, *41*, 294–303.
- Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, Inc., New Jersey, 620 pp.
- Zheng, Q., V. Klemas and N. E. Huang. 1984. Dynamics of the slope water off New England and its influence on the Gulf Stream as inferred from satellite IR data. *Rem. Sen. Environ.*, *15*, 135–153.

