Condition of laboratory-reared and wild-caught larval Atlantic menhaden *Brevoortia tyrannus* as indicated by metabolic enzyme activities

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ABSTRACT: As part of the South Atlantic Bight Recruitment Experiment (SABRE), the condition of larval Atlantic menhaden *Brevoortia tyrannus* from Onslow Bay, North Carolina, USA, was determined. The activities of the metabolic enzyme lactate dehydrogenase (LDH) were assayed in larval Atlantic menhaden to determine nutritional condition of laboratory-reared and wild-caught larvae on cruises in 1992 to 1994. In laboratory calibrations, larvae whose first feeding was delayed had depressions in protein-specific LDH activities, and LDH activity appeared to scale with length. Wild larvae had LDH activities within the range of activities found in laboratory-reared larvae and were classified into 3 nutritional categories based on length and LDH activities. Fewer than 30% of larvae collected from the majority of stations were classified in superior condition. No differences were detected between larvae collected during the day and those collected at night. Significant decreases in condition were evident with increasing distance from the Gulf Stream Front. LDH activities indicated that a substantial percentage of wild-caught menhaden larvae were poorly nourished during the period examined.

KEY WORDS: Larval menhaden · Lactate dehydrogenase · Nutritional condition · Onslow Bay

INTRODUCTION

The major natural cause of population fluctuations observed in marine fish stocks is interannual variability in recruitment success. Subtle changes in mortality rates, whether due to predation or starvation episodes during early life history stages, may play a significant role in subsequent recruitment variability (Harding 1974, Cushing 1983, Hunter 1984, Bailey & Houde 1989). Seemingly minor shifts in growth rates, stage duration, and survivorship may generate effects several orders of magnitude greater upon recruitment success into the adult population (Houde 1987).

Food assimilation rates, energy budgets, and behavioral aspects of feeding have also been extensively studied in order to gain insight into survival parameters for marine fish larvae (Blaxter & Ehrlich 1974, Laurence 1977, Houde & Schekter 1980, Cetta & Capuzzo 1982, Kentouri & Divanach 1982, Frank & Leggett 1985). The interactions between food availability and other biotic factors, such as predation (e.g. through decreased predator avoidance capabilities of poorly nourished larvae) or competition, are complex. Larval fish and egg populations are highly aggregated, both spatially and temporally (Laurence 1974, Hunter 1981). Fine spatial scale patchiness from meters to tens of meters may be of importance to larval fish because it corresponds to the effective environment ('ambit') of zooplankters which is defined by their limited swimming ability (Wiebe 1970, Haury et al. 1978, Haury & Wiebe 1982, Davis et al. 1992).

Many techniques have been utilized to determine the nutritional status of larval fish in the context of estimating starvation-induced mortality. Traditional approaches, however, preclude the shipboard analyses

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of large numbers of samples necessary to construct near real-time synoptic field maps of nutritional condition. Furthermore, in many cases these techniques have been time consuming, and large numbers of analyses could not be performed easily (Theilacker 1980, 1986, Hay 1981, 1982, Jennings 1991, Hjorleifsson & Klein-MacPhee 1992). Clarke & Walsh (1993) and Clarke et al. (1992) have used metabolic enzyme activities to characterize the condition of zooplankton during laboratory experiments and suggest that these methods may be useful in analyzing field-caught specimens. These investigations were based on the well-documented effects of feeding on the activities of juvenile and adult fish enzymes (Moon 1983, Lowery et al. 1987, Lowery & Somero 1990, Yang & Somero 1993).

Atlantic menhaden *Brevoortia tyrannus* is a highly abundant and economically important fish species. It also comprises the forage base for many pelagic game fish inhabiting the Western North Atlantic (Reintjes & Keney 1975, Ahrenholz et al. 1987, Smith et al. 1987). The Atlantic menhaden is an estuarine-dependent clupeid species whose egg and larval stages occur offshore, on the continental shelf. Transport of pelagic stages is predominantly westward across the shelf, affecting eggs and larvae of up to approximately 15 mm standard length. Larvae are planktonic for at least 1 mo, possibly up to 3 mo, from time of hatching. Late-larval stages and juveniles between 15 and 20 mm (standard length) immigrate through coastal inlets and subsequent development occurs in estuarine habitats (Ahrenholz 1991). Flexion occurs between 8 and 10 mm, and transformation into juveniles occurs at approximately 30 mm after estuarine immigration. Cross-shelf movement of *B. tyrannus* larvae results from interactions between nearshore, vertical, and estuarine circulation (Lewis & Wilkens 1971, Fore & Baxter 1972, Pietrafesa & Janowitz 1988, Hoss et al. 1989). During this cross-shelf transport, the larvae face a myriad of conditions and food availabilities. Therefore, in this study we use metabolic enzyme activities calibrated in laboratory experiments to characterize the condition of field-caught menhaden larvae during this cross-shelf transport.

METHODS

Sample preservation and biochemical methods. Cod-ends were quickly removed from plankton nets following short-duration tows (5 to 10 min) and emptied into ice-cold seawater (maintained at approximately 2 to 3°C by previously frozen gel-packs). Larvae were quickly sorted from the sample and standard lengths measured. The tail was removed from the head and gut, briefly rinsed in chilled 280 mM sucrose, 10 mM sodium HEPES (N-[2-hydroxyethyl]piperazine-

N'-[2-ethanesulfonic acid]), pH 8.0 and frozen in liquid nitrogen. Ice-cold 50 mM sodium-HEPES buffer pH 7.5 was added for tissue sonication (Kontes Ultra-Sonic Cell Disrupter) followed by centrifugation at $13\,000 \times g$ for 20 s (Eppendorf Model 5415C Microcentrifuge). Crude supernatants were used directly for lactate dehydrogenase activity assays according to methods of Clarke et al. (1992). In our prior studies on larvae, and others on adults, 2 enzymes showed particular utility in assessing condition, namely citrate synthase (a Kreb's cycle enzyme involved in aerobic catabolism) and lactate dehydrogenase (LDH; the terminal step of anaerobic glycolysis, a particularly important pathway for larval fish burst locomotion, Kaupp & Somero 1989). Preliminary investigation (Fiedler 1994) indicated that LDH was most suitable for application to larval menhaden due to its high activity even early in development, and thus it was chosen for this study. Total soluble protein was measured in the same homogenates by a modification of the Lowry et al. (1951) method using bovine serum albumin (BSA) as a standard. LDH activities (picomole product produced per minute) were normalized to microgram (µg) protein from this method (i.e. protein-specific LDH activity).

Delayed feeding experiment. Laboratory eggs of *Brevoortia tyrannus* were obtained from W. F. Hettler, National Marine Fisheries Service, Beaufort Laboratory (Beaufort, NC) on 4 April 1992. Larvae were reared at the Rosenstiel School of Marine and Atmospheric Science on Virginia Key, Florida. Air temperature was maintained at 20 ± 0.5°C with room air conditioners; tank water temperature was measured daily and remained between 18.5 and 20.0°C. A photoperiod of 12 h light:12 h dark was provided with fluorescent lights and timers. Salinity was also measured daily with an optical refractometer and fluctuated between 36 and 36.5 ppt. Equal volumes (3.6 l) of *B. tyrannus* eggs from a single spawning on 3 April 1992 were added to each of six 380 l tanks on 4 April 1992 at an approximate density of 10 to 15 eggs l^{-1}. Food densities were maintained at 2 wild copepod nauplii ml^{-1} + 2 cultured rotifers *Brachionus plicatilis* ml^{-1} $tank^{-1}$, based on previous studies in our laboratory (Clarke et al. 1992). The wild nauplii were obtained during ebb and flood tides from the RSMAS dock in Bear Cut, Biscayne Bay, by short duration tows (<10 min) with a 53 µm mesh net, quantified, and added to the tanks until final concentrations were as stated. Ammonia accumulation in the closed system was minimized and zooplankton maintained by the daily addition of 1 l of *Isochrysis galbani* (Tahitian strain). Tank bottoms were siphoned to remove accumulated debris as necessary. There were 6 experimental treatments corresponding to the time at which food was first presented to the fish (hatching day and 1, 3, 4, 5 and 6 d after hatching;

DAH). Food intake was verified by visual inspection of the gut. Five individual larvae per tank were sampled each day. Larvae were then dissected, cryopreserved and analyzed as above.

LDH stability in net simulation. Larvae collected in the wild by towed plankton nets spend several minutes at ambient temperatures following expiration, before being cryopreserved. A simulated flow-through plankton net was constructed to test for any effects of net capture. Air temperature was maintained at $20 \pm 0.5°C$ for the duration. Ambient seawater temperature was 19.5°C. Ten individual *Brevoortia tyrannus* larvae (14 DAH) were placed in a cone of 202 µm mesh netting affixed to a cylindrical PVC pipe. Larvae were then subject to running seawater for discrete time periods of 10, 15, 20, 25, and 30 min, then dissected, cryopreserved and analyzed as described above.

