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Biological and Physical Observations on Larval Spot (*Leiostomus xanthurus*) Recruiting to Oregon and Ocracoke Inlets North Carolina

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**BIOLOGICAL AND PHYSICAL OBSERVATIONS ON LARVAL SPOT
(*LEIOSTOMUS XANTHURUS*) RECRUITING TO OREGON AND OCRACOKE
INLETS, NORTH CAROLINA**

by

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B.A. May 1992, Saint Anselm College

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
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ABSTRACT

BIOLOGICAL AND PHYSICAL OBSERVATIONS ON LARVAL SPOT (*LEIOSTOMUS XANTHURUS*) RECRUITING TO OREGON AND OCRACOKE INLETS, NORTH CAROLINA

Thomas R. Wasaff
Old Dominion University, 2000
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Dr. Cynthia Jones

Patterns of abundance, length, age, and growth of larval spot (*Leiostomus xanthurus*) were compared to assess the variability between spot larvae ingressing to two North Carolina inlets. The source of variability for the recruitment of larval fishes to estuarine nurseries has been linked to environmental stochasticity. Wind data and sea-surface temperature satellite images were analyzed as two influential environmental variables that may help explain recruitment variability. As part of the South Atlantic Bight Recruitment Experiment (SABRE), spot larvae were collected between October 1994 and April 1995 as they recruited to Pamlico Sound through Oregon Inlet, located north of Cape Hatteras, and Ocracoke Inlet, located south of Cape Hatteras, North Carolina. Spot larvae first recruited to Ocracoke Inlet in small numbers for approximately seven weeks before both inlets experienced peak abundance. Following this peak recruitment event, patterns of abundance between inlets rarely coincided. However, on any given collection date, the length and age of spot larvae recruiting each inlet was similar. Results from a multivariate analysis of variance (MANOVA) indicate mean incremental otolith growth patterns between inlets were similar during early ages but significantly different in later ages. The initial similarities in otolith growth patterns

suggest larvae recruiting to both inlets originated from the same population. Spot larvae are spawned and transported through warm shelf water but then are eventually subjected to colder coastal waters which influence their recruitment into different inlets. Winds from a northerly direction are an important mechanism for cross shelf-transport. However, the mechanisms influencing estuarine recruitment are more complex. Along-shore transport has received recent attention and appears to be important for larval spot recruitment at Oregon Inlet. Warm water filaments from the Gulf Stream are another potential mechanism used by spot larvae for recruitment. It is possible that adult spot travel and spawn with these warm water filaments as they move north. This behavior would help ensure larval recruitment to estuaries in the Middle Atlantic Bight (MAB)

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INTRODUCTION

Purpose

During the fall and winter, spot (*Leiostomus xanthurus*) spawn offshore over the continental shelf of the United States' East Coast. Within one or two months after birth, the larvae must be transported inshore to settle in estuarine nurseries. The convergence of two western Atlantic gyres off North Carolina's Outer Banks supplies the nearby inlets with fish larvae from both temperate and sub-tropical environments. Three main inlets break apart the Outer Banks and connect Pamlico Sound with the Atlantic Ocean (Fig. 1). The northern most is Oregon Inlet and links Pamlico Sound with the temperate oceanic gyre located in the Middle Atlantic Bight (MAB). South of Cape Hatteras, are Hatteras and Ocracoke Inlets which link Pamlico Sound with the sub-tropical oceanic gyre located in the South Atlantic Bight (SAB). Each gyre acts as a retention mechanism for larval fishes and other planktonic organisms. However, larvae are often found simultaneously in each gyre. This may be the result of transport mechanisms from one gyre to another or separate spawning populations (one in the MAB and one in the SAB). The abundance of larvae recruiting to each inlet varies but those inlets that receive the most recruits during a season are believed to be closest to the spawning location or locations. Inlets receiving the youngest and smallest larvae also reveal their proximity to the spawning location. In this thesis I use demographic data from larvae collected at inlets north and south of Cape Hatteras to examine mechanisms that influence transport.

Environmental variability presumably influences the larval recruitment success of spot and several other fishes of economic importance spawning south of Cape Hatteras, North Carolina. These larvae are spawned in offshore waters but depend on estuarine nurseries as juveniles. During the fall and winter these larvae must rely on favorable environmental conditions for shoreward transport to their estuarine nurseries.

Understanding the influence of environmental conditions on the recruitment success of fish larvae was the objective of the South Atlantic Bight Recruitment Experiment (SABRE).

The focus of SABRE was the commercially important Atlantic menhaden (*Brevoortia tyrannus*) although several other fishes (croaker, flounders, pinfish, and spot) share a similar life history. The seasonal migration of menhaden follows the coastline north in the spring then south in the fall and winter (Dryfoos et al. 1973, Nicholson 1978, Warlen 1994). Numerous studies (Higham & Nicholson 1964, Kendall & Reintjes 1975, Lewis et al. 1987) have documented the seasonality of menhaden spawning. Menhaden spawn off New England from late spring through early summer and then again in early fall. In the fall and spring, spawning occurs off the mid-Atlantic states. From October through March spawning takes place off the southeastern states. However, peak spawning probably occurs between December and February in an area south of Cape Hatteras.

Menhaden migratory behavior is cued by ocean temperature (Quinlan et al. 1999). They prefer temperatures between 15-20°C. From late spring through early fall the waters off New England are conducive for spawning. Larvae spawned at this time and location, along with fall spawning off the mid-Atlantic states, probably supply the MAB (i.e. Delaware and Chesapeake Bays) with new recruits. However, Quinlan et al. (1999)

believe transport mechanisms are not conducive for the continued supply of menhaden larvae in the MAB as the season progresses and as adults migrate into the SAB.

Many studies (Harrison et al. 1967, Nelson et al. 1977, Miller et al. 1984, Reish et al. 1985, Warlen 1992, Stegmann & Yoder 1996) lend support to the idea of cross-shelf transport of menhaden larvae. However, Quinlan et al. (1999) propose a new transport paradigm based on the SABRE results. They suggest the along-shore component reported by Hare et al. (1999) is more influential for larval fish recruitment than cross-shelf transport.

Spot, of lesser economic importance than menhaden, has a relatively short life span of five years or less making its recruitment especially vulnerable to consecutive years of unfavorable environmental conditions. In addition, it is not known whether spot ingressing inlets in the MAB and SAB are from the same spawning population. Separate spawning populations might be influenced by different environmental conditions. It is therefore important to know the source and subsequent transport of spot larvae ingressing Pamlico Sound, North Carolina through Oregon and Ocracoke Inlets.

Otoliths collected from spot larvae that were captured at Oregon and Ocracoke inlets provide retrospective insight into the transport period of spot's early life history. This includes information on age, hatching date, and growth obtained from otoliths. Throughout a fish's life, calcium is continually deposited on their otoliths. Campana and Neilson (1985) and Jones (1986) have shown many larval fishes deposit a new layer each day. These layers appear as alternating dark and light increments when viewed under a microscope. Enumerating these increments reveals the age of an individual larva. When an individual's date of capture is known, its age can be used to provide a date of hatching

or spawning. The width between consecutive increments is influenced by growth rate. A narrow increment suggests slower growth whereas a wider increment suggests faster growth. Growth is influenced by environmental conditions such as water temperature. Thus, faster growth might result from transport in warmer water.

Wind and sea-surface temperature data may be compared with the otolith time line to reconstruct conditions encountered during transport. General data on wind direction and magnitude and surface-water temperature are readily available for most of the coastal United States. Favorable wind events of a consistent northerly direction have been hypothesized as necessary mechanisms for cross-shelf and shoreward transport of larvae along the U.S. East Coast (Nelson 1977, Miller et al. 1984, and Checkley et al. 1988). Ingress of larvae to inlets at younger ages might be the result of a preponderance of favorable wind events, which have reduced transport time. Ingress of larvae to inlets at older ages might be the result of less favorable wind events and longer transport. Temperature is also an important factor, as cold water stresses larvae entering coastal and estuarine waters and depresses larval growth rates. This study incorporates some of these data into the otolith time line of larval spot spawned in the SAB and their significance on recruitment abundance is assessed.

The aggregation of spot occurring off North Carolina's continental shelf and west of Diamond Shoals has not been adequately described. Tagging studies of adults conducted by Pearson (1932) and Pacheco (1962) indicate spot from Delaware and Chesapeake Bays travel south as temperatures decline and aggregate south of Cape Hatteras. The occurrence of early stage spot larvae in this area suggests this adult aggregation may develop for spawning purposes. However, the question remains as to

whether spot spawn as they migrate south from the MAB or spawn in one aggregation when they join other spot in the SAB. Different seasonal patterns in age and growth of spot larvae ingressing Oregon Inlet in the MAB can indicate a separate spawning population. This study clarifies potential source locations by comparing age, growth, and transport mechanisms of larvae ingressing Pamlico Sound at Oregon Inlet in the MAB with Ocracoke Inlet in the SAB.

Description of Spawning Location

The Gulf Stream is a well studied frontal zone, flowing north along the East Coast and coming in close proximity to North Carolina's continental shelf. Aggregations of spot are found off North Carolina's coast, and spawning occurs over the continental shelf west of the Gulf Stream in the South Atlantic Bight (Hildebrand & Cable 1930, Nelson 1977). Coastal waters adjacent to the Gulf Stream frontal zone are warmest, cooling as shore is approached. According to Govoni (1994), frontal zones are the surface expression of sharp gradients in physical properties. Characteristics of these zones are enhanced primary productivity, accumulation of plankton, and increased abundance of nekton (Bowman & Iverson 1978, Owen 1981, LeFèvre 1986). Thus, the Gulf Stream frontal zone offers an ideal spawning environment for spot because of the enhanced food that is available to their larvae.

The Gulf Stream also serves as the eastern boundary of two oceanographic circulation systems, separated by the shallow subsurface topography of Diamond Shoals, located southwest of Cape Hatteras, North Carolina. South of Cape Hatteras is the

northern extent of the SAB. Here, water movement is driven by a dynamic pressure gradient resulting from the combined effects of runoff, cross-shelf thermal gradients, prevailing winds, and the frictional drag of the Florida Current (Bumpus 1955). Water over the outer continental shelf moves northeastward (Bumpus 1955), while water on the inner shelf moves southward (Steffansson et al. 1971, Bumpus 1973). Water in the MAB flows southward until reaching its southern extent where it becomes entrained in the northward flowing Gulf Stream (Ford et al. 1952, Fisher 1972, Lillibridge et al. 1990).

Spawning

The spawning location of spot apparently is in water that is warmed by the Gulf Stream and is high in nutrients. Spot spawning takes place between mid-October and mid-March (Flores-Coto & Warlen 1993). Suitable temperatures for spawning and developing larvae are found near the Gulf Stream between 75 and 95 km off North Carolina's coast, south of Cape Hatteras and Onslow Bay (Flores-Coto & Warlen 1993, Warlen & Chester 1985). At this location inshore of the Gulf Stream, water temperatures range between 18° and 25°C (Fahay 1975, Hettler & Powell 1981). Northeasterly winds (Oey 1986, Checkley et al. 1988, Pietrafesa et al. 1994) generate upwelling of nutrients and promote growth of microzooplankton, an excellent food source for larvae. According to Norcross & Bodolus (1991), in the fall these conditions can be found in the MAB but is not found there during the winter when spot's peak spawning activity occurs, thus indicating that spawning is restricted to the SAB.

Developing spot larvae must endure starvation and cold stress to insure survival (Hoss et al. 1988). The pelagic eggs average 0.8 mm in diameter, and hatch in approximately 48 hours at 20°C. Upon hatching, larvae measure 1.6 - 1.7 mm SL (Powell & Gordy 1980, Powell & Chester 1985). These newly hatched preflexion larvae are susceptible to starvation because energy at this stage is allocated to growth rather than to storage reserves (Powell and Chester 1985). Survival of larvae is also affected by cold stress as respiration increases as temperatures lower to 10°C (determined to be a critical temperature) while feeding decreases. Continued cold exposure can lead to an energy deficit and ultimately death (Hoss et al. 1988). Interestingly, Atlantic croakers do not show the same signs of thermal stress as exhibited by spot (Hoss et al. 1988).

Larval Transport

Govoni & Pietrafesa (1994) provide a detailed review of four hypotheses, which attempt to explain the transport of winter-spawned larvae from an offshore aggregation in the SAB. Nelson et al. (1977) believe currents with an onshore component are essential for transporting young menhaden into estuaries along the central and southern U.S. coast. They argue that larval menhaden remain in the upper mixed layer and are therefore subjected to horizontal transport processes (i.e. wind and run-off) occurring near the surface. Their hypothesis is supported by matching average monthly zonal (east-west) Ekman transport with year class strength of young menhaden in Chesapeake Bay. They found at two points within the Middle Atlantic Bight, average monthly Ekman transports were twice as large in 1957-58 compared to 1963-64. They believe this may help explain

the unusually productive 1958-year class in Chesapeake Bay. However, these correlations have failed in subsequent years. Checkley et al. (1988) also attempt to explain the transport of young menhaden shoreward. They believe processes other than Ekman transport influence larval menhaden on a scale of days rather than monthly averages. They hypothesize that menhaden use winter storms to enhance larval survival and transport. Associated with these winter storms are northeasterly winds, which upwell warm water from the Gulf Stream and push it shoreward. As the water travels shoreward it cools along the mid-shelf front, sinks and then moves in the opposite direction off the shelf into deeper water. Miller et al. (1984) also propose that larval transport uses multi-layered water flow. During the passage of winter storms they found that wind is predominantly out of the northwest. Nearshore surface water is cooled causing it to sink and move offshore. This movement of water offshore in the surface and bottom layers is balanced by a warm saline middle layer (6 m to near bottom) moving in the opposite direction (onshore) and potentially transporting larvae of winter-spawning fishes. Finally, once larvae are transported inshore internal waves may concentrate larvae in surface slicks (Shanks 1988). Under special circumstances, such as internal bores, internal waves may move larvae through inlets (Shanks 2000).

Recruitment

Recruitment in the marine environment is a variable process. Early life survivorship in marine water is considerably less than in freshwater. Only 0.12% of a typical marine fish cohort is expected to be alive and able to enter the juvenile stage

compared to 5.30% of a typical freshwater fish cohort (Houde 1994). High larval mortality rates of 5-10% per day eventually translate to large variation in survivorship between cohorts (Jones 1989). In the context of this paper, recruitment refers to the period during which spot larvae ingress Oregon and Ocracoke Inlets just prior to settlement.

