Entrainment of redfish (Sebastes spp.) larvae off the Scotian Shelf

K. Drinkwater, S. Lochman, C. Taggart, K. Thompson, and K. Frank

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Satellite images show large volumes of cold shelf water lying offshore of the Scotian Shelf in the spring of 1991. The seaward boundary of the shelf water was highly convoluted and indicated that shelf water was being entrained offshore into the slope water region by warm-core Gulf Stream eddies. An interdisciplinary field study of this region in late April and May found relatively high concentrations of redfish (*Sebastes* spp.) larvae in the entrained shelf waters, 100 km offshore of the shelf. Historical data indicate that these larvae were most likely spawned along the edge of the Scotian Shelf. Based on weight-at-length relationships, the larvae off the shelf were in poorer condition than those on the shelf. We suggest the larvae swept offshore eventually die, a result consistent with earlier studies that entrainment by Gulf Stream eddies negatively affects redfish recruitment.

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K. Drinkwater, K. Frank: Bedford Institute of Oceanography, Box 1006, Dartmouth, N.S., Canada B2Y 4A2; S. Lochman, C. Taggart, K. Thompson: Oceanography Dept., Dalhousie University, Halifax, N.S., Canada B3H 4J1. Correspondence to: K. Drinkwater, tel: +1 902 426 2650; fax: +1 902 426 6927; e-mail: drinkwaterk@ mar.dfo-mpo.gc.ca.

Introduction

The exchange between the continental shelf waters and the adjacent offshore slope waters induced by the presence of Gulf Stream eddies in the Northwest Atlantic is well documented (Morgan and Bishop, 1977; Smith, 1978; Trites, 1981; Churchill et al., 1986). The exchange plays a significant role in the heat and salt balance for the shelf region (Smith, 1978) and affects biological production and distribution. Warm-core eddies transport tropical and sub-tropical fish species onto the shelves (Markle and Frost, 1980; Wroblewski and Cheney, 1984). It has also been hypothesized that the shelf water entrained by eddies can transport sufficient large numbers of fish eggs and larvae offshore to reduce significantly the recruitment of those fish that normally recruit to the shelf (Wroblewski and Cheney, 1984; Flierl and Wroblewski, 1985). Myers and Drinkwater (1989) provided evidence for the Scotian Shelf region consistent with this hypothesis. Investigating recruitment variability of five commercially exploited species of groundfish including Atlantic cod (Gadus morhua), haddock (Melanogrammus aeglefinus), pollock (Pollachius virens), redfish (Sebastes spp.), and yellowtail flounder (Limanda ferruginea), they found for 16 of 17 stocks examined that reduced recruitment occurred in years when there were higher numbers of eddies in closer proximity to the Shelf. Observations of fish larvae of shelf origin in offshore entrainment features remain rare, however. Wroblewski and Cheney (1984) collected substantial numbers of larval and juvenile white hake (Urophycis tenuis) 140 km seaward of the south-western tip of the Scotian Shelf. Friedlander and Smith (1983) observed sand lance (Ammodytes sp.) larvae in an entrainment feature approximately 136 km offshore of the Hudson Canyon in the Middle Atlantic Bight. We know of no reports of significant numbers of eggs or larvae in entrainment features for any of the five species of groundfish examined by Myers and Drinkwater (1989) that would provide a test of their hypothesis.

While conducting an interdisciplinary field study of the circulation and the distribution of cod larvae on the Scotian Shelf, the opportunity arose to investigate the influence of offshore entrainment on redfish (*Sebastes* spp.) larvae. Over the course of the following month we visited one entrainment feature three times. We describe



the changes in hydrographical characteristics in relation to the vertical and horizontal distribution of the redfish larvae and compare the length-weight relationship of the larvae encountered with available information from shelf waters. The results are discussed in light of the hypothesis that entrained larvae are lost to the population.