Field collections. As part of the SABRE program, Atlantic menhaden larvae were collected in Onslow Bay, North Carolina, during the winter spawning months of 1992, 1993, and 1994. Cruise dates, quantity of individual larvae obtained, and number of stations sampled are described in the appropriate figure legends. Larvae were collected by surface (area of greatest menhaden abundance) plankton tows with a 60 cm diameter 333 µm mesh paired bongo net. Sampling was conducted both in the daytime and at night, whenever the ship arrived at a station. Fluorescence measurements taken during Cruise 3 were converted into chlorophyll *a* (chl *a*) concentration (µg l^{-1}) by calibration of standards performed by the National Marine Fisheries Service (NOAA) Beaufort Laboratory, NC.

RESULTS

Delayed feeding experiment for *Brevoortia tyrannus* larvae

No significant differences (ANOVA, $p > 0.05$) in LDH activity were found between treatments on DAH (days after hatch) 1 through 4, although there was a significant increase on 1 DAH (Fig. 1). However, larvae began to exhibit significant increases in LDH activity within 2 d following first feeding. Larvae fed on the day of hatch exhibited significantly elevated protein-specific LDH activities compared to all other treatment groups on all sampling days following 4 d post-hatch (ANOVA, $p < 0.05$). Intermediate LDH activities were observed for the group of larvae fed on 3 DAH. This treatment group exhibited enzyme activities significantly less than the 0 DAH group and significantly greater than the 6 DAH treatment (ANOVA, SNK, $p < 0.01$) for all sampling periods following 4 d post-hatching.

The fish which were fed on 6 DAH had significantly lower activities than all other groups following 4 d post-hatch. For the purpose of developing a laboratory calibration to relate enzyme activity and feeding in field caught larvae, 3 representative treatment groups (first fed on 0 and 1 DAH, 3 and 4 DAH, and 5 and 6 DAH) were selected since the entire range of data values were represented. Regression analysis (ANCOVA, $p < 0.05$) found significant differences in the increase in LDH activities among these 3 treatments, but not consistently between treatments differing by only 1 d.

Growth rates in terms of length were similar for all treatment groups (Fig. 2), excepting those individuals starved until 5 and 6 DAH. The 5 DAH treatment exhibited intermediate growth rates lower than the 4 groups fed earlier but slightly higher rates than the group fed on 6 DAH. The 6 DAH treatment group exhibited a significant decrease in mean length for the 3 sampling periods following 3 d post-hatching, possibly due to enhanced mortality in these older larvae, which require more food. Consequently, a disproportionate amount of smaller size-class individuals may have been sampled. Growth parameters for all treatment groups are given in Table 1.
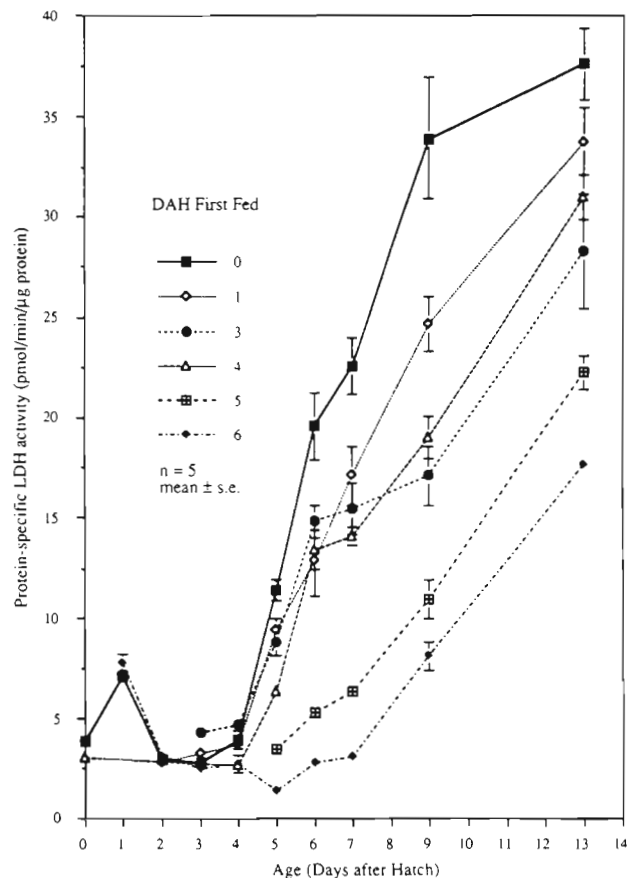

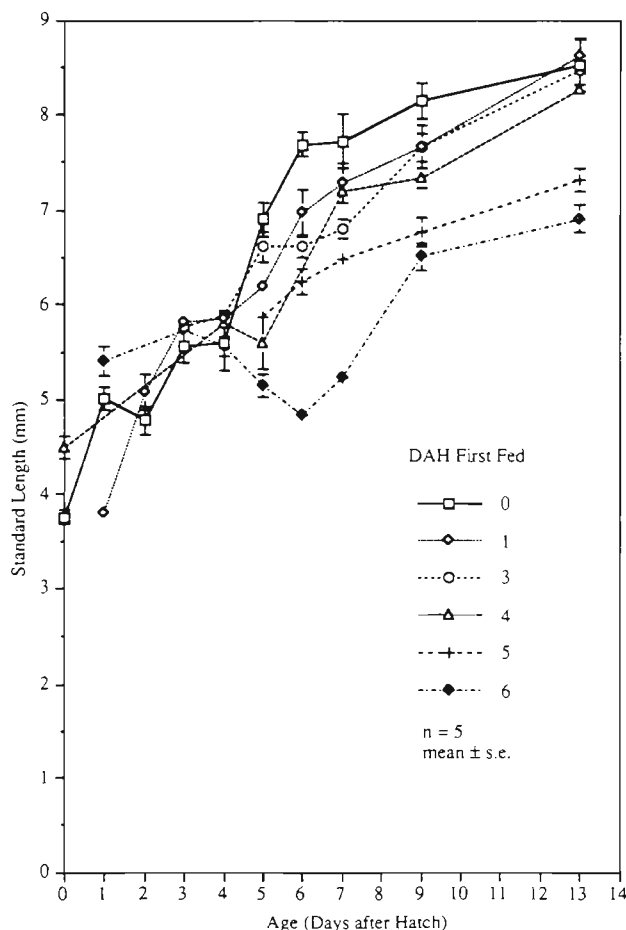Fig. 1. Delayed feeding effects on LDH activity

Fig. 2. Delayed feeding effects on standard length

Fig. 3. Delayed feeding effects on LDH activity versus length

The observed growth rates in *Brevoortia tyrannus* based on standard length (Fig. 2, Table 1) were curvilinear, and, therefore, an exponential model natural logarithmic transformation of the ordinate was necessary to linearize the data. All ln-transformed data produced highly significant non-zero linear regressions (ANOVA, $p < 0.001$). Approximately 16 % more of the variation was explained by the logarithmic equations than by the initial linear model. Groups fed on day of hatching and 1 DAH had significantly higher growth rates than all other groups. The 2 lowest growth rates were observed in those tanks fed on 5 and 6 DAH, evidenced by the lowest
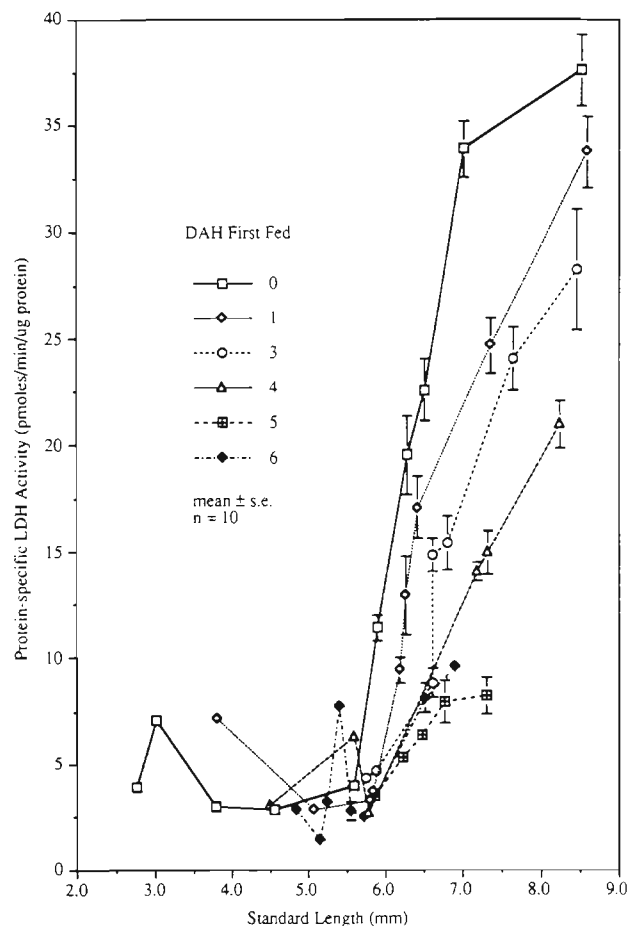
slopes. These 2 treatments had insignificant slope differences from each other (t-test, df = 63, p = 0.24). Groups fed on 3 and 4 DAH had slopes below those fed earlier, but significantly greater than tanks fed on 5 and 6 DAH (t-test, df = 98, p < 0.05). In summary, in addition to the observation of 3 groups of LDH activities, 3 groups of significantly different growth rates based on standard length increases were observed: fish first fed on 0–1, 3–4, and 5–6 DAH (see Table 1, note slopes for each treatment).