Fishes spawned during the warmer months have an advantage upon recruitment compared to spot and other fall-winter spawned fishes. Fishes spawning during the warmer spring and summer months have a twofold benefit upon estuarine recruitment according to Crawshaw et al. (1981). First, they experience rapid growth associated with higher metabolism and an abundant food supply. Second, predation by larger fish is reduced in shallow water. Larvae spawned during the fall-winter are at a disadvantage as they may encounter intolerable temperatures during transport towards shore and into estuaries. For example, mean water temperatures in the Newport River estuary, North Carolina between November and March range from 14° to 6°C (Hoss 1974). A particularly cold winter may result in a poor year class with only late arriving larvae recruiting to the fishery (Hoss et al. 1988).

Age and Growth

The age when larvae recruit to the lower estuary gives a good measure of transport time from offshore spawning grounds. Flores-Coto & Warlen (1993) found that the age of larvae varied inversely with distance from Beaufort Inlet, North Carolina, with the youngest larvae occurring over the outer continental shelf and within the Gulf Stream.

Entry age into the estuaries will vary as cross-shelf transport intensity varies. Transport time will vary as environmental conditions change with seasons and as fish move further offshore to spawn. Similarly, growth of spot larvae will reflect, in part, the conditions they have encountered during transport.

Age of young spot is determined from enumerating consecutive daily increments found on their otoliths. Otoliths from larval spot reared in the laboratory showed an average of one growth increment per day (Peters et al. 1978, Warlen 1984). Siegfried & Weinstein's (1989) fieldwork also confirmed that increments were deposited daily on larval spot otoliths. Hence, increment counts from field-captured larvae accurately reflect age. Growth can also be assessed as the relationship between fish size and age. Growth can be determined retrospectively by measuring otolith size at age as a proxy for fish size when there is a linear relationship between otolith size and fish size. Growth of larval spot has previously been described using nonlinear regression techniques. Nonlinear techniques allowed Warlen & Chester (1985) to fit the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel & Lasker 1976) for describing average growth of larval spot entering Beaufort Inlet, North Carolina.

METHODS

Collection

Spot larvae were obtained from samples collected during the South Atlantic Bight Recruitment Experiment (SABRE) by William F. Hettler, Jr. of the National Marine Fisheries Service (NMFS) in Beaufort, North Carolina. Larval fishes were sampled weekly while entering two major North Carolina inlets (Ocracoke, and Oregon) (See Fig. 1). As reported by Hettler (1998), the inlets were sampled for 27 consecutive weeks between October 1994 and April 1995, targeting larvae of six commercially important fall-winter spawning species (menhaden, croaker, spot, southern flounder, summer flounder, and pinfish). A single sampling station was centered in the main flood-tide channel of each inlet (Oregon Inlet: 35°46.3'N, 75°33.5'W, Ocracoke Inlet: 35°06.4'N, 75°59.5'W). Channel depth at each inlet was no greater than 7 m and width was approximately 300 m. Inlets were sampled once every week on adjacent nights. Sampling consisted of 12 repetitive oblique tows, spaced about 10 minutes apart. The sampling gear was a 0.8 m², 800 µm net on a 1 m diameter sled-mounted aluminum frame, which was deployed and retrieved using a hydraulic winch. The gear was towed for 4 minutes into the current at an average speed of 1 m sec⁻¹, filtering approximately 200 m³. Before each tow, the direction of tidal flow, temperature, and salinity was recorded using a SeaBird-19 CTD. Once retrieved, samples were preserved in 70 - 90 % ethyl alcohol on board the vessel.

Sorting

Samples collected by Hettler were loaned to ODU in 1996 for the extraction of all spot larvae. Each sample vial was checked for the presence of spot, removing all when found. Spot were placed into empty vials with 70% ethyl alcohol. Each vial contained a number corresponding to cruise number, tow number, and any additional information or comments, which may have appeared on the original NMFS vial.

The total numbers of spot larvae I removed from each NMFS collection before sub-sampling usually matched the numbers reported in their collection report (Table 1). Of the 13,773 spot larvae collected by NMFS (Fig. 2), I sorted out a total of 5,593 (41% of the total reported by NMFS). Of these, 4,058 came from collections made at Ocracoke Inlet and 1,535 came from collections at Oregon Inlet. There is an obvious discrepancy (missing 59%) between the number of spot larvae I sorted out of the sample vials and the numbers reported by NMFS. This discrepancy is only apparent for one day at each inlet. However, these were the days when each inlet experienced peak recruitment. I believe there were some large jars devoted to these two days of high abundance, which were not forwarded to me. This discrepancy should not present a problem since the biological analyses were conducted on a random sub-sample (Fig. 2).

Previous studies (Nixon and Jones 1997, Hoskin personal communication) on age and growth of larval croaker (*Micropogonias undulatus*) used a sample size of approximately 600 larvae to effectively reduce variation. I therefore decided to sub-sample approximately 300 spot larvae from each inlet (Oregon and Ocracoke), keeping my sample size similar to those previous studies. A sub-sample of 612 spot larvae was

Table 1. Numbers of spot larvae reported by the National Marine Fisheries Service, sorted at Old Dominion University, and sub-sampled for age and growth analyses.

Date	Cruise #	NMFS Collections		Sorted		Sub-sample	
		OC	OR	OC	OR	OC	OR
11/29 - 11/30	7	11	2	5	.	5	.
12/5/94	8	2	.	0	.	.	.
12/14/94	9	15	.	11	.	8	.
12/19/94	10	17	.	19	.	16	.
12/30/94	11	113	.	112	.	10	.
1/4 - 1/5	12	34	.	81	1	8	1
1/10 - 1/11	13	86	3	89	2	8	2
1/17 - 1/18	14	8704	985	1146	474	50	48
1/25 - 1/26	15	406	1	407	1	30	1
1/31 - 2/1	16	407	2	407	2	29	2
2/7 - 2/8	17	41	83	48	85	6	30
2/14 - 2/15	18	659	176	740	177	40	41
2/21 - 2/22	19	55	25	104	25	10	25
2/28 - 3/1	20	33	871	31	588	5	61
3/7/95	21	389	.	359	.	23	.
3/13 - 3/14	22	178	6	189	5	15	4
3/22 - 3/23	23	9	1	9	3	9	3
3/28 - 3/29	24	228	1	238	.	19	.
4/4 - 4/5	25	48	120	48	130	8	40
4/11/95	26	17	14	11	13	11	13
4/19 - 4/20	27	3	10	4	7	4	6
4/25/00	28	.	15	.	22	.	21
Totals:		11455	2315	4058	1535	314	298

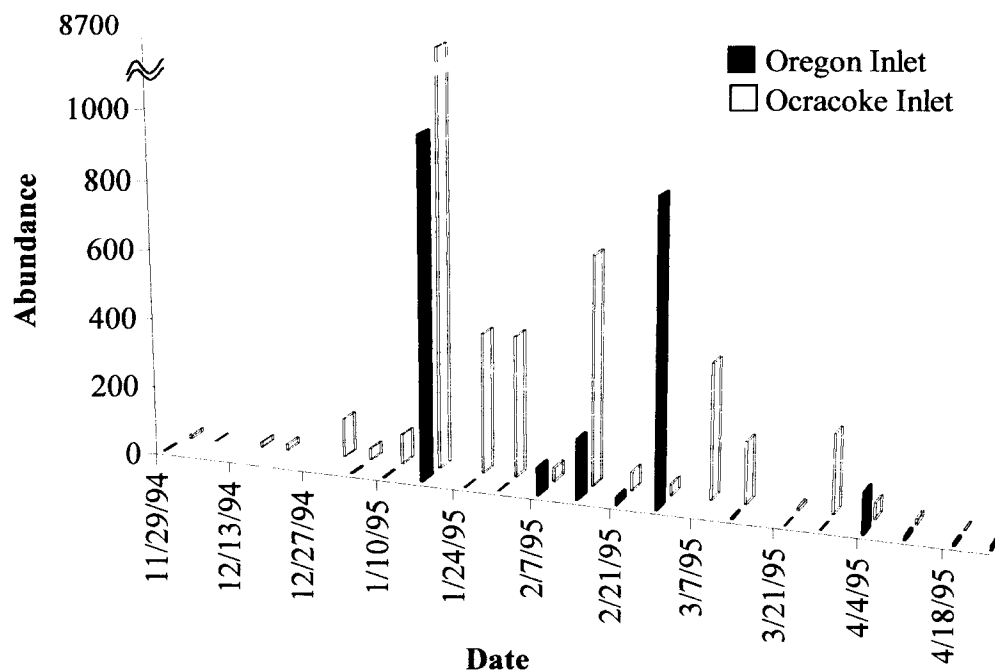


Fig. 2. Numbers of spot larvae collected by the National Marine Fisheries Service (NMFS) as they ingressed Oregon Inlet and Ocracoke Inlet. From mid-October 1994 through April 1995, NMFS collected 2,330 spot larvae ingressing Oregon Inlet (closed bars) and 11,455 spot larvae ingressing Ocracoke Inlet (open bars).

generated from 298 (5% of total spot larvae sorted by me) collected at Oregon Inlet and 314 (6% of total spot larvae sorted by me) collected at Ocracoke Inlet. I also attempted to sample in proportion to the numbers ingressing the inlets over the entire sampling period of the study (Fig. 3). Therefore, dates of high larval abundance have larger samples than dates of lower larval abundance.

I used simple random sampling to determine which tows to sub-sample. Because each day consisted of 12 tows, I used a random numbers table containing values from 1-12 to choose a single tow per day. Simple random sampling techniques were also used to determine which larvae from a tow were used for age and growth analyses. Larvae from a designated tow were placed on a clear plastic grid which had numbers etched on the bottom. Again, a random numbers table was used to determine which grid square to sample an individual larva. A total of 612 larval spot were sub-sampled, 278 from Oregon Inlet and 314 from Ocracoke Inlet.

Measurement

Spot larvae were measured to the nearest 0.1 mm standard length using image analysis. An Olympus SZH10 dissecting scope fitted with a Hitachi KP-DSO color video camera provided the image for use in Sigma Scan image analysis software. Sigma Scan was calibrated to measure standard length in millimeters. Standard length was measured from the tip of the snout along the lateral line and culminating at the hypural plate.

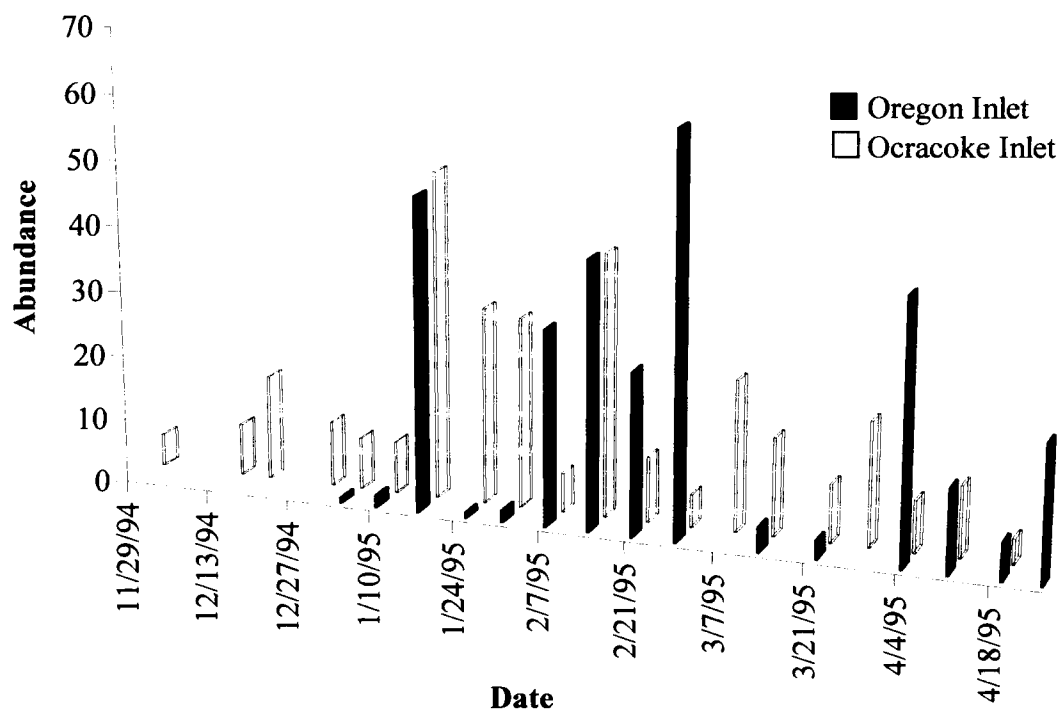


Fig. 3. Numbers of spot larvae sub-sampled from the NMFS collections. Closed bars represent 298 total larvae sampled from Oregon Inlet and open bars represent 314 total larvae sampled from Ocracoke Inlet.

Otolith Removal

Sagittal and lapillar otoliths were removed to determine which was best for ageing purposes. An Olympus SZH dissecting scope fitted with polarizing filters was used for locating and extracting otoliths. Larvae were clamped ventral side up with forceps and the anterior of the head removed, exposing the otoliths under polarized light. The two largest otoliths (sagitta and lapillus) were removed. Extracted otoliths were placed on microscope slides, air dried, and affixed using Krazy Glue™. Sagittae were ground with a 1200 grit lapping paper to expose daily rings and then polished using a finer (3µm) lapping paper. Lapillae were more delicate and susceptible to cracking and over grinding so only the finer paper was used for exposing daily rings. To compare ring counts, sagittae and lapillae were removed from a total of 65 spot larvae. A contingency table (Bowker 1948) was used to test for agreement between counts from the two different otolith types.

Ageing

Lapillar otoliths proved to be the easiest to process and read for ageing purposes. A total of 612 otoliths were aged twice, 298 were from Oregon Inlet and 314 were from Ocracoke Inlet. As stated above, a pilot study conducted by me indicated no significant difference in age readings between the sagitta and lapillus. I therefore decided to use the lapillar otolith for further ageing because it required less processing time than the sagittal

otolith. Also, increments on sagittae deposited in older larvae were often obscured and hard to read due to the formation of accessory primordia at the otolith edge.

A second contingency table analysis was incorporated to test age-reading precision. A total of 194 lapillae were aged twice, 112 from Oregon Inlet and 82 from Ocracoke Inlet. A time span of several months separated the first and second reading. The contingency table was used to determine whether there was agreement between the first and second reading. This analysis also allowed the reader to identify any bias, which may be influencing the results.

I tested for differences in age structure between inlets with a randomization test. Data were re-sampled with 1000 iterations. The randomization program pooled all ages from both inlets and then generated a new sample always keeping the original sample size of 298 for Oregon Inlet and 314 for Ocracoke Inlet. After 1000 iterations, the differences in mean age between inlets was compared. Statistical significance was determined by generating a t-distribution and using this randomized distribution to set confidence intervals. The probability benchmark of 0.001 was used to establish statistical significance.