Material and methods

During April to mid-May, 1991, a two-ship (CSS "Dawson" and the SS "Petrel V") multidisciplinary field study of the circulation and distribution of larval cod was conducted on Western Bank, a shallow (60 m) submarine plateau on the outer edges of the Scotian Shelf, off Nova Scotia (Fig. 1a). Low numbers of cod larvae led to speculation that they had been swept off the Bank through entrainment by Gulf Stream eddies. This hypothesis was consistent with observations of several eddies and entrainment features in the area, some just offshore of Western Bank. These had been visible in thermal satellite imagery for more than 2 months prior to our study.

We began a hydrographic and larval survey of the offshore waters from the "Dawson" on 20 April. Given that cod larvae are unlikely to tolerate the higher offshore temperatures (>10°C), we searched offshore for water with temperature and salinity characteristics similar to those on Western Bank (<4°C; <33.5). Such waters were located in the vicinity of 59.3°W and larvae were collected over a 24-h period. The samples revealed abundant redfish larvae but no cod larvae.

The "Dawson" returned to the offshore site on 30 April, undertaking further hydrographic and larval measurements. The "Petrel V" conducted a third visit on 8–9 May, during which several larval samples were collected. This ship also took samples from another, older offshore entrainment feature further to the southwest on 29–30 April and conducted a larval survey on the shelf over Western Bank during 1–4 May.

Surface thermal features from satellite imagery were obtained from the National Oceanic and Atmospheric Administration (NOAA) oceanographic analysis charts published three times per week. Additional imagery was available from Cribb (1993), who processed all available NOAA-11 AVHRR (Advanced Very High Resolution Radiometer) sea surface temperature (SST) images covering the period February to May, 1991.

Vertical profiles of temperature and salinity were obtained from the "Dawson" using a Seabird digital CTD (Conductivity-Temperature-Depth) profiler. Larval sampling was conducted using a 0.25 m² miniBIONESS, a half-scale version of the BIONESS (Sameoto et al., 1980); a multiple opening and closing net system fitted with seven 333 musignm nets, internal and external digital flowmeters, pitch and roll sensors, and a Seabird CTD. The miniBIONESS was typically deployed to 60 m depth, then used to sample three discrete depth strata in a stepped oblique manner toward the surface at 20 m intervals. This was followed by a depth-integrated sample from 0 to 60 m and a repeat series of tows toward the surface at 20-m intervals (replicates). Towing speed averaged 1 ms⁻¹ and each net was nominally deployed for 8 min to provide a filtered volume of \sim 70 m³ per net. After recovery, the nets were rinsed to the codends then samples were immediately sorted for larval fish and preserved in 95% ethanol. Plankton samples were preserved in 4% MgCO₃ buffered formalin in sea water.

Larval collections on the "Petrel V" were made using a 1 m² BIONESS fitted with ten 333-musignm mesh nets and a CTD and sensor package similar to that described above for miniBIONESS. The BIONESS was deployed first to collect a depth-integrated sample from surface to within 10 m of the bottom or 100 m maximum. The next set of nets sampled from the greatest depth to 40 m, 40-30 m, 30-20 m, and 20-0 m. The sampling procedure was then repeated (replicates) in reversed order for the remaining five nets. Towing speed averaged 1 ms⁻¹ and each net was nominally deployed for 10 min to provide a filtered volume of $\sim 450 \text{ m}^3$ per net. Recovery, sorting, and preservation techniques were as described above. The net samples were subsequently resorted on land and the remaining larvae were removed, enumerated, and preserved. Because of the difficulties in species identification, and consistent with most other redfish studies, larvae were identified to genus only. Two species (S. norwegicus mantella and S. fasciatus) are known to occupy the Scotian Shelf. Larval abundance estimates were depth-averaged, normalized by the filtered volume and expressed as number per 100 m^{-3} . The total length of each larva was determined using an ocular micrometer and no corrections related to preservation shrinkage were applied. Larvae were subsequently dried to constant weight at 60°C (\sim 24 h) and weighed to the nearest 0.1 µg with a Cahn Gram Electrobalance (model G, Ventron Corp., Paramount, CA, USA) and a Perkin-Elmer AD4 balance.