When analyzed on a per length basis, protein-specific LDH activities demonstrated a strong increase (Fig. 3) versus standard length. Highly significant non-

Table 1. *Brevoortia tyrannus*. Growth rate parameter variation

| | Day after hatch first fed | | | | | | Group | | |
	0	1	3	4	5	6	0/1	3/4	5/6
SL increase (mm)	4.7	4.8	4.7	4.5	3.6	3.2	4.81	4.60	3.36
Slope for ln Y	0.053	0.051	0.034		0.022	0.018	0.052	0.038	0.020
R^2 (ln Y)	0.826	0.838	0.957	0.929	0.945	0.437	0.613	0.778	0.841
Y-intercept ln Y	1.707	1.696	1.822	1.731	1.840	1.785	1.702	1.776	1.812

zero slopes (ANOVA, p < 0.05) were found for all groups, indicating an increase in anaerobic potential with size throughout this developmental period. Larvae first fed on the day of hatch had significantly greater changes in protein-specific LDH activity (t-test, df = 98, p < 0.05) than all other treatment groups. LDH activity was inversely correlated with the time between hatching and first feeding. Parameters for regression analyses are given in Table 2. Treatment groups did not show any significant differences until 5.6 mm standard length and then exhibited linear increases as demonstrated by highly significant F values (ANOVA) and large correlation coefficients.

In summary, protein-specific LDH activities and growth rates are significantly affected by the timing of first feeding in *Brevoortia tyrannus* larvae, and highly significant nutritional effects upon LDH activities are seen both as a function of age and standard length (after 6 mm). During the course of the 14 d experiment, LDH activities increased nearly 10-fold, a broad envelope for field values to fall into.

LDH stability in net retention simulation

No significant differences in protein-specific LDH (ANOVA, $F = 1.4142$, p = 0.221) levels were found during simulated plankton net experiments up to 30 min in duration (Table 3).

Field-collected larvae in Onslow Bay, NC

Wild Atlantic menhaden larvae were collected in conjunction with the SEFC Beaufort Laboratory, in Onslow Bay, North Carolina (76.4–77.8° W, 33.8–34.6° N), during the winter spawning months of 1992, 1993, and 1994. Stations (Fig. 4) are identified by cruise year followed by station number (e.g. 9308). The 2 stations sampled on Cruise 4 (February 1994) have been designated 94258 and 94259 to distinguish them from January 1994 stations. No significant differences were found in the numbers of larvae collected per station among all 4 cruises (Welch ANOVA, $F = 1.1761$, p = 0.3885), but the large sampling variability and difference in number of samples obtained would in any case virtually preclude any statistically rigorous intercruise comparison (Table 4). Cruises 1, 2, and 3 encompass 95.3% of the field collections since only 2 stations were sampled on Cruise 4.

Larvae collected from Cruises 2 and 3 were significantly longer (7.5 ± 0.1 and 7.4 ± 0.1 mm) than on cruises 1

Table 2. Protein-specific LDH activity versus length in delayed feeding experiment

DAH fed	Slope ± SE	F ratio	prob. > F	R^2
0	11.23 ± 2.49	20.306	0.0108	0.835
1	9.95 + 1.12	77.778	0.001	0.928
3	9.44 ± 0.99	90.329	0.002	0.947
4	6.32 ± 0.89	49.447	0.0059	0.943
5	3.51 ± 1.15	9.226	0.0229	0.605
6	3.39 ± 0.65	26.647	0.0141	0.899

Table 3. Mean protein-specific activities for net retention test

Min	n	LDH activity (mean ± SE)
5	10	45.659 ± 8.304
10	10	38.164 ± 7.289
15	10	44.947 ± 6.062
20	10	44.855 ± 7.168
25	10	49.565 ± 6.213
30	20	42.971 ± 3.006

and 4 (7.1 ± 0.1 and 7.0 ± 0.1 mm, Welch ANOVA, $F = 13.639$, p = 0.001; Tukey-Kramer HSD). The range of mean standard lengths was however comparatively small, only 6.7 to 7.9 mm. The mean standard length per station for all cruises was between 6.7 and 7.9 mm with the exception of Stn 9301 in which the mean standard length (9.5 mm [n = 4]) was significantly greater (ANOVA, p < 0.003, $F = 23.658$). No statistical relationship was detected between standard deviation of mean length per station and numbers of fish collected per station using all data (ANOVA, $F = 0.8902$, p = 0.317, $r^2 = 0.02$). When only stations with 4 or more larvae were included (61% of field stations) a significant negative linear relationship was seen between length variability and abundance per station (ANOVA, $F = 18.0140$, p = 0.003, $r^2 = 0.44$). Those stations at which the greatest numbers of larvae were collected (Stn 9212: n = 33; Stn 9213: n = 29) were most homogeneous. On the other hand, there was no statistically significant relationship between size, as measured by standard length, and abundance at stations of n > 3 (ANOVA, $F = 0.0484$, p = 0.827, $r^2 = 0.001$).

Table 4. Mean number of larvae per station

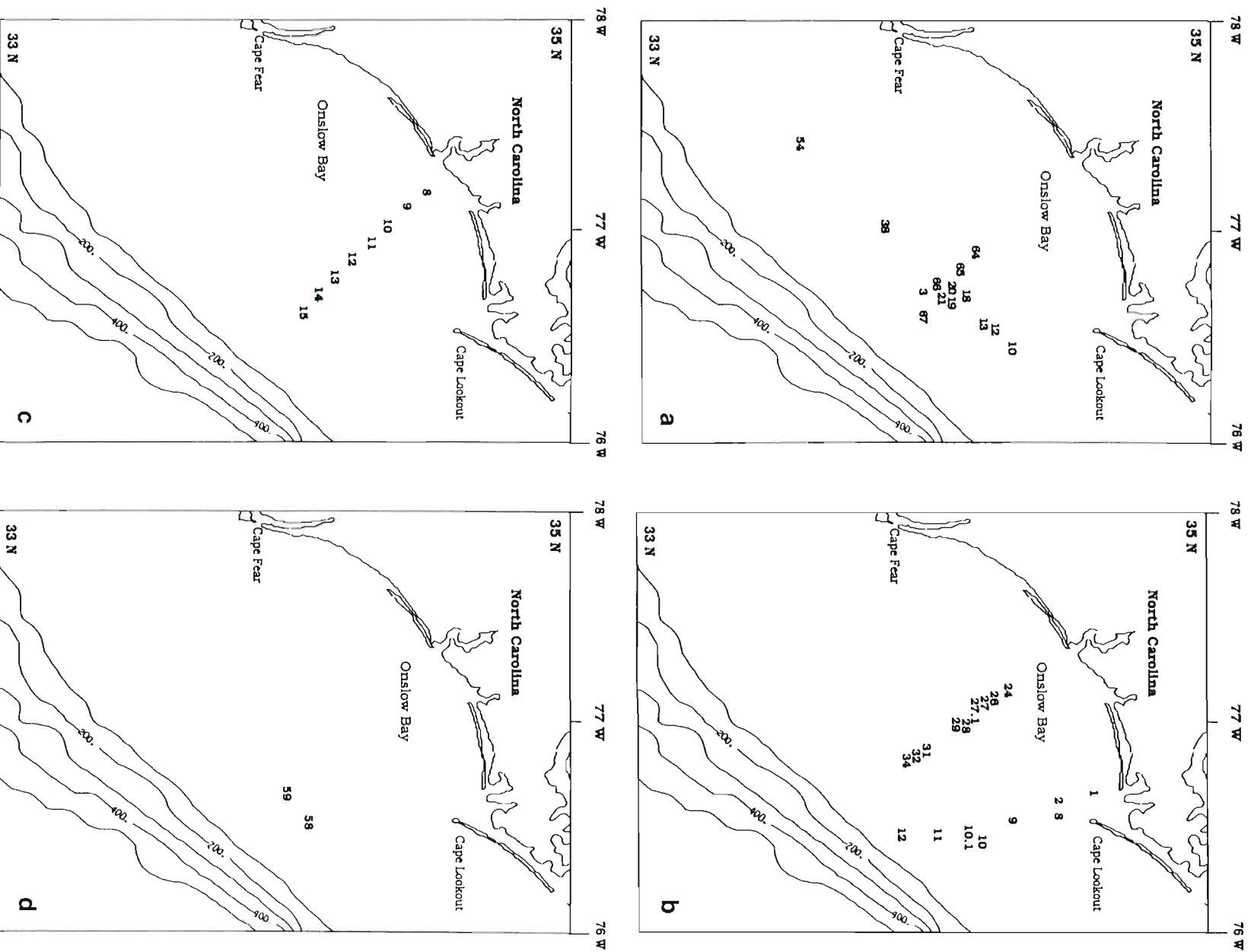| Cruise	Cruise ID	Cruise dates	n	No. of stations	Larvae per station
1	AL-92-12	16–20 Dec 1992	112	14	8.0
2	AL-93-01	8–15 Jan 1993	102	17	6.0
3	OII-93-08 leg 2	11–20 Jan 1994	88	8	11.0
4	OII-93-08 leg 5	3–6 Feb 1994	15	2	7.5