Spawning Date

Spawning date distributions were reconstructed based on the sub-sample of 612 spot larvae. Spawning dates were calculated by subtracting the number of rings counted plus five from date of capture. Five days were added to the counts because it has been shown that the first ring is laid down 5 days post hatching (Peters et al. 1978). I

reconstructed spawning dates for all spot larvae collected based on the 612 spot larvae aged. A proportion of the total spot larvae collected on a given day was determined from my sub-sample of aged larvae. For example, on January 10, 1995, 86 spot larvae were collected at Ocracoke inlet. Of these I sub-sampled and aged eight. Dividing 86 by eight gives a value of 10.75 which is the number of larvae designated to each individual back-calculated spawning date from the sub-sample of eight. This methodology was repeated for all collection dates and for both inlets. Once this information was obtained larval abundance by spawning date was chronologically sorted, compiled, and then graphed.

Growth

Growth rates were calculated using both linear and nonlinear techniques. Average growth ($\text{mm}^{-\text{day}}$) rates of the 612 spot larvae were determined from size-at-age data. The standard length (mm) of the spot larvae divided by age (number of increments) provided a simple average growth rate for the individual. In addition to the average growth rate, instantaneous growth rates of larval spot were fit to the Laird-Gompertz growth equation to age-at-capture data. The model incorporates 3 parameters (L_0 , A_0 , α) into the equation. L_0 is the hypothetical length (SL) at hatch, A_0 is the age specific growth rate at hatching, and α is the rate of exponential decay of the specific growth rate. These three parameters were calculated using SAS non-linear regression procedures. Parameter values published for larval spot ingressing Beaufort Inlet to the south of Oregon and Ocracoke inlets were used to initiate the non-linear procedure.

Increment Widths

Retrospective age and growth analyses were conducted on 69 lapillar otoliths (32 from Oregon Inlet and 37 from Ocracoke Inlet) obtained from simple random sampling techniques. Optimas 6.1 image analysis software was used to measure radii and consecutive increment widths of spot otoliths. Otolith radii were measured as the distance from core to edge. Successive daily-increment widths were measured as the distance from one dark band to the next. Measurements were recorded electronically. A MANOVA (Chambers & Miller 1995) was used to determine differences between daily otolith increments.

Physical Data

Wind data and sea surface temperature imagery were used to reconstruct environmental conditions influencing transport of larval fishes spawned offshore. Wind data were obtained from the NOAA Diamond Shoals weather buoy located close to the spawning location of spot. The NOAA buoy is located 35°15'00" N latitude and 75°30'00" W longitude and provided air temperature (Celsius), sea surface temperature (Celsius), hourly average wind speed ($\text{m}^{-\text{s}}$) over an eight-minute period for buoys, and hourly average wind direction (degrees clockwise from N) during the same period used for average wind speed. Vectors of wind direction and magnitude were generated using S-Plus software. Dr. Jon Hare also provided NOAA satellite images covering the same period as the buoy data. However, images from many days were missing or unusable due

to cloud cover or solar glare. The satellite imagery provided sea surface temperature imagery for North Carolina's Outer Banks region including the western edge of the Gulf Stream.

RESULTS

Larval spot ingressing Ocracoke Inlet were collected earlier and at greater abundance than those ingressing Oregon Inlet. A total of 13,773 larval spot were collected between October 18, 1994 and April 26, 1995 in SABRE. Of these, 11,455 larvae were collected ingressing Ocracoke Inlet and 2,318 were collected ingressing Oregon Inlet (Fig. 2, Table 1). Spot larvae were first collected at the same time for both Oregon and Ocracoke Inlets (2 and 11), on November 29 and 30, 1994. Following these dates, spot larvae continued to be collected at Ocracoke Inlet but not at Oregon Inlet. Approximately five weeks elapsed before spot were again collected at Oregon Inlet on January 4, 1995. Two weeks later on January 17 and 18, 1995 larval abundance ingressing Oregon and Ocracoke Inlets peaked at 985 and 8,704 respectively. These peaks accounted for 42% (985) of the total larvae collected at Oregon Inlet and 76% (8,704) of the total larvae collected at Ocracoke Inlet. The numbers of new recruits dropped drastically (1 and 2 collected) at Oregon Inlet during the two weeks following peak abundance. This was not the case for Ocracoke Inlet where numbers of new recruits remained abundant (approximately 400 collected each week). This mismatch continues throughout the sampling season.

With the exception of the initial peak recruitment events, patterns of abundance between inlets rarely coincide. By mid-April spot larvae were no longer ingressing Ocracoke Inlet although they continued to be collected at Oregon Inlet. The only obvious pattern, which can be interpreted from the abundance data, is that Ocracoke Inlet experiences more larval recruits than Oregon Inlet (83% of the total compared to 17%).

A similar range and mean (Fig. 4) were associated with length frequency distributions from both Oregon and Ocracoke Inlets. The mean standard length of larvae ingressing Oregon Inlet (13.5 mm) is only slightly larger than the mean of larvae ingressing Ocracoke Inlet (13.3 mm). These distributions were not determined to be statistically significant (t-test $p > 0.05$). The smallest sized larva collected was 7.3 mm SL, while the largest was 28 mm SL.

Standard lengths of larvae recruiting to Oregon and Ocracoke Inlets were similar for each collection date and gradually increased over time (Fig. 5). Lengths of spot larvae ranged from 8-13 mm standard length during the peak recruitment abundance of mid-January. Variability in length was greatly reduced at this time compared to the preceding weeks. From mid-November through early December 1994, larval spot recruited to Ocracoke Inlet at 8-23 mm standard length.

Statistical analyses determined that lapillae and sagittae ages are not different and there was precise agreement between consecutive readings. A contingency table (Bowker 1948) test of symmetry indicated no significant difference ($n=61$, $p > 0.05$) in age readings between the sagittae and lapillae of spot larvae (Table 2). The lapillus was thus chosen to conduct all further ageing. Analyses show that lapillar ages are precisely measured. The average percent error (Beamish & Fournier 1981) for 32 sagittae was 9.69% and the APE for 32 lapillae was 9.25%. An additional contingency table analysis (Bowker 1948) indicated no significant difference ($n=194$, $p < 0.05$) between two age readings (Table 3).

Proportionately more spot larvae of significantly older ages were collected ingressing Oregon Inlet. The age ranges for both inlets are similar, ranging from approximately 21 days through 121 days (Fig. 6). Although the oldest larva was collected

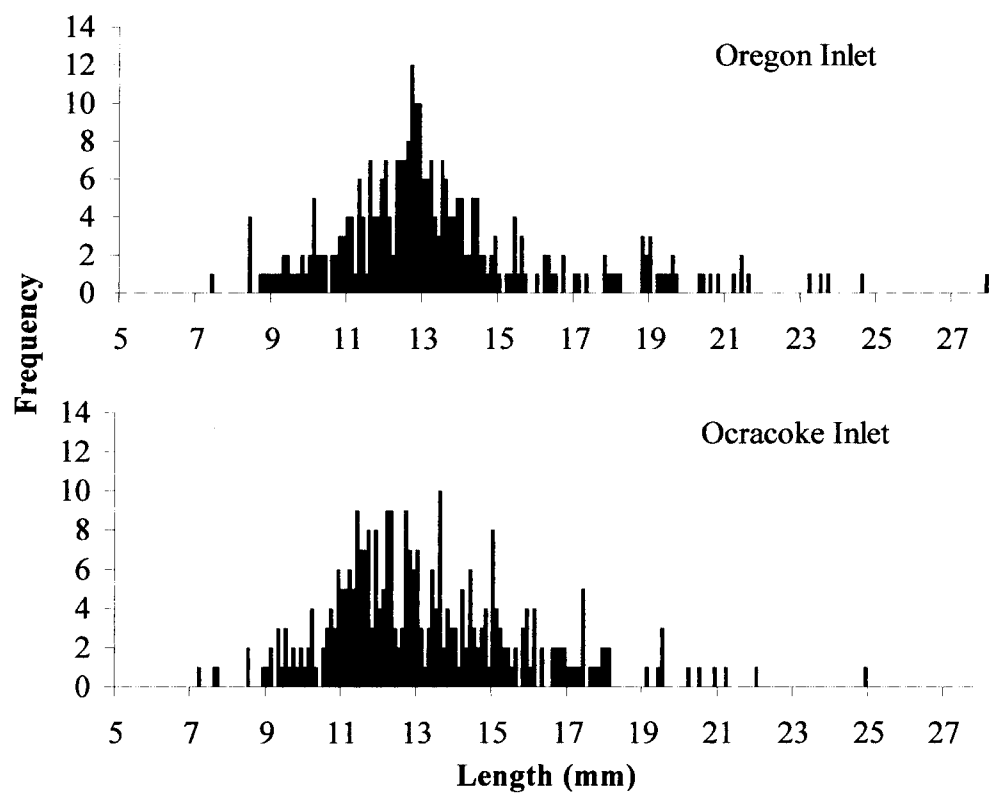


Fig. 4. Length frequency distributions of 298 spot larvae collected at Oregon Inlet and 314 spot larvae collected at Ocracoke Inlet. The means at Oregon (top) and Ocracoke (bottom) Inlets are 13.5 mm and 13.3 mm respectively. The distributions are not significantly different.

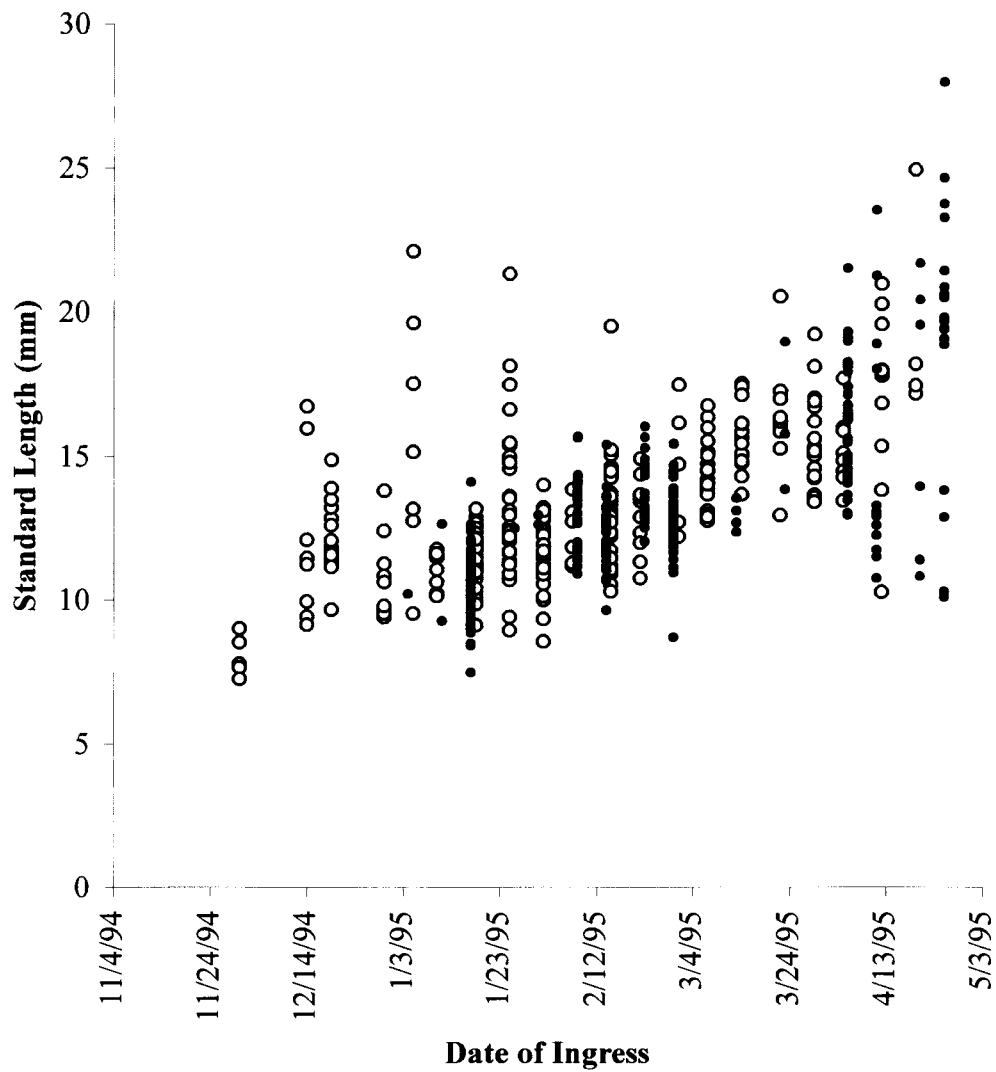


Fig. 5. A comparison of standard length (mm) between Oregon and Ocracoke Inlets at time of recruitment. Closed circles represent size of spot larvae collected at Oregon Inlet and open circles represent spot larvae collected at Ocracoke Inlet.

Table 2. Contingency table analysis to determine whether differences exist between ageing the sagitta compared to the lapillus. Results suggest either otolith will give comparable ages.

		Sagitta										
		21-26	27-32	33-38	39-44	45-50	51-56	57-62	63-68	69-74	75-80	81-86
Lapillus	21-26		1									
	27-32		1									
	33-38		2	4	1							
	39-44			3	2	1		1				
	45-50			2	4							
	51-56		1		5	4						
	57-62				1	1	3	3	1			
	63-68						1	3	4	3	1	
	69-74						1	1				
	75-80										1	2
	81-86							2		1		

n = 61

alpha = 0.05

chi square = 28.8

d.f. = 21

table value = 30.144

28.8 < 30.144, Do not reject H_0 , thus there is no asymmetry

Table 3. Contingency table analysis to determine whether differences exist between the first and second ageing. Results suggest consecutive readings are precise.