Figure 2a,b shows the transects with station numbers sampled during the two cruises on 21–22 April and 30 April–1 May, respectively, relative to the position of the waters of different origin, as derived from satellite imagery.

Results

On 19 April 1991 the shelf/slope front off the Scotian Shelf was highly convoluted and included a large





Figure 2. CTD stations (numeric identifiers) occupied relative to the position of the shelf and slope (shaded) waters and Gulf Stream eddies, as derived from satellite imagery (a) during 21–22 April 1991 (satellite imagery 22 April) and (b) during 30 April–1 May 1991 (satellite imagery 1 May). The positions of fronts between the shelf and slope waters as derived from CTD measurements are denoted by heavy solid lines.

"hammerhead" feature located south of Western Bank (Fig. 1a). Four Gulf Stream eddies occupied the slope water region between the Gulf Stream and the shelf water (eddies A, B, C, and D). The highly dynamic nature of the region is indicated by changes in positions of the shelf/slope front, the Gulf Stream, and warm-core eddies between 19 April and 8 May (Fig. 1b), a period which overlaps our field measurements. For example, on 22 April the eastward extension of the hammerhead was wrapped around eddy C and was being pulled offshore toward the Gulf Stream. By 26 April this extension had disappeared, presumably through mixing with slope water, while the remainder of the hammerhead was being entrained around eddy B. By 1 May, eddies B and C were approaching each other, while a new eddy E had become established. By 8 May there was nothing left of



Salinity

Figure 3. Contours of temperature and salinity compiled from CTD profiles collected at stations 69 to 97 offshore of Western Bank (see Fig. 2a) during the visit on 21-22 April 1991.

the original hammerhead feature, while eddy B had merged with eddy C.

When running the transect on 20–21 April (Fig. 2a), the hammerhead contained waters of temperatures $<6^{\circ}$ to 8°C and salinities of 33.5–34.5, slightly warmer and saltier than the waters over Western Bank (T<5°C, S<33.5; Fig. 3). This feature was approximately 50 m deep and lay above warm slope waters (T>8°C, S>34.5). East of the hammerhead lay surface waters of slope

Figure 1. Charts showing the location of the shelf/slope front between shelf water (SH) and slope water (SL), the Gulf Stream (GS), and different Gulf Stream eddies (A, B, C, D, E): (a) on 19 April 1991 with indication of the primary study area (shaded) and (b) during the period 22 April to 8 May 1991.

water origin (CTD stations 80 and 81). Farther east, we passed through the shelf/slope front (between stations 81 and 82) into shelf water with hydrographic characteristics similar to those found on Western Bank. A transect along 59.2°W indicated the southern limit of the shelf/slope front was near 42.8°N, while measurements along 43°N showed that the shelf water extended to our easternmost observation (station 97, 58°W).

There was relatively good agreement in the surface thermal structure derived from the CTD and from the 22 April NOAA satellite image, although there were discrepancies (Fig. 3). The largest difference was the absence of slope water at the surface along the CTD transect west of 60°W, where the NOAA charts suggested that slope water separated the western arm of the hammerhead from the main body of shelf water.

When we returned to the area 9 days later (30 April–May 1; Fig. 2b) temperatures in the hammerhead feature had increased to between 6.5° and 8° C. Warm slope water (>10°C) still separated this feature from the cold shelf waters to the east. Temperatures in the latter shelf waters had generally risen by 0.5° to 1° C since our earlier visit, although salinities had not changed appreciably. Figure 4 provides the vertical profiles of temperature and salinity along one of the north–south transects, along 59.2°W. The southern extension of the shelf-slope front was located to the south of 42.7°N and slightly south of its 22 April position. Good agreement was again found between the position of the shelf/slope front from the CTD measurements and the NOAA charts (Figs 2b, 4).

Temperature and salinity characteristics of the different water masses during the cruise on 8–9 May were similar to those found during the previous two visits, although the shelf water did not extend as far offshore as before (Fig. 1b).