Fig. 4. (a) Cruise 1—December 1992 field stations, (b) Cruise 2—January 1993 field stations, (c) Cruise 3—January 1994 field stations, (d) Cruise 4—February 1994 field stations

Atlantic menhaden larvae collected from all 4 cruises demonstrated a highly significant linear correlation (ANOVA, $F = 704.98$, $p < 0.001$, $r^2 = 0.68$) between standard length and total protein content per larva (Fig. 5). This fit to the data was better than other relationships tested, including curvilinear plots. Notably this relationship was the same for laboratory-reared larvae, suggesting that it would be reasonable to normalize enzymatic activities to protein content to account for larval size differences.

A total of 317 individuals were assayed from 4 field cruises representing 41 different stations. Enzyme activities were normalized to total protein content as discussed above to account for size differences and to make them comparable to activities for laboratory-reared larvae. Although there were no replicate determinations on single individuals, reproducibilities of both enzymatic activity and total body protein determination is approximately ±5% (unpubl. data, Fiedler 1994). These differences are small compared to the variation in the data. Significant differences were found in protein-specific LDH (ANOVA, $F = 4.5828$, $p = 0.001$) activities among field stations (Fig. 6). Significant differences also exist between cruises with respect to LDH activity with Cruise 4 larvae (n = 15) having the lowest mean activities (ANOVA, $F = 8.868$, $p = 0.001$, Tukey-Kramer HSD). Among the first 3 cruises, Cruise 3 activities were significantly greater than Cruise 1. Enzyme activities in field-collected larvae had values comparable to those determined
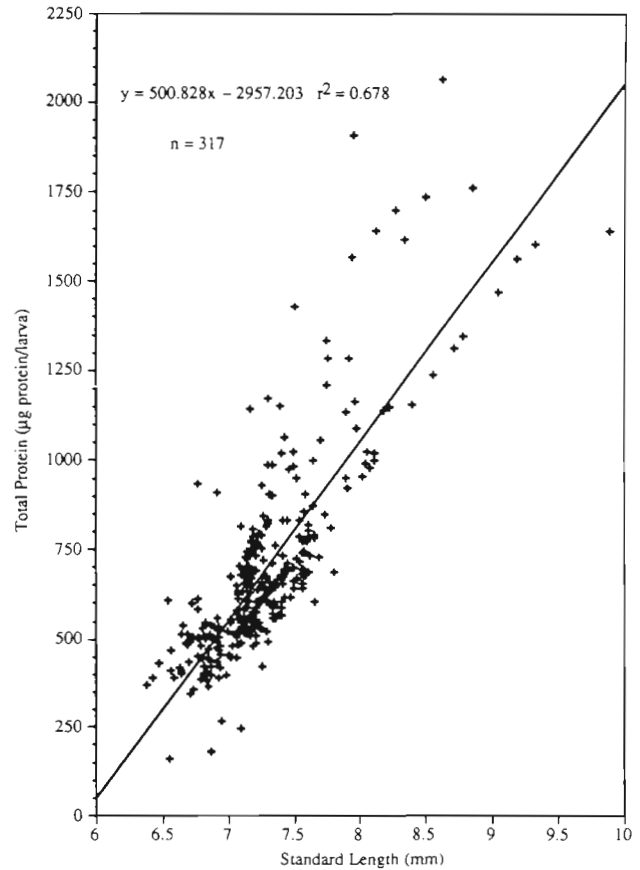

Fig. 5. Total protein versus standard length in field-caught larvae

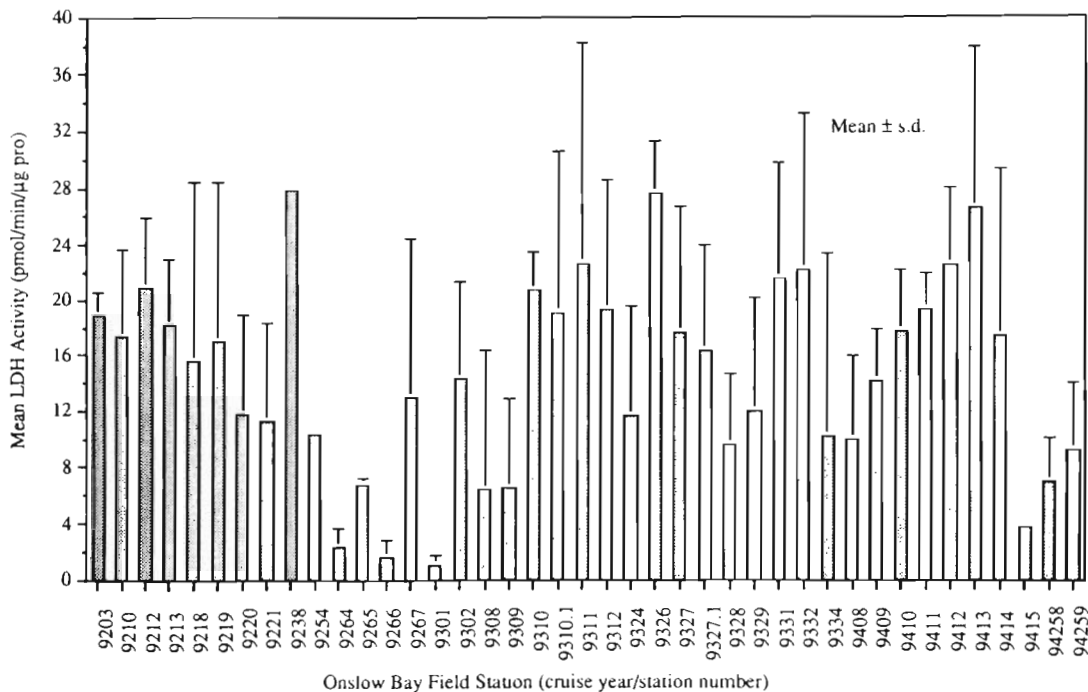$y = 500.828x - 2957.203$ $r^2 = 0.678$

$n = 317$

Fig. 6. Protein-specific LDH activity for field stations in Onslow Bay, NC, USA

from laboratory-reared larvae in the delayed feeding experiment. Stations with fewer than 3 larvae were omitted from station analyses, but included in all individual-based analyses. LDH activities exhibited a greater range in the field data than in the laboratory experiments. No significant correlation was detected between standard length and protein-specific LDH activity (ANOVA, $F = 0.1971$, $p = 0.6574$, $r^2 = 0.006$). Out of 317 larvae collected, 218 (68.8%) were gathered during daylight hours. No significant differences were found between day and night collections when analyzed with respect to standard length (ANOVA, $F = 0.040$, $p = 0.8415$) or protein-specific LDH activity (ANOVA, $F = 0.001$, $p = 0.971$). Mean values for these measurements were extremely close for day and night calculations.

Field condition analyses

LDH values seen in wild-caught larvae were compared to LDH for laboratory-reared larvae to assess nutritional condition (Figs. 3 & 6). Larvae were placed in 1 of 3 somewhat arbitrary nutritional conditions by normalizing their protein-specific LDH activity to their standard length as follows. Fish with activities above the lower 95% confidence interval (CI) about the linear regression describing the treatment fed on 1 DAH, including the day of hatch treatment, were classified as 'healthy'. Larvae which were below the lower 95% CI for the 1 DAH group (worse condition than fed on 1 DAH) but above the lower 95% CI for the 4 DAH treatment exhibit the condition of fish fed on 2, 3, or 4 DAH and were classified as 'average'. Wild-caught larvae with activities below the lower 95% CI for the 4 DAH treatment (representing the 5 DAH treatment or below) were classified as 'starving'. These were poorly fed individuals similar to those fed on 5 or 6 DAH. During Cruise 4 only 2 samples were obtained. These had insignificant differences in nutritional condition distribution (chi-squared, $\chi^2 = 0.096$, $p = 0.7565$). Both sites had a majority of starved larvae (89% for Stn 94258, 83% for Stn 94259) and lacked any healthy individuals.