		Lapillus First Ageing																
		15-20	21-26	27-32	33-38	39-44	45-50	51-56	57-62	63-68	69-74	75-80	81-86	87-92	93-98	99-104	105-110	111-116
Lapillus Second Ageing	15-20	1																
	21-26	1	2	2														
	27-32		1	9	4													
	33-38		1	1	5	5												
	39-44				4	12	5	1										
	45-50				1	6	9	5										
	51-56					1	7	9	3	2								
	57-62					2		5	10	4				1				
	63-68					1	1	1	2	5	2			1				
	69-74					1		1	2	3	2	2						
	75-80								1	1	2	3	2					
	81-86						1		2	3		3	2		3			
	87-92										1	5	2	4				
	93-98												1	4				
	99-104															2	2	
	105-110											1			1	1		
111-116												1		1		1		

n = 194

alpha = 0.05

chi square = 51.132

d.f. = 40

table value = 55.758

51.132 < 55.758, Do not reject H_0 , thus there is no asymmetry

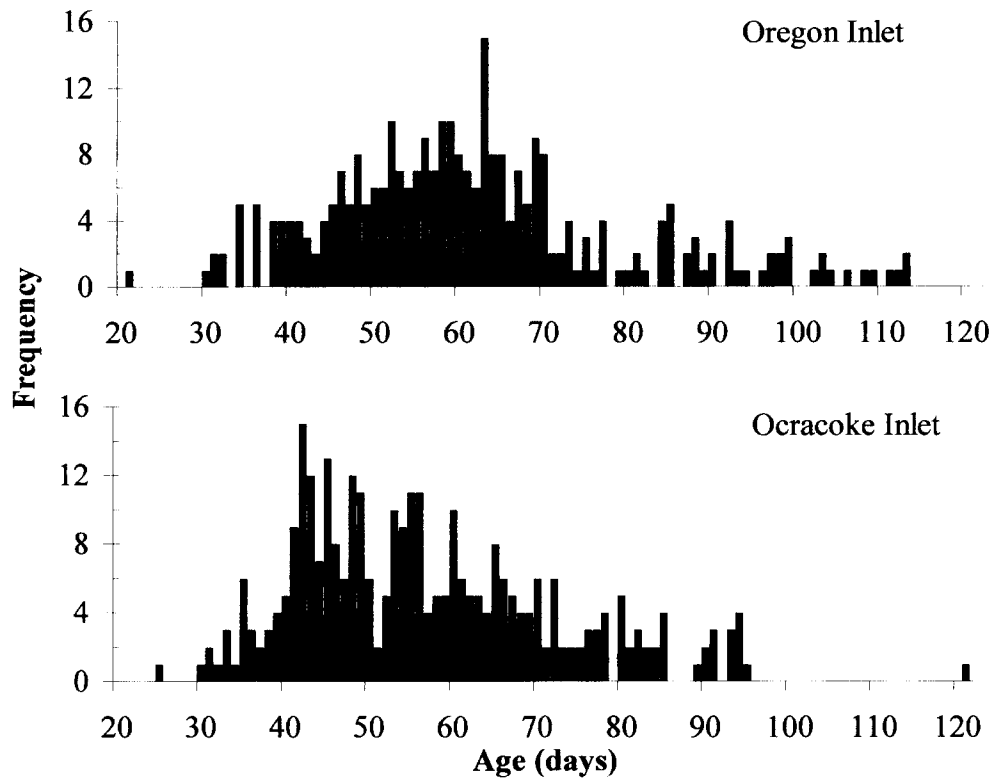


Fig. 6. Age frequency distributions of 298 spot larvae collected at Oregon Inlet and 314 spot larvae collected at Ocracoke Inlet. The mean age at Oregon Inlet (top) is 62 days and the mean age at Ocracoke Inlet (bottom) is 57 days, a seven day difference. The two distributions are significantly different.

at Ocracoke Inlet, older aged larvae were more abundant at Oregon Inlet. The frequency distributions show an older mean age for larvae collected at Oregon Inlet (62 days) compared to larvae collected at Ocracoke Inlet (57days). Randomization tests indicate a significant difference in age structure between inlets. This is evidenced by the greater number of young larvae at Ocracoke Inlet seen when comparing age and time of recruitment between the two inlets (Fig. 7).

The reconstructed birth-date distribution for spot larvae suggests spawning takes place intensely over a relatively short period (Fig. 8). Larvae collected at Oregon Inlet were spawned from mid-November through early March. Larvae collected at Ocracoke Inlet were spawned from mid-October through early March. Peak spawning activity for larvae collected at both inlets occurred during the month of December 1994.

Simple calculations were conducted to describe growth of larval spot recruiting to Oregon and Ocracoke Inlets. Average growth rates ($\text{mm}^{-\text{day}}$) based on length at age data show growth slows with age (Fig. 9). Growth is initially higher (<40 days), ranging between 0.25-0.4 $\text{mm}^{-\text{day}}$ and then decreases to 0.2 $\text{mm}^{-\text{day}}$ as larvae reach 60 days of age. Length-at-age data suggests linear growth (Fig. 10) rather than sigmoidal growth as often described for larval fishes.

A high coefficient of determination resulting from the regression of standard length on otolith radius suggests that back calculation techniques are appropriate (Fig. 11) and that otolith increment width reflects fish growth. Because no fish were smaller than 7.2 mm, I have assumed this linear relationship holds from the size at hatch (1.6 mm). Such assumptions have been used when small fish were not available (Ralston et al. 1995). Length data for smaller larvae not collected in the sampling gear can be

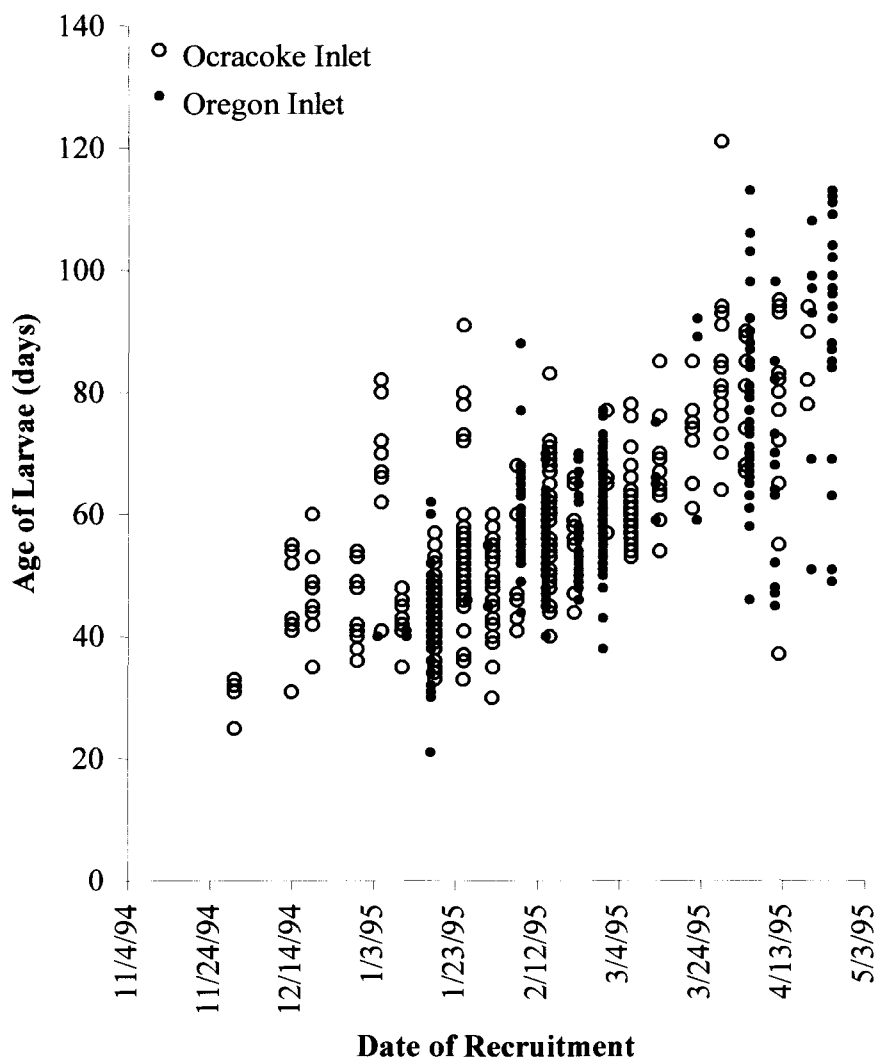


Fig. 7. A comparison of age (days) between Oregon and Ocracoke Inlets at time of recruitment. Closed circles represent age of spot larvae collected at Oregon Inlet and open circles represent spot larvae collected at Ocracoke Inlet.

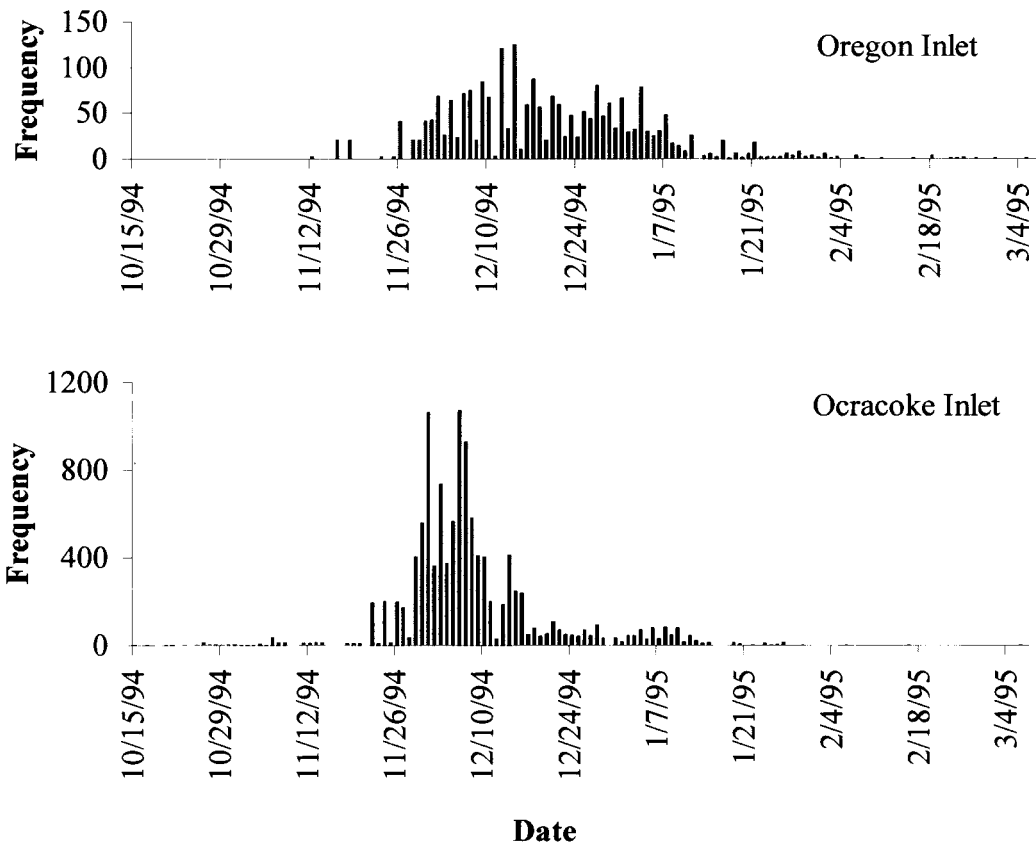


Fig. 8. Spawning date distributions projected from a subsample of 298 spot larvae collected at Oregon Inlet and 314 spot larvae collected at Ocracoke Inlet. The two distributions span a similar temporal scale, suggesting all larvae entering Pamlico Sound are from a single population.

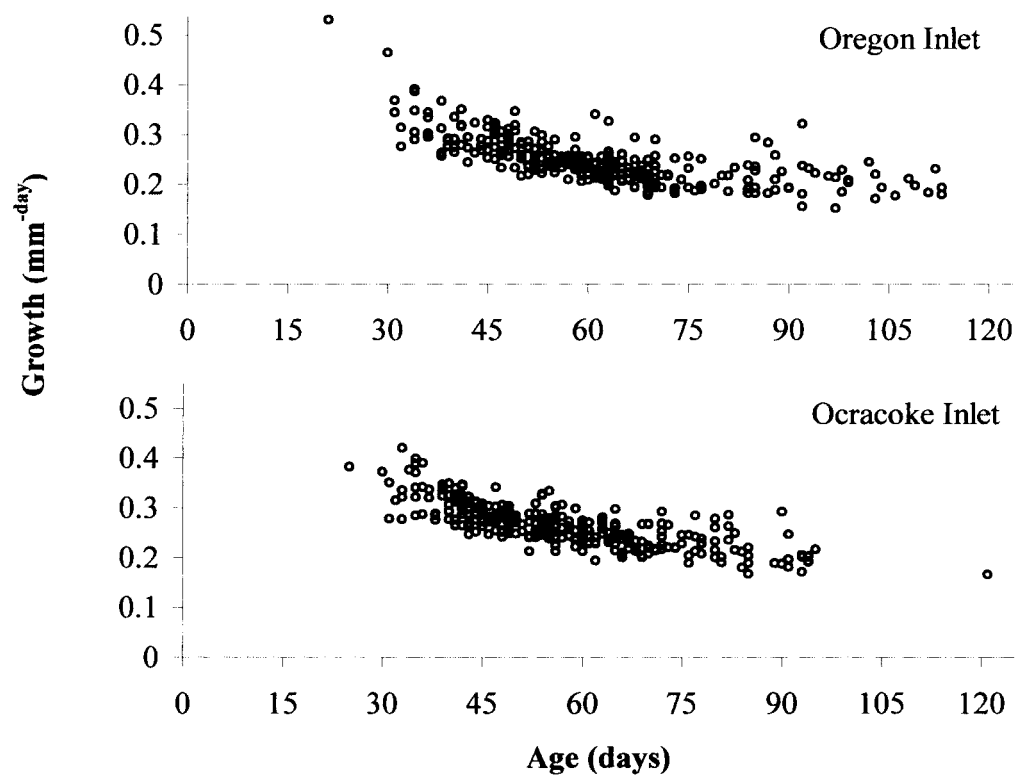


Fig. 9. Average growth ($\text{mm}^{-\text{d}}$) determined from size at age data for 298 spot larvae collected at Oregon Inlet and 314 larvae collected at Ocracoke Inlet.