The redfish larvae collected during the three occupations of the offshore feature were found almost exclusively in the upper 40 m, where the hydrographic characteristics resembled those on the shelf ($T < 5^{\circ}C$ and S<33.5; Fig. 5). Average concentrations in the upper 40 m by station and cruise (Fig. 6) indicate that during the first occupation larval concentrations were maximum ($\sim 7/100 \text{ m}^3$) near 43°N, 59°W (tow #227) and decreased to the east and west. The lowest concentrations were observed immediately to the south of the shelf/slope front in slope waters with temperatures >10°C. During the second occupation, larval concentrations were higher and exceeded $\sim 11 \text{ larvae}/100 \text{ m}^3$ in shelf waters at two sites along approximately 42.8°N. The lowest concentrations (0.3 larvae/100 m³) were again recorded in slope water near the shelf/slope front. On the third occupation, all samples were collected in shelf waters varying from 2° to less than 6°C. Larval concentrations were lower than on the second occupation, but similar to those recorded during the first visit and ranged from a high of $\sim 10 \text{ larvae}/100 \text{ m}^3$ to $<0.1/100 \text{ m}^3$. Concentrations during the first and third visits were similar to those recorded over Western Bank at the beginning of May (range 0 to $\sim 12 \text{ larvae}/100 \text{ m}^3$).

The weight-at-length relationships for the redfish larvae from each occupation of the offshore feature, as well as from Western Bank, show lengths ranging between 3.5 and ~9 mm and weights between <0.1 and ~1 mg (Fig. 7). While the lengths were approximately normally distributed, weights were skewed toward lighter larvae, with the majority in the 0.1–0.4 mm range. The last two occupations of the offshore feature revealed longer and heavier larvae relative to the first occupation. Larvae collected on Western Bank had similar lengths to those found offshore, but weights at a given length were significantly greater.

As larval physiological condition can be indexed from a weight-at-length relationship, we used such an index to compare the condition of the larvae collected offshore with those collected on the shelf (Western Bank) and in an older entrainment feature. All data were initially pooled to determine an overall weight-at-length relationship using a linear regression of log-transformed weight on length. Residuals (log-weight anomalies) from this regression were then calculated for each larva and used as an index of relative condition. The frequency distributions of the residuals (Fig. 8) during the three occupations of the offshore feature were similar, i.e. the mean and median residuals for all three visits were negative and significantly different from zero (p=0.05). This contrasts sharply with Western Bank larvae, of which the majority showed positive residuals, and thus are considered to be in better relative condition.

During the "Petrel V" cruise, five additional BIONESS collections were made south of Western Bank in the area of the hammerhead feature along 61.3°W between 42.15°N and 41.75°N. Temperatures in the range of 6-8°C indicated a mixture of predominantly shelf water with some slope water. This mixing is also consistent with the gradual disappearance from the satellite imagery of the hammerhead feature. Redfish larvae concentrations (total of 27 larvae for the five stations combined) were significantly lower relative to either the offshore feature to the east or on Western Bank. The ichthyoplankton collections in the area were dominated by myctophids (69% of all larvae), while redfish constituted 26%. This species composition contrasts with the main offshore feature described above, where redfish dominated (82-100%) and few myctophids were found. Myctophids are mesopelagic fish that normally occupy slope waters and are not generally found on the shelf. The redfish larvae in the hammerhead were primarily 7-9 mm in length and weighed between 0.3 g and 1 g. Using an assumed initial size of 4–6 mm and a growth rate of $\sim 1\%$



Figure 4. Contours of temperature and salinity along 59.2° W during 30 April 1991. CTD station numbers appear directly above the plots. Horizontal lines above the station numbers indicate the location of the BIONESS tows; the number below each line is the BIONESS station number and the number above the line the concentration (number per 100 m³) of redfish larvae in the upper 40 m.

per day (Anderson 1984), these larvae were estimated to be 1 to 2 months old. From the generalized weight-atlength relationship described above, they were in better condition (i.e. greater weight at a given length) than the larvae in the other offshore feature, but in worse condition than those collected on the shelf.