Cruise 1—physical features and larval condition

Cruise 1 occurred between 18 and 20 December 1992 in Onslow Bay (Figs. 4a & 7a). The satellite data show a large filament of warm water (21 to 23°C) extending from Raleigh Bay into Onslow Bay, which had developed from an onshore meander of the Gulf Stream offshore of Cape Hatteras. It was subsequently entrained into a trailing frontal eddy whose

core was located off Raleigh Bay. A strong frontal gradient was seen due to this filament in Raleigh Bay between Cape Lookout and Cape Hatteras. Between Cape Lookout and Cape Fear, however, the Gulf Stream Front was more highly dispersed, generating a broad temperature gradient (14 to 23°C) across horizontal distances of approximately 40 km. One small-scale feature occurred approximately 30 km south of Cape Lookout in which a meander of the western edge of the filament generated a southward intrusion of cold shelf water into the warmer mixed region, producing a strong east-west frontal boundary.

Larval condition was estimated at each of 14 stations composing 2 transects (Fig. 8a, b). Continuous temperature profiles for both transects were taken and were used to accurately locate frontal regimes. Salinity measurements varied minimally (36.10 to 36.40 ppt) and added little additional insight (as compared with temperature or, where available, fluorescence) as to the origin of specific water masses. This is not unexpected during the winter season (T. Lee pers. comm.).

The 32.7 km transect of Cruise 1, running northeast-southwest, consisted of 5 stations of 4 or more larvae. Significant differences in the distribution (chi-squared, $\chi^2 = 24.137$, $p < 0.01$) of nutritional conditions were observed (Fig. 8a) across stations. The general pattern suggested better feeding conditions toward the northern extent of the transect near Cape Lookout as evidenced by a comparatively large percentage of non-starving larvae at Stns 10 to 13. Fewer than 25% of the fish collected at the 3 northeastern stations exhibited enzyme activities within the 'starved' grouping. The northeastern stations 9210, 9212, and 9213 occurred in the near vicinity but a few kilometers shoreward of the frontal boundary produced by the warm filament. If this front were the leading edge of a convex meander structure, convergence might be expected. Samples from this region of convergence also exhibited extremely high percentages of non-starving larvae (81, 97, and 93%, respectively). Stns 9218, 9219, and 9220 were located 6.2 km to the seaward side of the strong east-west front directly south of Cape Hatteras. Larvae collected from this offshore zone were in comparatively poor nutritional condition with over 60% starving and no 'average' individuals at any of these stations.

A second transect perpendicular to the first also was sampled in Cruise 1 running 26.4 km northwest-southeast (Fig. 8b). Statistical evaluation of the nutritional condition distributions indicated no significant differences among stations (chi-squared, $\chi^2 = 5.791$, $p = 0.44$) with continuous temperature records indicating no strong frontal features as compared with the 32.7 km transect.

Cruise 2—physical features and larval condition

Satellite SST images (Fig. 7b, c) were available for 2 and 15 January 1993 (JD 2 and 15) before and after the net sampling (8 to 13 January 1993). On 2 January, a large warm (21 to 23°C) filament occurred in Onslow Bay. The filament wrapped around a colder frontal eddy, which was partially obscured by cloud formation. Sampling stations were located on both sides of this frontal boundary. The next usable satellite image (Fig. 7c, 15 January) revealed that the frontal eddy had been advected downstream (northeasterly) into Raleigh Bay. A very broad frontal region with weak temperature gradients was situated in Onslow Bay. Continuous temperature and salinity data however did reveal localized frontal regimes for both transects where larvae were collected. Accordingly, any explanation of nutritional condition relative to the physical features in Onslow Bay is somewhat
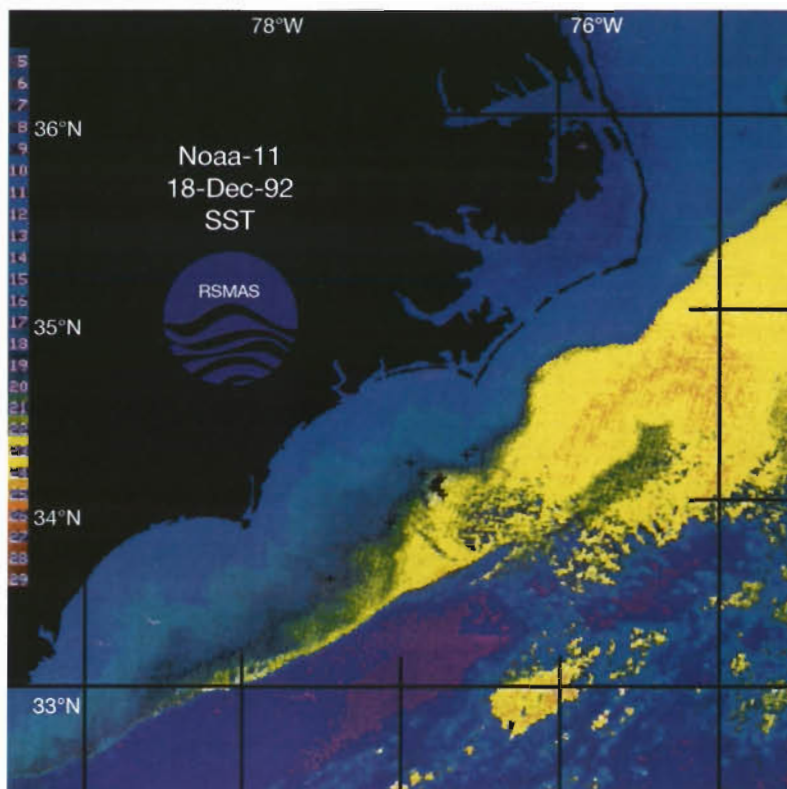

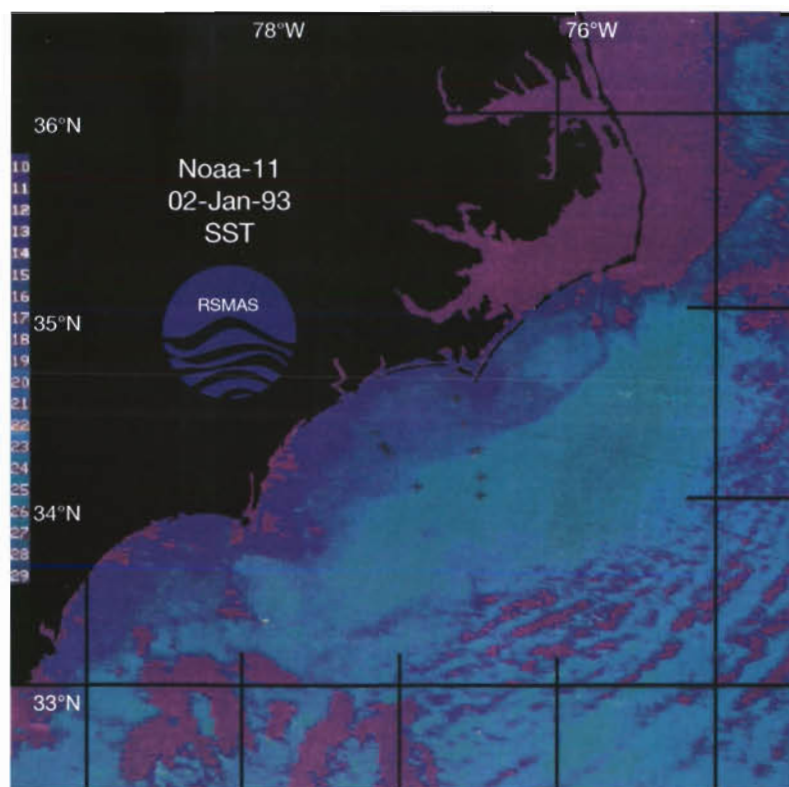Fig. 7. (a) Satellite VHRR image December 18, 1992 during Cruise 1

Fig. 7. (b) Satellite VHRR image January 2, 1993 during Cruise 2

inferential since only previous and following days' images are usable and the temperature profile could not provide full coverage of the sampling region.