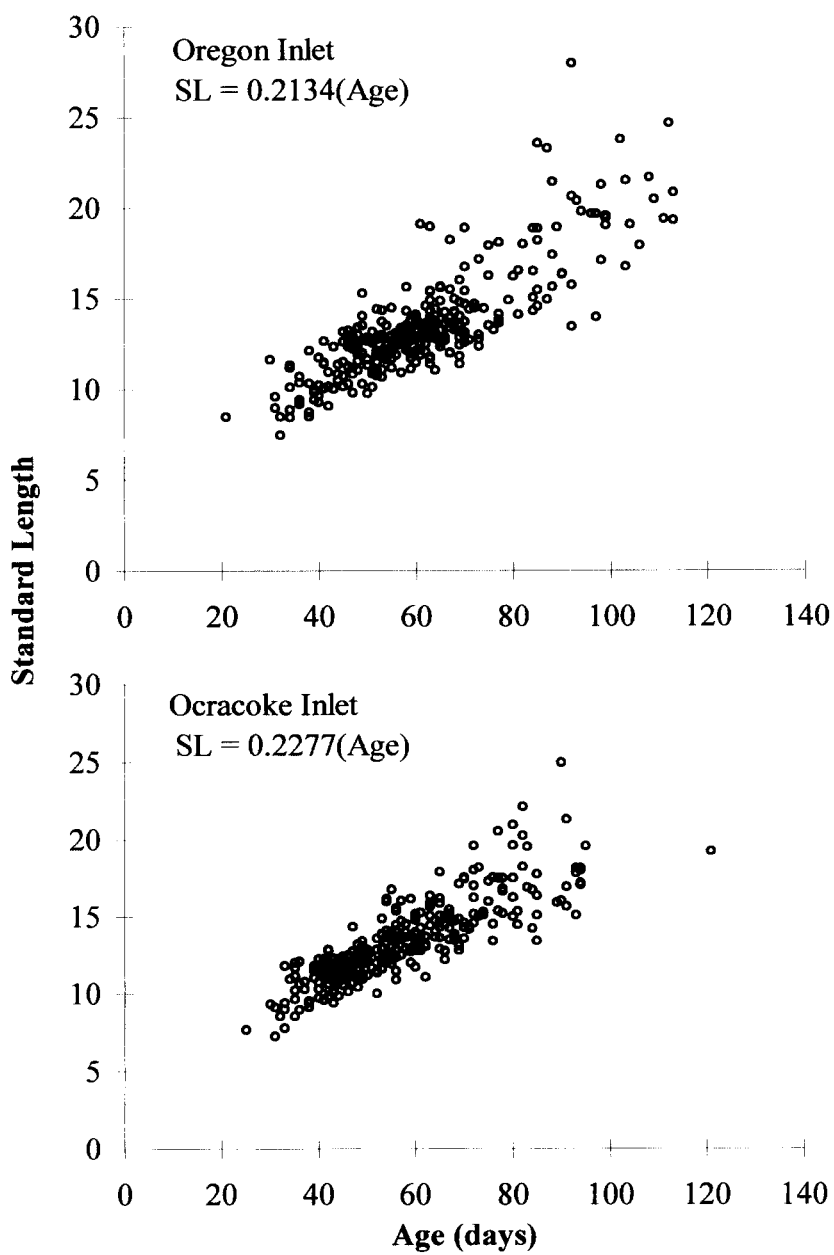


Fig. 10. Length-Age regressions representing growth rates of larval spot.

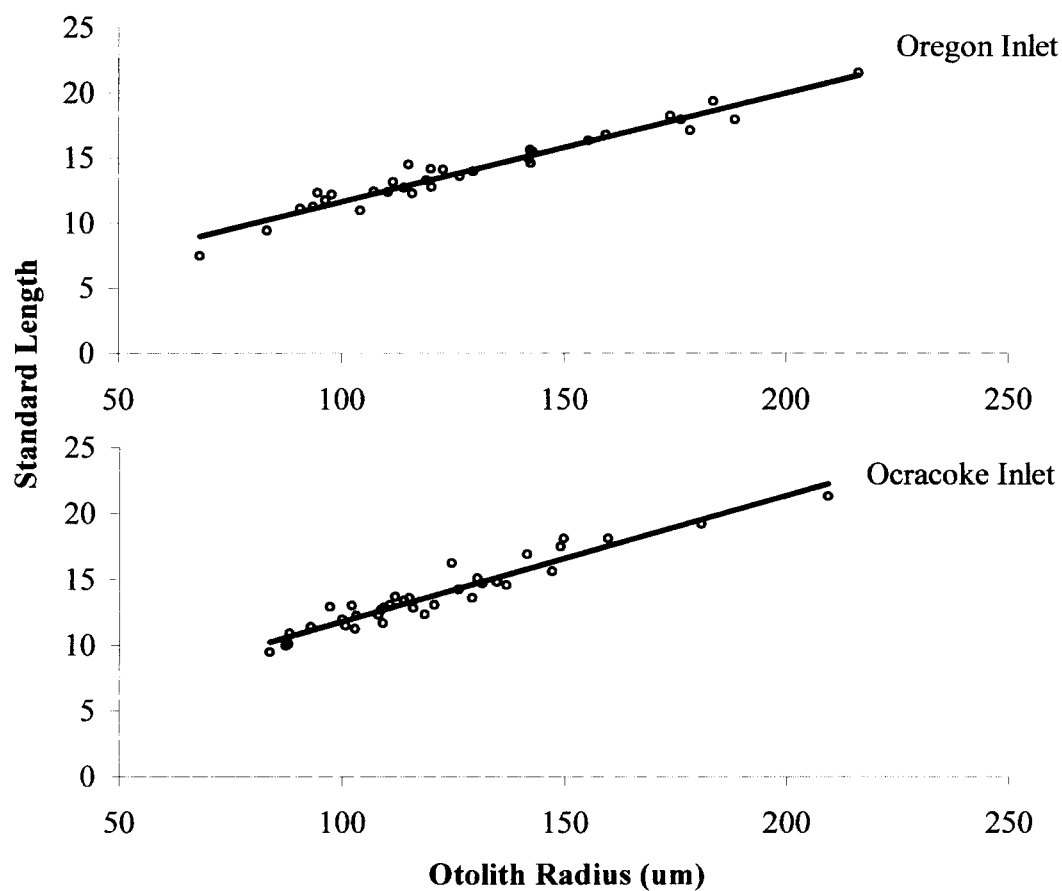


Fig. 11. Regressions of larval spot standard length on otolith radius. The regression accounts for 95% and 91% of the total variation occurring at Oregon and Ocracoke Inlets respectively. The top graph represents 32 larvae from Oregon Inlet and the bottom graph represents 36 larvae from Ocracoke Inlet.

easily generated from back calculation techniques. Ninety-one percent of the total variation was accounted for when standard length was regressed on otolith radius for fish collected at Ocracoke Inlet ($n = 32$). Based on this relationship, length at age information can be obtained from back calculation techniques with a high degree of confidence. A higher percentage (95%) of the total variation is explained by the same regression using spot larvae collected at Oregon Inlet ($n = 37$).

A retrospective daily record and understanding of growth is contained within individual otoliths ($n = 69$), showing periods of both rapid and slow growth measured as the distance between consecutive daily increments (Fig. 12). Growth during the first 25 days is slow with the distance between consecutive increments averaging $2 \mu\text{m}$. Growth increases after 25 days averaging $2.7 \mu\text{m}$ at 30 days. For the next 15 days growth fluctuates around $2.5 \mu\text{m}$. Although similar initially, after 40 days, growth patterns between inlets are very different. Results from the MANOVA (Fig. 13) indicated differences in growth patterns were statistically significant ($p < 0.05$).

Wind direction remained variable throughout the entire sampling period (Fig. 14). There were no obvious periods in which the wind was consistently from the same direction for an extended time. This makes it difficult to match peaks in recruitment with specific wind events. Instead, the numbers of northerly wind events, thought to be favorable to transport mechanisms, were tallied for each month of the sampling period (Table 4). During December, there were 12 northerly wind events, compared to zero in February, four in November, and eight in March.

Northerly wind events were considered possible mechanisms for shoreward transport and recruitment of spot larvae into Oregon and Ocracoke Inlets. The duration

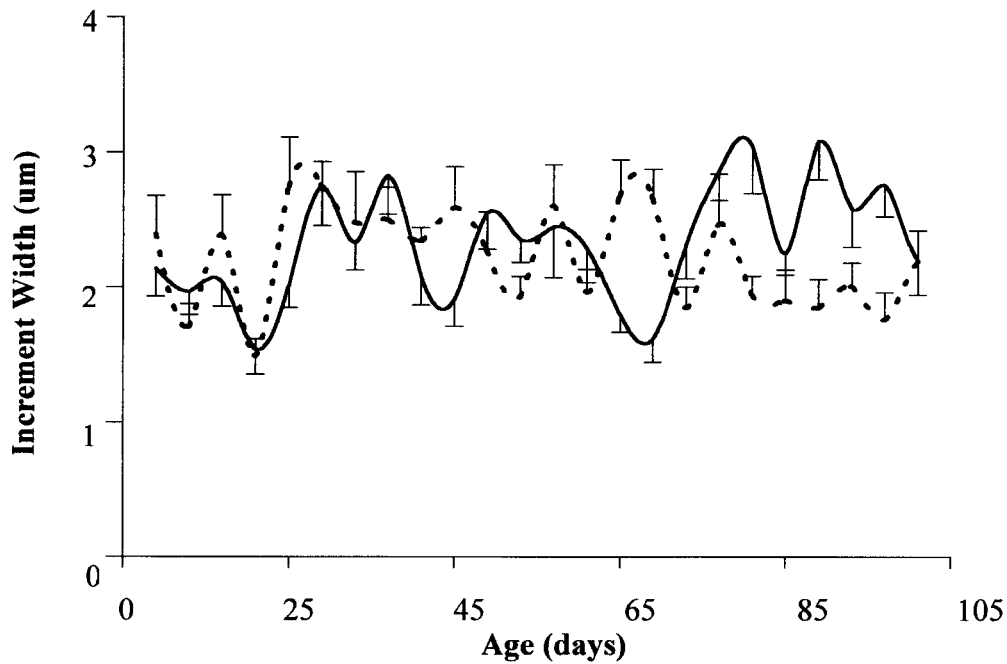


Fig. 12. Daily incremental otolith growth between inlets shows similar patterns up to 40 days post-hatch. After which growth patterns diverge and no longer track each other. Incremental growth of 32 spot larvae collected at Oregon Inlet is represented by the dashed line and the continuous line represents incremental growth of 37 spot larvae collected at Ocracoke Inlet. Error bars represent standard error of the mean.

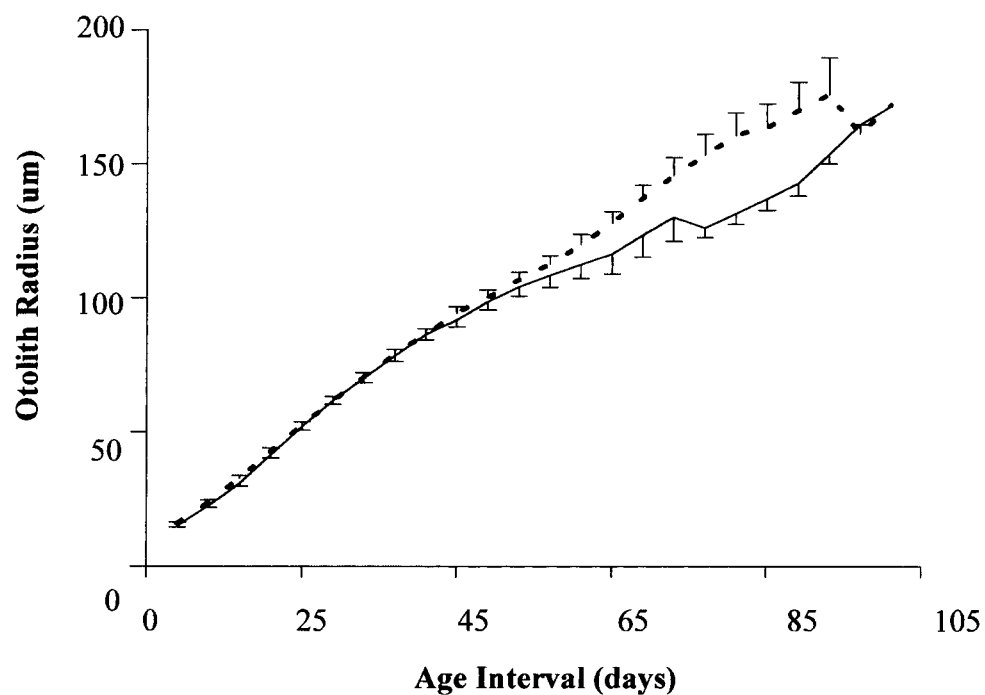


Fig. 13. Repeated measures MANOVA results suggest significant differences in growth of daily increments occurs after 40 days. Otolith growth is slightly faster for 32 spot larvae collected at Oregon Inlet (dashed line) compared to 37 spot larvae collected at Ocracoke Inlet (continuous line). Error bars represent standard error of the mean.

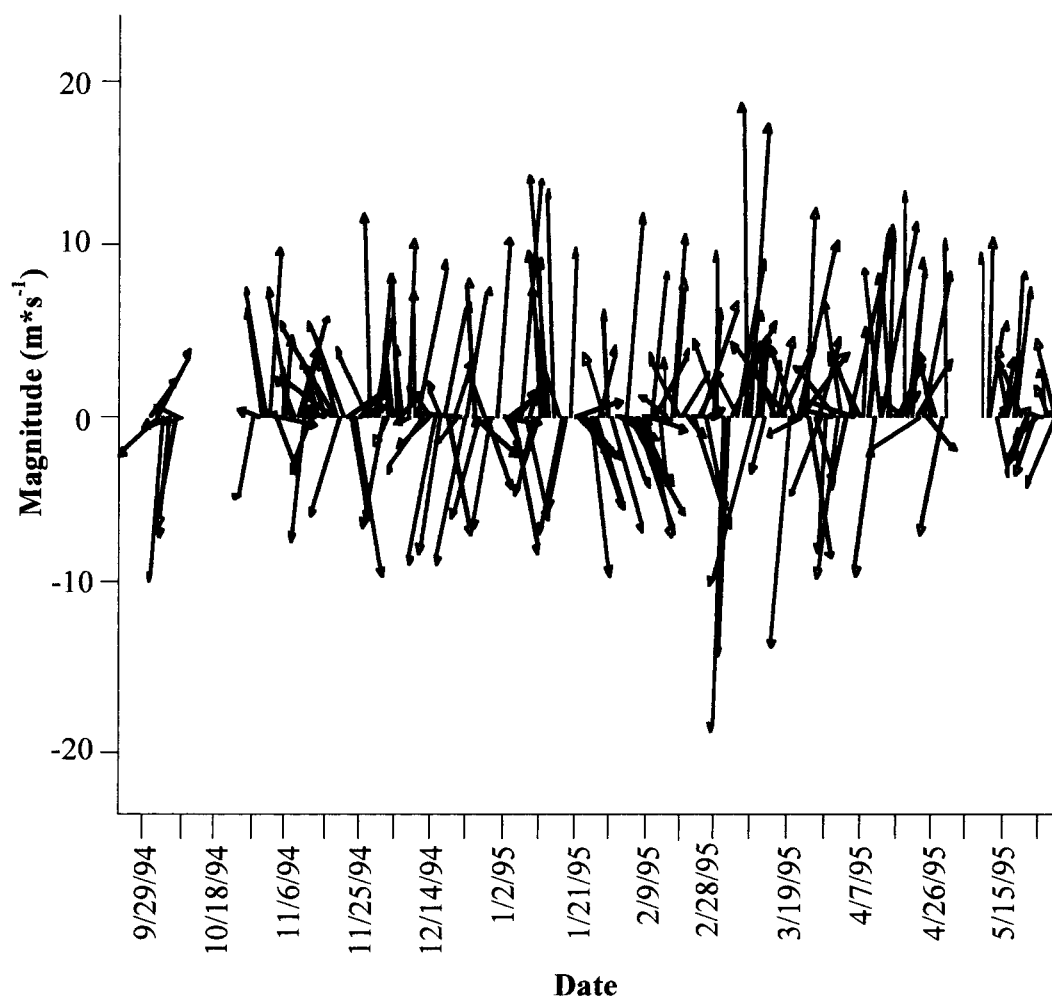


Fig. 14. Mean daily vectors describe wind direction and magnitude from October 1, 1994 through May 31, 1995. Vectors point in direction wind is traveling.