Discussion

The three consecutive surveys during a 19-d period revealed significant numbers of redfish larvae offshore of

the Scotian Shelf, approximately 100 km seaward of the shelf-break. Larval concentrations were comparable to those on the shelf over Western Bank during the same period. The offshore larvae were almost exclusively found in the upper 40 m in temperatures $<5^{\circ}$ C and salinities <33.5, i.e., properties consistent with waters of shelf origin. Almost no larvae were found in the warmer, saltier slope waters and multi-net sampling revealed a sharp gradient in larval concentrations across the narrow shelf-slope front.

Previous studies have observed few redfish larvae off the Scotian Shelf. Kenchington (1984) provides the most



Figure 5. Contours of larval redfish concentrations (large font; number per 100 m^{-3}) as a function of depth and temperature, averaged over the tow length. Darker shading indicates higher concentrations and the small font numbers are the measured concentrations for each individual tow.

extensive analysis based on 34 cruises between 1976 and 1982. Although most sampling was restricted to the shelf area, no redfish larvae were found in the relatively few samples collected seaward of the shelf break. During the 1914–1915 Fisheries Expedition in Atlantic waters led by J. Hjort, redfish were widely distributed over the shelf (Dannevig, 1919). However, of the 21 stations taken beyond the shelf break, only two contained redfish larvae and concentrations were relatively low. Those stations were off the northeastern Scotian Shelf and, similar to our study, the hydrographic properties indicated the larvae were in waters of shelf origin. Templeman (1959) in his extensive review of redfish in the North Atlantic notes the absence of larvae seaward of the 200 m isobath off the Scotian Shelf and attributes it to a lack of suitably low temperatures. To our knowledge, our measurements are the first to show significant concentrations of redfish larvae seaward of the continental shelf.

Where did the larvae observed offshore originate? Redfish on the Scotian Shelf tend to release their larvae (redfish are ovoviviparus; i.e., they release their larvae near the end of the yolk-sac stage) between March and September, with the majority doing so in May through August (Kenchington, 1984). In April, larvae are released primarily along the shelf break, but by May they are released over the Shelf. The larvae we collected offshore most likely originated near the shelf break in



Figure 6. Average concentration (numbers per 100 m^3) of redfish larvae in the upper 40 m at each BIONESS station for: (a) 21 April; (b) 1 May; and (c) 8–9 May 1991. The slope waters based on the satellite data are shaded and the heavy solid lines denote the positions of the front based on CTD measurements.

shelf waters, and these waters, along with the larvae, appear to have been transported seaward through entrainment by Gulf Stream rings, perhaps aided by other processes (e.g. wind forcing).

Newly released larvae tend to range in length from 4 to 9 mm (Kenchington, 1984) and rise towards the surface subsequent to release. Larval lengths observed during our study fell within this range. For the two redfish species on the Scotian Shelf, newly released larvae of *S. mantella* tend to be in the 7–9 mm length



Figure 7. Weight–length relationship for redfish larvae from the three visits to the offshore feature and from Western Bank (horizontal line corresponding to a weight of 0.5 g provided to facilitate comparisons).

range, while S. fasciatus is typically <7 mm. The high percentage of larvae <7 mm in the offshore feature (84%, 72%, and 87% of all larvae collected during consecutive visits, respectively) and on Western Bank (85%) suggest that at both sites the larvae were S. fasciatus. A lower percentage of smaller larvae ($\sim 44\%$) were observed within the offshore hammerhead feature. We suggest these larvae were also S. fasciatus but had been released 1-2 months earlier. This is consistent with the measured lengths, given published growth rates, and the release time is consistent with the date (early March) when the hammerhead feature was first observed in the satellite imagery. Temperature and salinity characteristics as well as the high number of myctophids in the hammerhead feature are consistent with extensive mixing of shelf and slope waters and provide further evidence that the redfish larvae we collected were unlikely to have been recently released.



Figure 8. Percent frequency distributions of residuals from the overall linear weight-length relationship (expressed as log weight) for redfish larvae from the three visits to the offshore feature and from Western Bank (solid bars: negative residuals – less-than-average condition; shaded bars: positive residuals – better-than-average condition).