The larvae collected during Cruise 2 consisted of 2 transects running north/northwest-south/southeast from 8 to 13 January. The 72.6 km eastern transect (Figs. 4b & 8c) consisted of 6 stations with 3 or more larvae. A highly significant difference in the distribution of the larval nutritional conditions (chi-squared, $\chi^2 = 22.621$, $p < 0.05$) among stations was observed. The 3 northern stations had between 77 and 100% starvation with only Stn 9308 having any non-starving larvae (23%). These stations (9301, 9308, and 9309) were far inshore, away from any convergent frontal feature. The relatively cold water temperatures (12 to 15°C) at these stations suggest that they were in shelf waters, well shoreward of any front. In the front (Stns 9310, 9310.1) the percentage of 'healthy' individuals increased to 67% and there was also a relatively high proportion of 'average'

fish just beyond the front at Stn 9312. Stns 9310 and 9310.1 are located on the shoreward side of the front and had more healthy larvae than Stn 9212 seaward of the front which had a higher percentage of non-healthy fish.

A second southern transect was also performed during Cruise 2 lying approximately parallel to the first transect. Seven stations provided 3 or more larvae for statistical analysis. The distribution of larval condition among the stations along the 41.1 km transect was highly significant (chi-squared, χ^2 = 28.435, p < 0.01) although the pattern observed was more complex than on other transects. 'Healthy' larvae increased (Fig. 8d) from 0% at the northwest end to 67% in the southeast (offshore). Also with the exception of Stns 9328 and 9334, 'average' condition larvae exhibited a continuous decrease from north to south. Approximately 33% were classified as 'average' with the remainder 'starving' at northwest inshore Stn 9324, while only 7% were 'average' at the southeastern
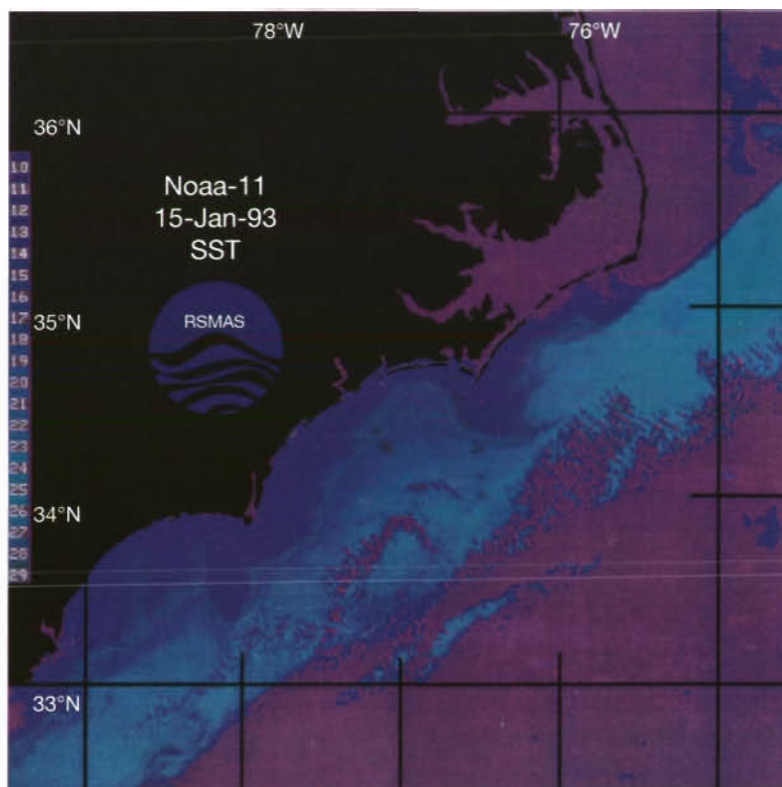

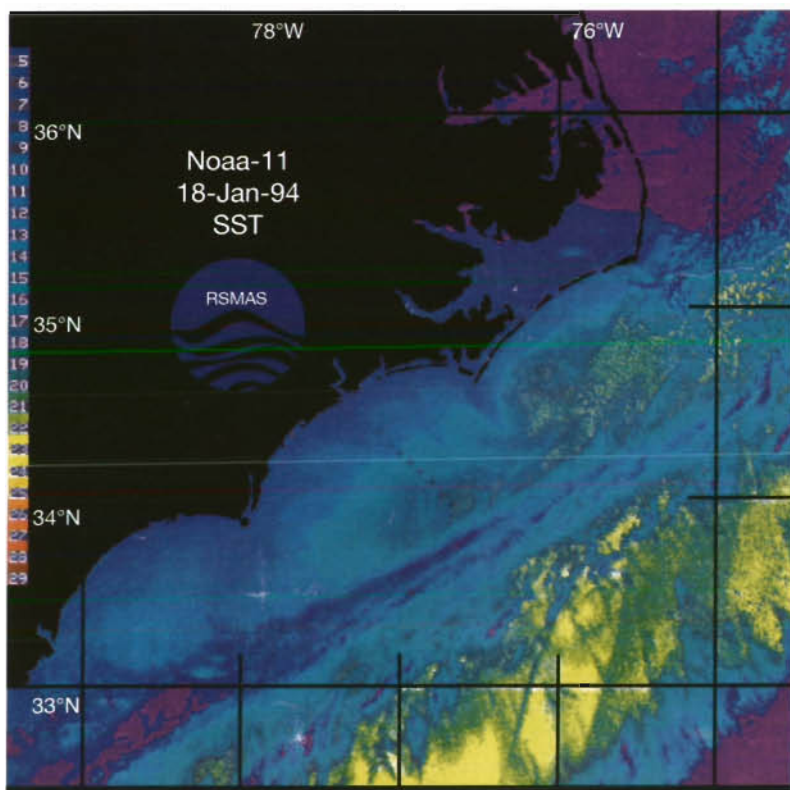Fig. 7. (c) Satellite VHRR image January 15, 1993 during Cruise 2

Fig. 7. (d) Satellite VHRR image January 18, 1994 during Cruise 3

end of the transect (Stn 9334). The center, Stn 9328, of the transect had no 'average' larvae, but an abnormally large percentage (87%) of 'starving' fish when viewed in relation to the transect.

Stns 9331 and 9332 were identical (approximately 65% healthy) in geographic location, and sampling differed by only approximately 15 min. This similarity was evident in the nearly identical nutritional distributions, water temperatures and salinities. The small distance between Stn 9334 (79% starving) and these 2 stations indicates small-scale variability (scales of 1000s of m), suggesting that this region may have been extremely close to a frontal boundary on 13 January. Stns 9331 and 9332 also had nutritional distributions similar to Stns 9310 and 9310.1, possibly resulting from convergence associated with the same frontal feature. The inshore (nonfrontal) samples, Stns 9324 and 9327, again revealed a greater percentage of starving and non-healthy larvae.

Cruise 3 — physical features and larval condition

Satellite images during the period of Cruise 3 (January 1994) were available for the single day (Fig. 7d) when all samples were collected (18 January). No other images were available due to cloud coverage several days prior to and subsequent to our field sampling. On 18 January, a large warm (19 to 21°C) filament was located in Onslow Bay, extending from Cape Hatteras to east of Cape Fear. The filament was presumably separated from the axis' flow by a narrower stream of cold (12 to 14°C) water; however, cloud banks extending along the Gulf Stream frontal zone prevented SST data collection, and our ship track did not extend so far seaward. The western boundary of the filament produced a strong temperature front recorded in both the satellite image and surface shipboard temperature measurements. Between the western edge of this front and the cold (8 to 10°C) inshore shelf water, the satellite image indicated a broad zone of mixed water. Salinity measurements at sampling sites revealed a minor increase from inshore to
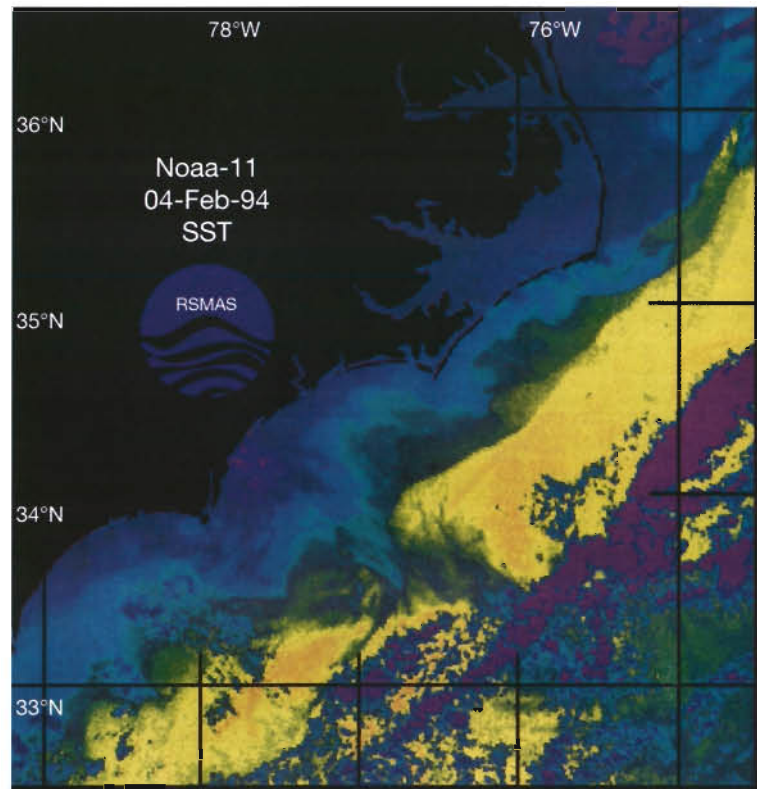