Table 4. Numbers and direction of wind events occurring from November 1, 1994 through March 31, 1995. Dominant wind direction for each month is indicated by an asterisk.

MONTH	WIND DIRECTION			
	NE (0-89°)	SE (90-179°)	SW (180-269°)	NW (270-359°)
November	4	12*	10	4
December	12*	10	6	3
January	4	8	8	11*
February	0	2	12	14*
March	8	8	13*	2
TOTAL	28	40	49	34

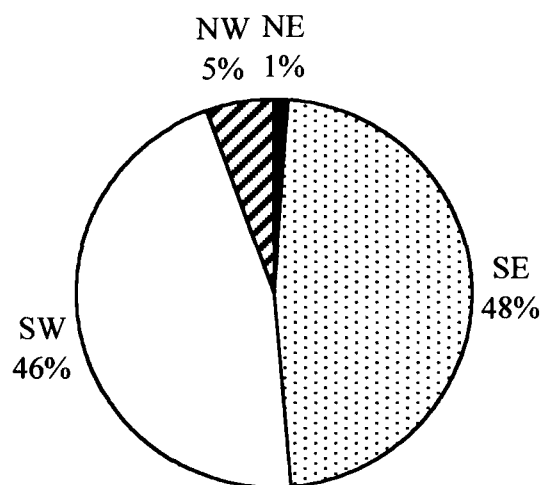
and magnitude of such wind events are obvious factors to consider. However, I arbitrarily decided to look at the impact of northerly winds lasting three or more days. Several investigators have attributed northerly wind events to the shoreward transport of larval menhaden (Nelson 1977, Miller et al. 1984, and Checkley et al. 1988). Two such wind events occurred during the sampling period. An additional wind event of importance lasted only two days but had winds of high magnitude ($>14 \text{ m}\cdot\text{s}^{-1}$). The first of these wind events occurred from January 21, 1995 through January 27, 1995. Predominant wind direction during this period was northwesterly with magnitudes ranging from $7.2\text{-}12.4 \text{ m}\cdot\text{s}^{-1}$. The second northerly wind event occurred from January 31, 1995 through February 13, 1995. Also during this time, predominant wind direction was northwesterly ranging in magnitude from $4.5\text{-}15.7 \text{ m}\cdot\text{s}^{-1}$. The third wind event was northeasterly and occurred on March 2 and March 3, 1995 with magnitudes of 19.1 and $14.6 \text{ m}\cdot\text{s}^{-1}$ respectively.

During southerly wind events the proportion of larvae recruiting to Oregon Inlet overwhelms the number of larvae recruiting to Ocracoke Inlet (Fig. 15). The proportion of total larvae recruiting to Oregon Inlet on southwesterly and southeasterly wind events is 46% and 48% respectively compared to 5% and 1% during respective northwesterly and northeasterly winds.

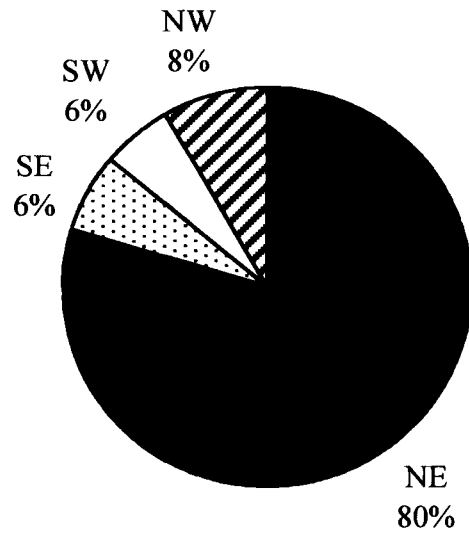
Sea surface temperatures obtained from satellite imagery from January 1, 1995 through March 2, 1995 were analyzed for distinctive features, which may correlate to peaks in larval ingressation at Oregon and Ocracoke Inlets. Appendix I documents the water temperatures near Oregon and Ocracoke Inlets obtained from the 24 images that were readable. Four warm water events occurred during this time and may have contributed substantially to the abundance of spot larvae recruiting to Oregon Inlet

Figure 15. Wind direction and corresponding percentage of total spot larvae collected by the National Marine Fisheries Service at each inlet.

Oregon Inlet



Ocracoke Inlet



(Plates I-IV). The first of these events was between January 4 and January 10, 1995. The second was a two-day event between February 1 and February 2, 1995. The third occurred in middle of the month (February 12-13, 1995) and the final was at the end of the month (February 26, 1995).

DISCUSSION

Larval spot use different mechanisms to recruit to inlets in the MAB and SAB compared to other fall-winter spawning fish. This is evidenced by their abundance and demography. During the fall, menhaden and croaker larvae are more abundant at Oregon Inlet in the MAB than spot (Hettler 1998). Although spot share a similar life history and range as these other fishes, their pattern of larval recruitment is different.

Length data suggest the supply of new recruits to Oregon and Ocracoke Inlets are from a single aggregation of spot spawning during a single protracted season in the SAB. This spawning behavior is different when compared to menhaden, which spawn over several seasons both in the MAB and SAB. Spot larvae recruit to Oregon and Ocracoke Inlets simultaneously at their seasonal peak abundance in mid-January. At this time spot larvae are the same size at each inlet (Fig. 5). This was perplexing, as the abundance data indicated a time lag of seven weeks between the first substantial numbers of larvae recruiting to Ocracoke Inlet compared to Oregon Inlet. Based on menhaden and croaker, recruitment, it was assumed that spot larvae were spawned south of Cape Hatteras and transported north by similar mechanisms, which will be discussed later. Larvae recruiting to Oregon Inlet were expected to be larger in size compared to larvae first recruiting to Ocracoke Inlet seven weeks earlier. However, the length data shows these larvae recruiting to Oregon Inlet are not significantly larger in size than those recruiting to Ocracoke Inlet (means of 13.5 and 13.3 mm standard length). Surely, an additional transport time of seven weeks would be apparent with larger sized or older larvae recruiting to Oregon Inlet. Larvae remained similar in size at each inlet for the entire

sampling season. The only difference was increased variability in size at the beginning and end of the season.

The mean lengths of young spot recruiting to Oregon and Ocracoke Inlets are similar to those reported for spot recruiting to the Newport River estuary in North Carolina. Warlen and Chester (1985) reported the average size of spot larvae recruiting to Beaufort Inlet is 13.6 mm standard length (range 11.3 – 15.6 mm). Flores-Coto & Warlen (1993) report the average size of spot larvae near Beaufort Inlet is 17.2 mm standard length (range 9.2 – 22.2 mm). This information suggests that larvae are not spawned any further south than Beaufort Inlet. If they are, the sizes of spot larvae recruiting to Beaufort Inlet would be smaller and there will be an increase in length as they recruit to inlets further north (i.e. Ocracoke and Oregon). The lengths reported in both references are larger than what I have reported for spot larvae recruiting to Oregon and Ocracoke Inlets. This may indicate spot are spawning closer to these inlets (more northerly) than previously thought.

Lengths of spot recruiting to estuaries increase proportionally to the north and south of Oregon and Ocracoke Inlets. The lengths of spot larvae recruiting to Virginia and South Carolina estuaries are larger and similar to each other in size. Data collected by Beckman & Dean (1984) show spot larvae recruiting to North Inlet Estuary, South Carolina range in size 11-42 mm standard length. Numerous studies (Welsh & Breder 1923, Hildebrand & Schroeder 1928, Orth & Heck 1980, Olney 1983, Weinstein & Brooks 1983, Olney & Boehlert 1988) show spot recruiting to the Chesapeake Bay at a similar size ranging from 11-37 mm standard length. This information also suggests that spot larvae are spawned from a single aggregation off North Carolina's coast. Larvae

transported equally quickly to locations north and south of this location are therefore of similar lengths.

Complementary to length data, spot larvae are also of similar ages when they recruited to both Oregon and Ocracoke Inlets (Fig. 13). Again, it was expected that the seven-week time lag between the end of November, when larval spot are first abundant at Ocracoke Inlet, and the end of January, when spot larvae are first abundant at Oregon Inlet, would be apparent with differences in age between inlets. That is, if spawning took place south of Cape Hatteras North Carolina, in the SAB, then the seven-week lag period is the time it took for larvae to be transported into the MAB and through Oregon Inlet. Larvae ingressing Ocracoke Inlet are expected to be younger in age due to reduced transport time from spawning location, whereas Oregon Inlet is farther from the spawning location so larvae are expected to be older in age. Significant differences were found in overall age distributions between Oregon and Ocracoke Inlets, but only with a mean of five days.

The age of spot larvae increases equally in the MAB and SAB as the distance from spawning location increases. The youngest spot larvae were initially collected in North Carolina's estuaries, while estuaries of states to the north and south contained older larval spot. Warlen & Chester (1985) reported the average age of spot larvae recruiting to the Newport River estuary, North Carolina, through Beaufort Inlet; was 59 days (range 40 – 74 days). In another study, Flores-Coto & Warlen (1993) determined the mean age of larvae near Beaufort Inlet was 82 days (range 37 – 108 days). Beckman & Dean (1984) reported the youngest larvae recruiting to the North Inlet estuary, South Carolina, were 60 days old. Siegfried & Weinstein (1989) also reported the youngest aged spot

recruiting to Chesapeake Bay, Virginia were 57 days old. Thus, it appears to take an extra 20 days to travel comparable distances to the north and south of the spawning location. The different oceanography of the MAB does not appear to hinder the transport time of larvae into northern inlets (i.e. Chesapeake Bay, Virginia) any more so than larvae traveling equal distances to inlets in the SAB (i.e. North Inlet, South Carolina).

Contrary to other fishes sharing a similar life history (i.e. menhaden and croaker), spot do not appear to be spawning as they migrate out of the MAB into the SAB. Spot share the same geographic extent, migratory patterns, and some of the same spawning location as menhaden and croaker. However, their spawning behavior appears different. Unlike the other two fishes, fewer spot larvae were collected at Oregon Inlet (MAB) compared to Ocracoke Inlet (SAB). In addition, these larvae were not smaller or younger than those collected at Ocracoke Inlet. All this information indicates spot do not spawn in the MAB. I offer the following three hypotheses: 1) Insufficient spawning activity takes place in the MAB during their southern migration. 2) Spot leave the estuaries and coastal waters later in the fall than menhaden and croaker. By this time, waters in the MAB are too cool and are not conducive for spawning activity. 3) Spot migrating out of the MAB do not contribute significantly to larval abundance and recruitment. Instead, it is the spot, which move out of the estuaries and offshore in the SAB that add most new recruits to the population. Spawning date distributions support all three hypotheses. Peak spawning occurs throughout December when waters in the MAB are too cold for spawning. The similar unimodal, protracted, and overlapping distributions of both inlets suggests there is only a single spawning population. This population has to be located in the SAB because of water temperature.

Similar spawning date distributions suggest that larval spot ingressing Pamlico Sound at Oregon and Ocracoke Inlets are from a single population. Reconstructed spawning dates from otolith back calculation describe similar unimodal, protracted, and overlapping distributions for both Oregon and Ocracoke Inlets. The similarity suggests larvae originate from the same spawning population. Two distributions separated temporally might indicate spawning populations in both the MAB and SAB. However, a separate population in the MAB would be forced to spawn earlier than the data suggests, before water temperatures decline.

The supply of larval spot to Oregon Inlet in the MAB is from a single spawning aggregation in the SAB. New recruits of menhaden are supplied to Delaware and Chesapeake Bays as adults migrate south out of the MAB and into the SAB. Models by Quinlan et al. (1999) suggest that once these adults reach the SAB, they no longer can contribute new recruits into the MAB. My data suggests spot do not spawn as they migrate south. However, there are still a considerable number of recruits which ingress Oregon Inlet. Contrary to what Quinlan et al. (1999) concluded, spot spawning in the SAB must supply new recruits into the MAB.

Length-at-age data suggest growth of spot larvae ingressing Oregon and Ocracoke Inlets are similar to what has previously been reported for spot larvae ingressing North Carolina's inlets. Calculations made by Warlen & Chester (1985) indicate that spot are approximately 1.6 mm SL at hatching, reaching 17.0-19.0 mm at 90 days. Through linear regression, I too show spot larvae reach 17.0 – 19.0 mm standard length at 90 days. This estimation of hatching size agrees with the laboratory observations of Powell & Gordy (1980). Data collected by Flores-Coto & Warlen (1993) and fit to the Laird-Gompertz

model predicted a smaller hatching age (1.2 mm SL) with larvae reaching 19.1 mm in 95 days for spot entering Beaufort Inlet. Larval spot experience their maximum growth rate at approximately 9.3 mm SL and 46 days (Flores-Coto & Warlen 1993). It is at this size and age that spot are first seen ingressing Beaufort Inlet. However, growth rate drastically declines once spot enter North Carolina's estuaries. By the time larvae recruit to the cool waters of the lower estuary (often $<10^{\circ}\text{C}$), growth rate (length) has slowed considerably from an initial rate of 7%/day to 1.5%/day (Warlen & Chester 1985).

An analysis of otolith microstructure from larval spot shows differences in growth between Oregon and Ocracoke Inlets. Growth rates appear to slow quicker for spot larvae collected at Ocracoke Inlet compared to Oregon Inlet. My data show constant, sustained, and faster growth of larval spot otoliths collected at Oregon Inlet while otoliths of spot larvae collected at Ocracoke Inlet grow slower with age. One potential explanation is increased growth of spot larvae associated with warm water filaments. If these filaments are transporting spot larvae close to Oregon Inlet then the warm water and increased prey abundance may help sustain quicker metabolism and higher growth rates. Spot larvae reaching Ocracoke Inlet may not encounter conditions that allow for immediate ingress. Instead, the larvae may pile up outside the inlet in cold coastal waters until conditions are favorable and allow them to be pulsed through. Nonetheless, they show no growth cessation during this time.

My explanation of growth differences introduces the influence of environmental conditions on larval spot transport. I will now focus my discussion on transport of spot larvae towards Oregon and Ocracoke Inlets, offering two additional hypotheses, which incorporate environmental influence and recruitment abundance.