Substantial larval growth between our first and second visits to the offshore feature east of 60° is suggested by the presence of longer, heavier larvae in the second visit. Also, the increase in the median length from 6.1 mm to 6.5 mm between these visits matches the expected growth rate of 1% per day (Anderson, 1984). Although on the third visit the larger sizes of larvae were similar to those observed during the second visit, there were more small larvae. This resulted in a reduced median length (6.0 mm), which suggests either we were sampling a different patch of larvae or newly released larvae had entered the original patch.

The first of the two most important questions is what happens to the larvae that are transported off the shelf? Our results suggest that entrained larvae are most likely lost and do not recruit to the shelf population. We found the offshore larvae were in worse condition relative to those on the shelf over Western Bank. There is also a hint that condition may have deteriorated between our first and second visits, as there were more larvae in less-than-average condition during the second (68%) relative to the first (55%; Fig. 8). These values compare to only 19% below average on Western Bank. However, during the third visit the larval condition resembled that of the first visit. As previously mentioned, this may be due to sampling a different patch of larvae or the addition of younger larvae to the original patch.

Metamorphosis normally occurs at lengths of 40-50 mm, which at measured growth rates translates into a 4.5 month larval period (Kenchington, 1984; extreme range of 2-6 months). Given such long periods, larvae released near the shelf/slope front are unlikely to persist there for the 4-5 months. Satellite imagery shows the region to be highly dynamic with the shelf-slope front being constantly "pushed and pulled" by eddies and by the Gulf Stream. The shelf waters entrained offshore mix with the surrounding slope water, as indicated by the high percentage of larvae of mesopelagic species in the older hammerhead feature. Most redfish larvae in the cold shelf waters that came into sudden contact with the warm slope waters are expected to die owing to the abrupt temperature change, such as observed by Colton (1959) for cod larvae off Georges Bank. If the larvae did survive the initial contact, the higher temperatures would increase metabolic demands, which could result in reduced growth rates and ultimately death (Boehlert, 1981). Concentration, species, and particle-size of available prey would change and could result in a deterioration of larval condition. Such a phenomenon is simply another variation on the match-mismatch hypothesis (Cushing, 1972). The lack of larvae found in the slope water during our study is consistent with increased mortality. If the larvae did survive to metamorphose over depths of 2000-4000 m far offshore they are unlikely to be able to swim back to the shelf and would presumably be lost to the shelf population. In summary, we suggest that once entrained the probability of death or vagrancy (Sinclair, 1988) is increased through weakened condition, excessively high temperatures if transported into slope water, or undergoing metamorphosis too far off the shelf.

We do not think our observations are indicative of an unusual event. The shelf waters typically extend beyond the continental shelf (Drinkwater et al., 1994) and the front separating the shelf and slope waters is normally convoluted due to the presence of the Gulf Stream and its associated eddies. Entrainment of near-surface shelf waters into the slope region is a frequent phenomenon. Thus, redfish larvae may also be frequently transported offshore in the spring when they are released near the continental break. The lack of prior observational evidence for significant numbers of redfish larvae offshore is likely due to the limited offshore sampling, both at the proper time and in shelf-like waters. This is consistent with Marr's (1956, p. 169) forgotten suggestions that observations related to significant mortality processes are usually limited because "the chances that the observer will make the right observation at the right time and right place are greatly reduced".

The second important question is, can entrainment of shelf water by eddies transport enough fish larvae off the shelf to significantly affect recruitment variability? Larval survival, including that of redfish, is extremely low, around 1% or less (Anderson, 1984). Thus, losses due to entrainment of larvae offshore may simply be one mechanism accounting for reduced recruitment potential. However, the relationship of redfish recruitment to the presence of Gulf Stream eddies during the time when larvae were present as found by Myers and Drinkwater (1989) suggests that offshore transport is important. Unfortunately, recent attempts to update the relationship between ring activity and redfish recruitment have proved frustrating. Management units of redfish have changed, recruitment indices are not readily available and the relative proportion of the two main species of redfish over the shelf is not well established (R. Halliday, Bedford Institute, pers. comm.).

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