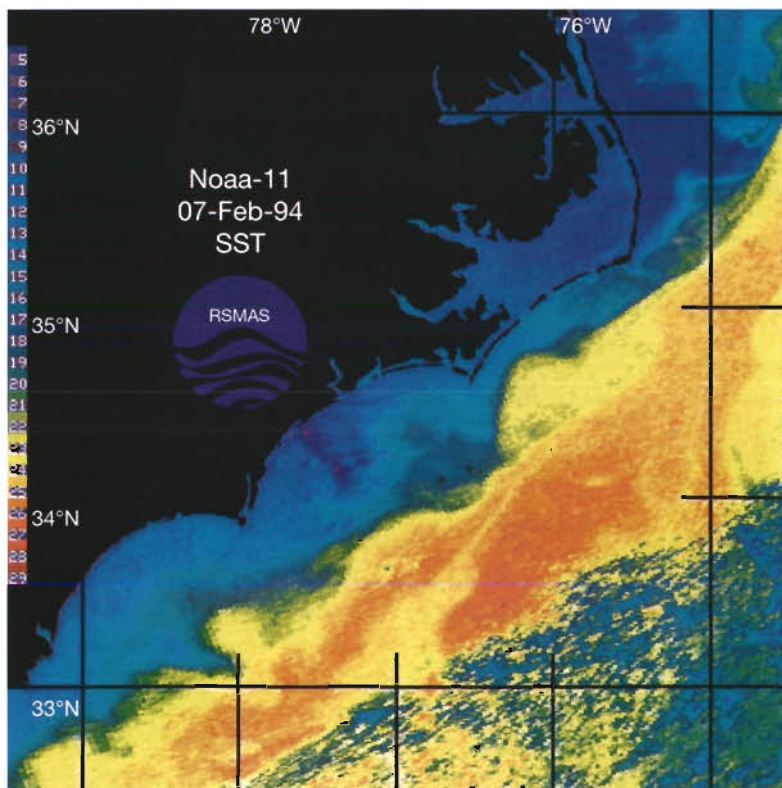Fig. 7. (e) Satellite VHRR image February 5, 1994 during Cruise 4

Fig. 7. (f) Satellite VHRR image February 7, 1994 during Cruise 4

offshore (36.11 to 36.39 ppt), although all salinities were nonetheless characteristic of Gulf Stream water.

Fluorescence-based chl a measurements at sampling stations showed a slight peak inshore (0.200 µg l⁻¹), presumably due to resuspension of shallow water sediments and other near-shore processes. Further offshore but west of the filament, chl a measurements were lower in the mixed waters adjacent to the front. The highest chl a measurements (0.277 and 0.329 µg l⁻¹) were taken in the immediate vicinity of the front produced by the western edge of this filament (Stns 9412 and 9413). Further offshore in the warm core of the filament, chl a measurements dropped slightly to 0.218 µg l⁻¹ (Stn 9415).

Condition of larvae was significantly different across the transect (chi-squared, χ^2 = 40.192, p < 0.01), with fish in superior condition in the center stations of the transect, which were located just shoreward of a marked temperature front where the horizontal temperature gradient was most acute. The 2 middle
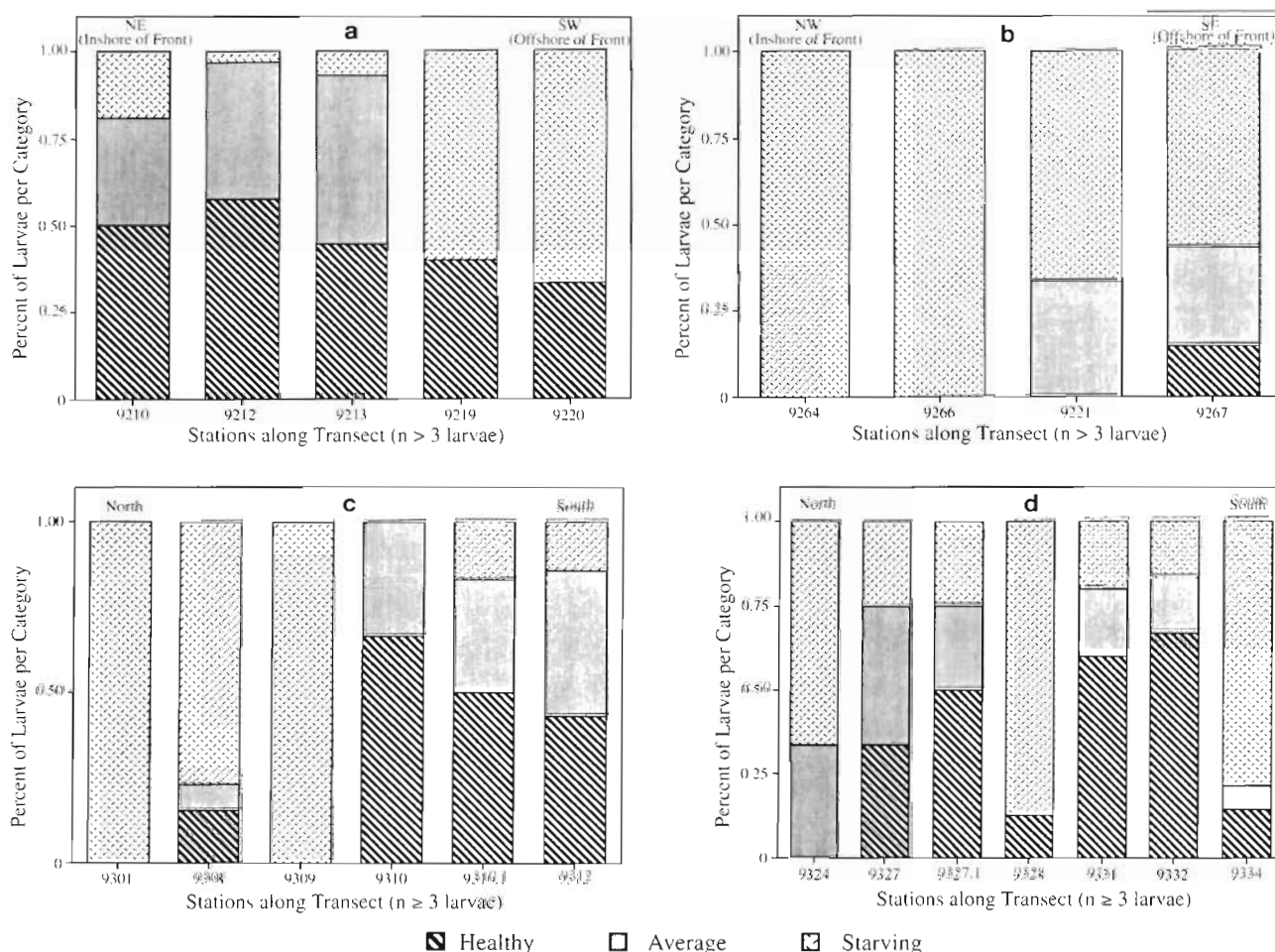
Fig. 8. Larval condition along (a) 32.7 km NE-SW transect of Cruise 1, (b) 26.4 km NW-SE transect of Cruise 1, (c) 72.6 km eastern N-S transect of Cruise 2, (d) 41.1 km western N-S transect of Cruise 2

stations, 9411 and 9412, were the only regions sampled having no 'starving' larvae collected. At these sites, 67 and 35%, respectively, of the individuals were 'healthy', the remainder 'average'

The next 2 stations away from the center (9410 and 9413) indicated minor signs of starvation, with 23 and 21%, respectively, 'starving'. Although similar in percentage starving, the non-starving larvae were distributed differently with 65%/12% at Stn 9410 but 7%/71% at Stn 9413 classified as 'average' and 'healthy' respectively. The endmost stations of the transect, Stn 9409 (inshore) and Stn 9414 (offshore), had the highest percentages of 'starving' larvae, 60 and 47%, respectively. Stns 9409 and 9410 were well inshore of the frontal zone in mixed shelf water. A similar distribution of nutritional conditions between these 2 stations and Stn 9414, located on the seaward side of the front, was observed. Only 7% were 'healthy' at Stn 9409, which was the lowest percentage along the entire transect.