Along-shore transport is a mechanism used by menhaden and croaker to supply new recruits to estuaries in the MAB during fall migration (Hare et al. 1999). The seasonal migration of Atlantic menhaden and croaker supplies new recruits to estuaries in the Middle Atlantic Bight. Menhaden migrate south out of the MAB as the waters off New England and the mid-Atlantic cool. During this seasonal fall migration, spawning takes place. Larval menhaden are first transported through inlets in the MAB where they overwinter in the estuaries. Studies show abundance of larvae is initially greater at Oregon Inlet in the Middle Atlantic Bight compared to Ocracoke Inlet in the South Atlantic Bight (Hettler and Barker 1993, Hettler 1998). This same scenario is even more pronounced with the abundance of Atlantic croaker larvae. Thus, it is believed that croakers also spawn in the MAB as they migrate south towards the warmer waters in the SAB.

Variability in recruitment has previously been associated with cross-shelf transport mechanisms. However, recent results of SABRE modeling (Hare et al. 1999) confirm earlier studies, which suggest along-shore transport is a more influential mechanism than cross-shelf transport. Lee et al. (1989) and Govoni & Pietrafesa (1994) reported along-shore flows off the Carolina coast are typically four to five times greater than cross-shelf flows. Cross-shelf transport is nonetheless important, possibly more so for spot larvae than menhaden. However, Norcross & Bodulus (1991) indirectly acknowledged the importance of along-shore transport for juvenile spot recruiting to Chesapeake Bay, Virginia. They suggest year class strength is dependent on the number of southerly wind events, which occur in the spring season. These winds push spot north along the coast into the MAB where they recruit to Chesapeake and Delaware Bays.

Young spot traveling a comparable distance south of the spawning area are similar in age when they recruit South Carolina estuaries (Beckman & Dean 1984). This also suggests the importance of along-shore transport in supplying southern estuaries with new recruits. My results indicate that along-shore transport established by southerly wind events is indeed an important mechanism used by spot larvae recruiting to Oregon Inlet but the importance of cross-shelf transport cannot be disregarded. Cross-shelf transport remains a necessary mechanism for pushing spot larvae inshore, particularly if spot spawn further offshore than menhaden and croaker.

Cross-shelf transport is a mechanism linked to winds blowing from a northerly direction. The importance of such winds is evident in the data. The month-long period of peak spawning activity occurring throughout December may result from numerous northeasterly wind events as hypothesized by Checkley et al. (1988). Although, spot were spawned continuously for approximately 5 months between mid October and early March, a distinct peak lasting the month of December suggests conditions were optimal for shoreward transport during this time. This peak in spawning activity may be the result of northeasterly wind events. Twelve northeasterly wind events were recorded during December, far more than the four recorded in November and January, zero recorded in February and eight recorded in March (Table 4). Oddly enough, none of these wind events lasted longer than two days and none were of magnitude greater than 12 knots. These observations seem to confirm Checkley et al.'s (1988) hypothesis, that wintertime larval fish transport in the SAB is influenced by northeasterly wind events associated with the passage of wintertime storms. These storms occur frequently providing a

mechanism for shoreward transport which develops and dissipates on a short temporal scale (days).

The hypothesis proposed by Checkley et al. (1988) may be the likely scenario for transporting bouyant eggs and newly hatched larvae across the shelf but does not necessarily explain recruitment of older larvae into the inlets. Tides, winds, local geometry, and bathymetry influence transport through an inlet (Luettich et al. 1999). Spot eggs and larvae are initially subjected to wind forcing and other conditions affecting surface waters. However, as the larvae age and are transported closer to shore, they may reposition themselves deeper in the water column. Miller et al. (1984) hypothesizes an intermediate layer of water moves onshore as surface and bottom waters move offshore during northwesterly winds. Govoni & Pietrafesa (1994) found larval spot and Atlantic croaker concentrated in the middle or lower water column, providing support for Miller et al. (1984) as a plausible mechanism of estuarine recruitment. According to Forward et al. (1999) spot are found throughout the water column and rely on selective tidal stream transport to move them up the estuary. Those spot in the middle layers may have an advantage moving through the inlet and up the estuary. The mechanisms affecting recruitment are unique at each inlet. What influences recruitment at one inlet does not necessarily do so at another.

In addition to pushing larvae shoreward, wind forcing may help larvae recruit estuarine nurseries. Blanton et al. (1999) found certain wind directions were statistically associated with peaks in the number of postlarval white shrimp and blue crab megalopae recruiting to North Edisto Inlet, South Carolina. Recruitment at Oregon Inlet is associated

with winds from a southerly direction. However, recruitment to Ocracoke Inlet appears to be associated with northeasterly wind events (Table 5).

Warm water filaments extending off the Gulf Stream may also be used as a mechanism to aid in estuarine recruitment. Rice et al. (1999) state that Gulf Stream influences may in fact be the most important mechanism potentially affecting cross-shelf transport. Unfortunately, the analysis of sea surface temperature imagery has been difficult due to an incomplete data set for the study period. This discussion therefore formulates conclusions based on a limited number of satellite images. There is evidence that warm water filaments encroaching Oregon Inlet may help contribute to peaks in recruitment abundance several days to a week after the initial warming trend appears. Warmer water (20-23°C) was found near Oregon Inlet (Plate I) on January 4th and 5th 1995. The next available image is 5 days later (January 10, 1995) which shows the warm water filament is still close to Oregon Inlet although reduced in size. Seven days later (January 17, 1995) Oregon Inlet experiences peak recruitment of spot larvae. Because the sea surface temperature imagery does not cover the entire period from January 4, 1995 through January 17, 1995 I cannot definitively attribute this warm water event to the peak recruitment of 985 larvae into Oregon Inlet although it is possible. From January 25, 1995 through January 31, 1995 water temperatures outside Oregon Inlet are cold reaching only 12°C. However, on February 1, 1995 warm water (20-23°C) encroaches north of Cape Hatteras. The next day (February 2, 1995) this water has warmed to 29°C (Plate II). This two-day influx of warm water may have contributed to another recruitment peak at Oregon Inlet on February 8, 1995 when 83 larvae were collected. From February 12th and 13th 1995 a warm water filament develops outside Oregon Inlet (Plate III) and lasts at

least two days. The duration this filament lasted is not known due to incomplete satellite imagery. However, its presence could have contributed to the 176 larvae collected on February 14, 1995. Finally, by the end of February there is a substantial “bump” (Plate IV) of warm water north of Cape Hatteras, which potentially contributed, to the second highest peak in recruitment abundance (871) experienced at Oregon Inlet on February 28, 1998.

Based on wind data and sea surface temperature imagery, I offer the final two hypotheses which address why Oregon Inlet recruits were initially collected seven weeks after Ocracoke Inlet recruits yet remained similar in age throughout the sampling season. First, although larvae may reach Ocracoke Inlet quicker than larvae transported north toward Oregon Inlet they do not always enter the inlet directly. Instead, larvae may pile up just outside the inlets waiting for certain conditions to send them through. Rice et al. (1999) also suggests larvae may remain near an inlet before actually immigrating. This behavior is indicated in other studies as well (Warlen 1992, Hettler & Hare 1998, Churchill et al. 1999, Luettich et al. 1999). While larvae are waiting outside Ocracoke Inlet, others are transported north toward Oregon Inlet. By the time these larvae reach Oregon Inlet, conditions at Ocracoke Inlet may also be favorable allowing similar aged larvae to enter the inlets. Second, adult spot move offshore in the northern SAB where they spawn. Significant numbers of their offspring recruit inlets only in the SAB (i.e. Ocracoke Inlet). Adults then encounter a warm water filament from the Gulf Stream, which provides suitable spawning temperatures. Spot continue spawning in this warm water as it moves north and in close proximity to Oregon Inlet. This warm water filament eventually dissipates exposing spawners to cooler waters, forcing them south where they

continue spawning in warm water. Spawning behavior might always be cued to follow warm water features north as a way of ensuring transport of larvae into the MAB.

CONCLUSION

Larval spot were spawned continuously over a five-month period from a single population in the SAB. Reconstructed hatch-date distributions indicate an intense peak in spawning activity that lasted the month of December 1994. Northeasterly wind events prevailed during this time suggesting they are indeed an important mechanism for cross-shelf shoreward transport as hypothesized by Checkley et al. (1988). Substantial recruitment of spot larvae first occurred at Ocracoke Inlet followed by recruitment into Oregon Inlet seven weeks later. Length and age frequency distributions also offer support for a single spawning population in the SAB. Spot larvae recruited to Oregon and Ocracoke Inlets at similar lengths, and ages. Recruitment into the inlets was not correlated with general meteorological or oceanographic events. However, peaks in recruitment abundance at Oregon Inlet may be associated with southerly wind events as proposed by Norcross & Bodulus (1991) for recruitment of spot larvae into Chesapeake Bay. Warm water features extending from the Gulf Stream may have also enhanced recruitment at Oregon Inlet. The influence of water temperature on growth of spot larvae may be reflected in otolith microstructure when the two inlets are compared. Otolith growth patterns between consecutive daily increments are similar during the early ages but then diverge significantly in later ages. Spot larvae spend their later larval ages in coastal waters, which vary in temperature extremes. For example, spot larvae may remain outside Ocracoke Inlet in cold coastal waters while others are transported towards Oregon Inlet in filaments of water warmed by the Gulf Stream. The initial similarities in otolith growth patterns suggest spot larvae are spawned in a specific location by a single population.

Recruitment variability of larval spot at Oregon and Ocracoke Inlets is not due to separate populations or locations. Length, age, and growth data all suggest spot larvae recruiting to these inlets are from the same spawning population. The variability, which exists between inlets, is influenced by environmental conditions. The individual physical characteristics of each inlet (geographical orientation, size of opening, depth, etc.) all need to be studied further before recruitment variability between inlets is understood.

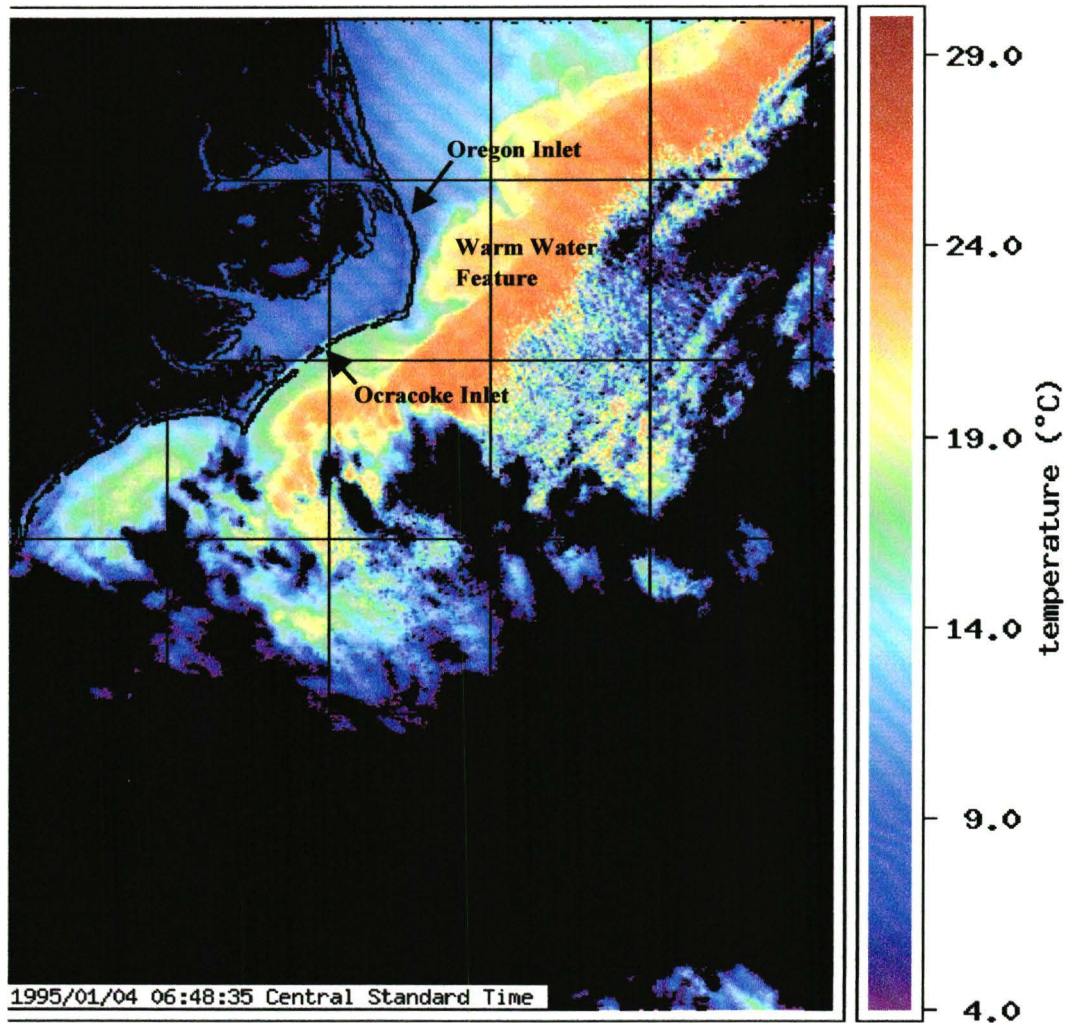


Plate I. Warm water extends from the Gulf Stream close to Oregon Inlet on January 4th, 1995 (6:48 am). This warm water feature may have enhanced transport and recruitment of the 985 spot larvae collected on January 17, 1995.

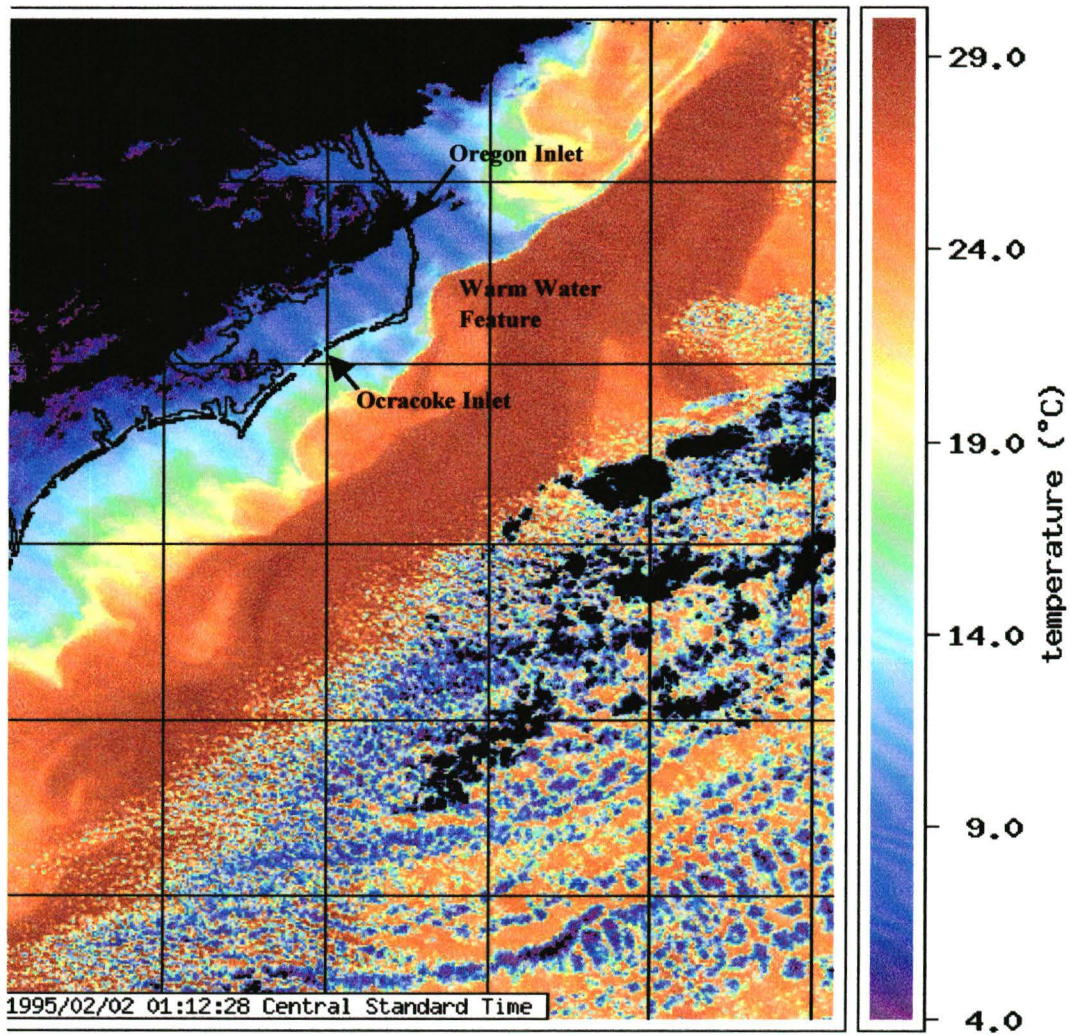


Plate II. Warm water encroaches north of Cape Hatteras on February 2, 1995 (1:12 am). This warm water feature may have enhanced transport and recruitment of the 83 spot larvae collected on February 8, 1995.

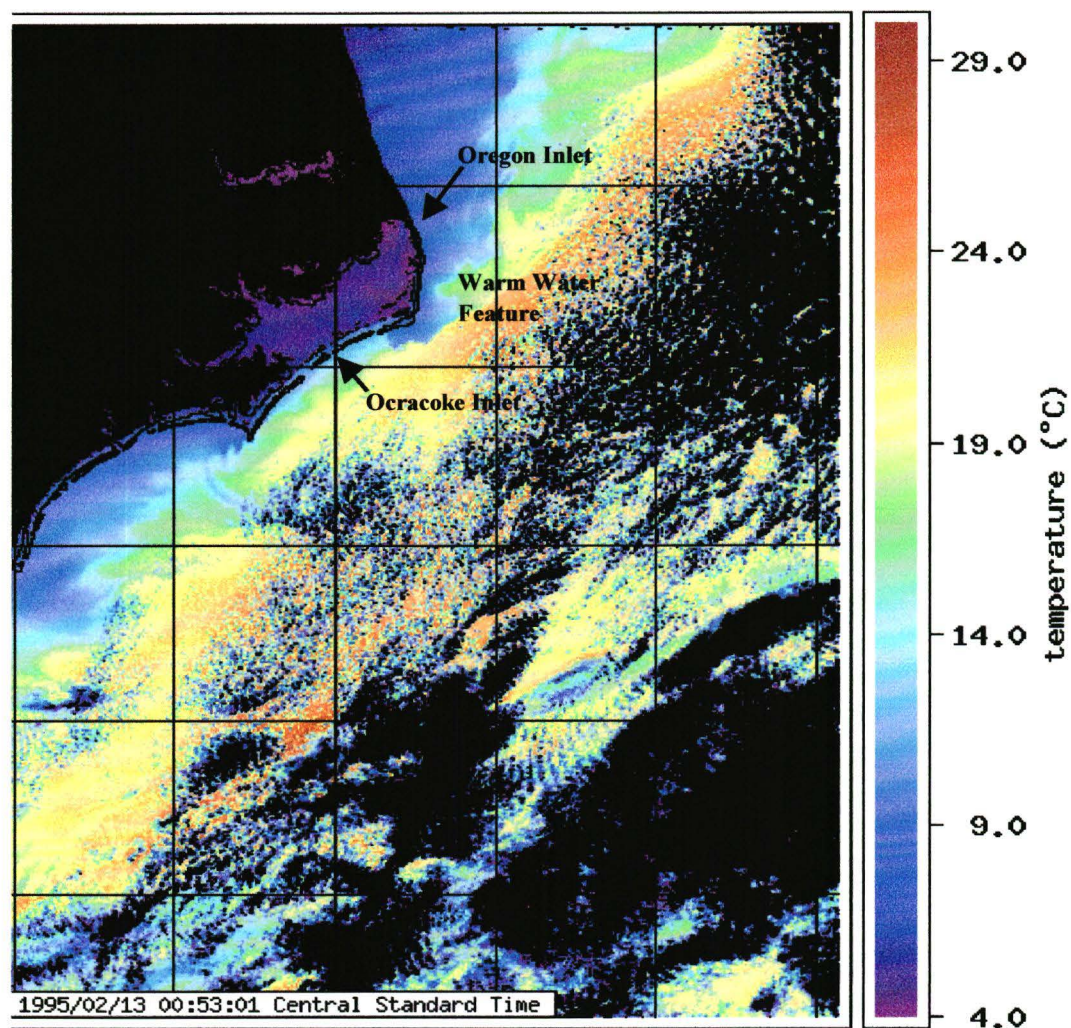


Plate III. Warm water extends from the Gulf Stream close to Oregon Inlet on February 13, 1995 (12:53 am). This warm water feature may have enhanced transport and recruitment of the 176 spot larvae collected on February 14, 1995.

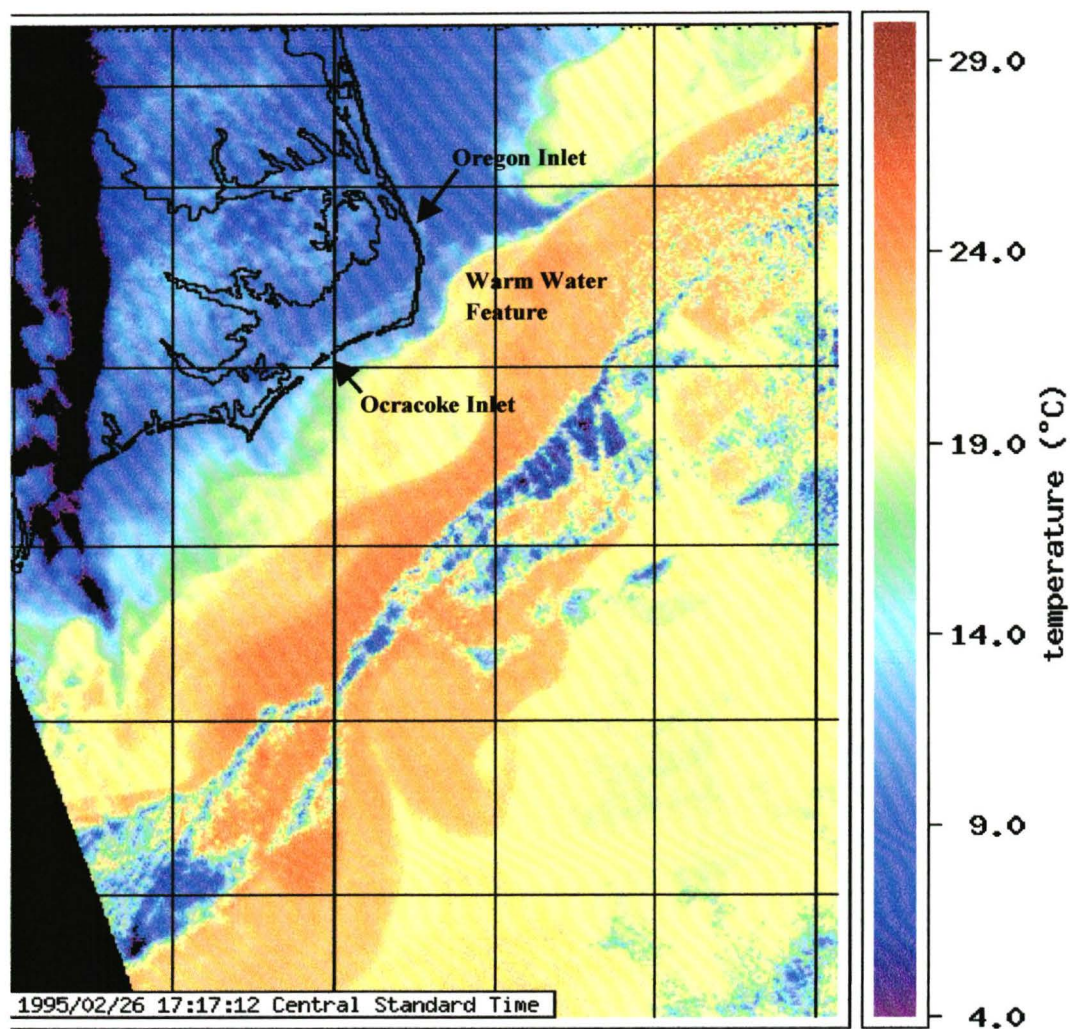


Plate IV. Warm water encroaches north of Cape Hatteras on February 26, 1995 (5:17 pm). This warm water feature may have enhanced transport and recruitment of the 871 spot larvae collected on February 28, 1995.

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APPENDIX

INCOMPLETE HISTORY OF SEA SURFACE TEMPERATURES FROM JANUARY 4, 1994 – MARCH 2, 1995

January 4, 1995. Water temperatures are warmer closer to Oregon Inlet (20-23°C) compared to Ocracoke Inlet (16-18°C).

January 5, 1995. Water temperatures at both inlets are cold (10°C). However, there is a warmer water filament (16-18°C) close to Oregon Inlet.

January 10, 1995. Warm water temperatures (20-23°C) are found close to Ocracoke Inlet. A much smaller filament of the same temperature is found encroaching Oregon Inlet.

January 22, 1995. Water temperatures are warmer north of Cape Hatteras and closer to Oregon Inlet (24-26°C). Water temperatures outside Ocracoke Inlet are 16-18°C.

January 25, 1995. Water temperatures have cooled north of Cape Hatteras near Oregon Inlet (10-12°C) but remain warmer to the south near Ocracoke Inlet.

January 26, 1995. Satellite imagery shows little change in sea surface temperatures outside Oregon and Ocracoke Inlets from the previous day.

January 27, 1995. Water temperatures north of Cape Hatteras remain cold (10-12°C) while water temperatures to the south remain slightly warmer (12-15°C).

January 31, 1995. Water temperatures at both inlets are the coldest to date (7-9°C).

February 1, 1995. Warmer water temperatures begin encroaching north of Cape Hatteras (20-23°C) close to Oregon Inlet. Water temperatures near Ocracoke Inlet remain cold (9-12°C).

February 2, 1995. Water temperatures north of Cape Hatteras continue warming (26-29°C), while water temperatures to the south near Ocracoke Inlet remain cold (9-12°C).

February 3, 1995. Water temperatures north of Cape Hatteras near Oregon Inlet have cooled to 16-18°C. For the third consecutive day, water temperatures south of Cape Hatteras near Ocracoke Inlet are cold (9-12°C).

February 5, 1995. Water temperatures near Oregon Inlet have drastically declined (7-9°C). A filament of warmer water temperatures (16-18°C) extends close to Ocracoke Inlet.

February 6, 1995. Water temperatures north of Cape Hatteras remain cold (7-9°C) while the warmer water filament to the south begins to dissipate.

February 7, 1995. Water temperatures are cool north and south of Cape Hatteras. To the south there is a small filament of warmer water (16-18°C) near Ocracoke Inlet.

February 9, 1995. Water temperatures north and south of Cape Hatteras are cold (9-12°C).

February 12, 1995. Water temperatures remain cold north and south of Cape Hatteras. However, there is evidence of a small filament of warm water (16-18°C) near Oregon Inlet.

February 13, 1995. The warm water filament north of Cape Hatteras is more developed and defined. Water temperatures south of Cape Hatteras remain cold (9-12°C).

February 21-23, 1995. Water temperatures north and south of Cape Hatteras have fallen to the coldest temperatures since January 31, 1995.

February 24, 1995. Although water temperatures remain cold, there is a small filament of warmer water (16-18°C) near Oregon Inlet.

February 25, 1995. The filament of warmer water located north of Cape Hatteras has cooled slightly (16-18°C) while the water outside Ocracoke Inlet remains cold (7-9°C).

February 26, 1995. Water has warmed substantially north and south of Cape Hatteras. To the north of Cape Hatteras is an obvious “bump” of warm water which extends eastward and close to Oregon Inlet.

March 2, 1995. Water temperatures have once again become cold both north and south of Cape Hatteras.

VITA

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EDUCATION

August 1995 – December 2000, MS in biology; Old Dominion University, Virginia
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PRESENTATIONS

Wasaff, T.R., C.M.Jones, and W.F. Hettler. 1999. Observations on the transport of larval spot, *Leiostomus xanthurus*, using biological and physical data. p. 171. *Presented at the 129th Annual Meeting of the American Fisheries Society*. August 29- September 2, 1999, Charlotte, North Carolina.

Wasaff, T.R., and C.M. Jones. 1999. Comparing age and growth of larval spot (*Leiostomus xanthurus*): implications on shoreward transport and population structure. *Presented at the 77th Annual Virginia Academy of Sciences, Biology Section*. May 26-28, 1999, Old Dominion University.

Wasaff, T.R., C.M. Jones, K.E. Carpenter, and W.F. Hettler. 1998. Age and growth of larval spot ingressing Ocracoke and Oregon Inlets, North Carolina. p.15. *Presented at the 22nd Annual American Fisheries Society, Early Life History Section, Larval Fish Conference*. July 9-12, 1998, University of Michigan.

CERTIFICATIONS

PADI certified open water SCUBA diver
Certified by the United States Power Squadrons for completion of their boating course

PROFESSIONAL SOCIETIES

Virginia Academy of Sciences
American Fisheries Society