Cruise 4—physical features and larval condition

Cruise 4 (February 1994) contained only 2 sampling sites with 15 total individuals collected. However, the nutritional condition of the larvae in these 2 sites did relate extremely closely to the prevalent physical regime. Two satellite images were available from 4 to 7 February near the sampling date (5 February) (Fig. 7e, f). These images showed the northeasterly drift of a frontal eddy. On 4 February, the offshore advection of shelf water (10 to 12°C) into the cyclonic circulation of this eddy centered south of Cape Lookout was clearly evident. The features depicted on 4 February presumably closely resembled those on the sampling day (5 February).

Two field stations were sampled during Cruise 4. The difference in sea surface temperature was only 1°C, with Stn 94258 at 17.8°C and Stn 94259 at 18.8°C. Neither site contained any 'healthy' larvae. Stn 94258, located 12.4 km shoreward of the Gulf Stream front,

had approximately 89% starving, while Stn 94259 (18.8 km shoreward of the front) had somewhat fewer (83%) in a state of starvation. Both stations were located in the mixed area trailing the frontal eddy. Based on the satellite picture, the 2 stations were nowhere near a strong frontal feature.

In summary, significant variation in larval condition was observed in all samples. On 3 of 4 cruises, significant variation in condition across transects was observed, and this variation appeared to correlate with oceanographic features. Larvae appeared to be in especially good nutritional condition when near frontal features.

DISCUSSION

Larval transport is regulated by complex circulation patterns both on the continental shelf and in the vicinity of inlets. As a result of the rapid along-shore Gulf Stream influence, eddy formation may increase retention periods near these inlets, increasing an individual's vulnerability to flood tides (Pietrafesa & Janowitz 1988). Westward Ekman transport in the South Atlantic region has also been reported (Reish et al. 1985) to show a significant relationship with recruitment, but the magnitude of this process is unclear (Myers & Drinkwater 1989). Winter storm events may further promote cross-shelf circulation and shoreward larval drift (Checkley et al. 1988) yet also disperse aggregations of planktonic prey as indicated by decreases in otolith-based individual growth rates.

Condition is almost certainly a factor in mortality since larvae in poor condition grow slower and suffer prolonged exposure to starvation, predation, and disease. Morphological, biochemical, otolith, and histological indices are used but with some shortcomings. Morphological techniques such as body depth and dry weight are often insensitive on short time scales and must be corrected for larval shrinkage (Hjorleifsson & Klein-MacPhee 1992). The RNA:DNA ratio also integrates growth rates over a period from 4 d to 1 wk (Lough 1984). Consequently starvation effects do not become evident until 3 to 4 d following food deprivation. Decreases in the ratio due to temperature effects (greater protein synthesis per ribosome) are also unclear. Histological techniques suffer from time- and labor-intensive paraffin embedding, staining, and sectioning (Theilacker 1978, 1986).

Our delayed feeding experiment revealed that LDH activities increased greatly during the first 2 wk of larval life, in agreement with other larval studies (Kaupp 1987, and references therein). The results suggest that increased protein allocation to these pathways may be instrumental during early life ontogeny.

Both length and nutritional effects were significant on protein-specific LDH activities. Weight-specific activity of LDH declines exponentially in menhaden (Power & Walsh 1992) in larger size-classes of larvae. Empirical and theoretical considerations of the scaling of these metabolic enzymes have been reviewed for adult (Somero & Childress 1985, Childress & Somero 1990) and larval fish including Reynolds number transitions (Kaupp 1987).

This study is the first reported analysis of enzyme activities in larval Atlantic menhaden obtained from field surveys. It indicates that starvation effects are evident in approximately 26 to 85% of larval Atlantic menhaden caught at sea. However, certain sampling stations did contain nearly 80% non-starving larvae, suggesting that microenvironments conducive to larval survival exist. With the exception of Cruise 4, which provided few samples, a consistent 25 to 35% of the larvae were classified as 'healthy', 18 to 35% were of 'average' nutritional condition, and approximately 25 to nearly 50% were 'starving' Larger scale projects (i.e. greater numbers of larvae analyzed) may support this finding that the percentage of larvae in poor nutritional condition varies tremendously from station to station, and that the upper limit of this percentage may be as high as suggested in some traditional views of larval biology.

The use of the enzymatic condition index reported here has promise in that growth rates are reflected in time scales of 18 to 36 h as confirmed by response to initiation of feeding, as well as lack of correlation with day versus night sampling period. The effect of temperature on the actual enzymatic rates may not be as critical as in other studies (Clarke et al. 1992, Clarke & Walsh 1993), since egg and larval stages of Atlantic menhaden naturally tolerate highly and rapidly varying salinity (10 to 30 ppt) and temperature regimes (10 to 25°C) (Ferraro 1980, Powell & Phonlor 1986). Second, the laboratory calibration was done at 19°C which was in the center of the range of observed field values (16 to 22°C). Third, a 3°C excursion on either side of the laboratory temperature would generally alter enzyme rates by less than 30%. Of the biological factors, predation is most likely not a significant source of mortality. *Brevoortia tyrannus* eggs and larvae appear to be too large for even large copepods (*Anomalocera ornata*) to ingest (Turner et al. 1985).

Shipboard assay of enzyme activity shows promise for obtaining near-realtime data. The equipment required (sonicator, microcentrifuge, and microtiter plate reader) is durable and compact, requiring only small amounts of bench space. The use of a microtiter plate reader speeds throughput. Larvae collected, for example, in a 12 h sampling regime could easily be assayed in the next 12 h.

Horizontal temperature gradients in Onslow Bay are large during winter due to the proximity of the Gulf Stream (>22°C) to cold (<10°C) inshore coastal waters. The heterogeneous and transient nature of the physical regime in the sampling area implies that location of spawning sites could have major effects on larval survival and growth. Wave-like meanders and eddies persist for approximately 2 d to 2 wk (Lee et al. 1984) in the region. Cold core frontal eddies with weekly periodicity are important for water mass, nutrient, and larval exchange (Pietrafesa & Janowitz 1979, Lee & Atkinson 1983, Lee et al. 1991). The outer shelf is controlled by Gulf Stream frontal disturbances, being primarily meanders and eddies (Lee 1981, 1983), which also partially affect the midshelf. Such meanders can be characterized by sea surface temperature and salinity fluctuations. Salinity data collected during the field component of this research indicate minimal variability in sampling stations since the overall range of data collected from all cruises was only 36.11 to 36.39 ppt, in contrast with reported values down to 27 ppt (Mathews & Pashuk 1986) during periods of high freshwater runoff.

Throughout the sampling region within any particular cruise, with the exception of Cruise 4 which consisted of only 2 stations, spatial heterogeneity was observed in larval condition. Protein-specific LDH activity varied greatly among sampling stations and continued to reveal spatial (assumed to be at least partially nutritional) differences as was found in the laboratory experiments and other experiments in our laboratories (Clarke et al. 1992). The range of observed metabolic activities with this enzyme system was similar to the laboratory calibration. As a consequence of highly variable field conditions, the range of enzyme values collected in the field far exceeds the controlled laboratory feeding experiment.

Condition of larvae seems related to location in Onslow Bay and position relative to physical features. The Gulf Stream front occurred between approximately 34 and 77 km from shore during the 4 field cruises and was a significant factor in the nutritional condition of the larvae. During Cruise 1, stations closer to the front contained a lower percentage of starving individuals. Similar decreases in nutritional condition with increasing distance from the front were also evident during Cruise 3 presumably due to frontal biomass accumulations (Franks 1992). Physical effects including tidal advection, upwelling and mixing at the front have been reported to enhance larval growth in the frontal region. As confirmed by this study, these effects are not fully understood since larval fish and prey density maxima are frequently found coincident with the front but occasionally several km on either side of the frontal region (Taggart et al. 1989), giving

rise to a comparatively poor nutritional environment in the immediate vicinity of the front. This occurrence as well as the lag in response of the enzymatic condition index may be responsible for explaining the presence of only starving larvae found bordering the front in the NW-SE transect of Cruise 1. Coastal fronts (often found between offshore and coastal waters) have a significant effect (Nakata 1989) on larval transport from spawning to nursery grounds. With the development of improved condition indices such as reported in this study, position of frontal boundaries may prove instrumental in the prediction and validation of larval transport and condition. While there is no single best index of condition for all circumstances (Ferron & Leggett 1994), laboratory and field research presented in this study mark an initial success in the use of metabolic enzyme assays for the prediction and determination of nutritional condition of wild marine larvae.

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