FURTHER SUPPORT FOR THE HYPOTHESIS THAT INTERNAL WAVES CAN CAUSE SHOREWARD TRANSPORT OF LARVAL INVERTEBRATES AND FISH

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ABSTRACT

In areas of mesotides (tidal range 2 to 4 m) and narrow continental shelves (<30 km) internal waves can transport (i.e., convey from one place to another) the larvae of coastal organisms shoreward. Research reported here was in an area of microtides (tidal range <2 m) and a wide continental shelf (>80 km), the South Atlantic Bight. Half of the sampled sets of internal waves were aligned parallel to shore and probably originated at the shelf break. The higher densities of larvae and flotsam in the slicks over these internal waves (convergence zones) than in the rippled water between slicks (divergence zones) indicates that these waves were transporting larvae and flotsam shoreward. All nontransporting internal waves were aligned at a sharp angle to shore and may have formed over shoals oriented perpendicular to shore.

To further test the hypothesis that internal waves can transport larvae, surface plankton were collected from the waters over, in front, and behind a set of internal waves. The density of *Portunus* spp. megalopae was significantly higher in waters in front of the set than behind. The average densities of a variety of larval fish and invertebrates were significantly higher over the internal waves than in front of the set of waves. These data indicate that internal waves can cause shoreward transport of larvae and flotsam. Precompetent larval fish were not carried shoreward by this set of waves while competent stages (i.e., juvenile through postflexion) were transported shoreward.

Recent papers have suggested that the planktonic larvae of some coastal invertebrates and fish (Shanks 1983, 1985, 1986; Jillett and Zeldis 1985; Kingsford and Choat 1986; Shanks and Wright 1987) as well as flotsam (e.g., an oil spill, Shanks 1987) can be transported (i.e., conveyed from one place to another) by internal waves. As the tide ebbs off the continental shelf or across some other sharp change in the bottom relief (i.e., a reef or bank) a lee wave is formed (Lee and Beardsley 1974; Gargett 1976; Maxworthy 1979). When the tide changes to flood this lee wave is "released" and propagates away from its point of origin (see for example Chereskin 1983). Most of the waves formed at the continental shelf break propagate shoreward. As the original internal wave moves onshore it evolves from a solitary wave into a set of waves (Osborne and Burch 1980). Stripes of glassy water, slicks, are surface manifestations of currents over the internal waves, and they delineate zones of converging and downwelling currents situated between the crest and the trough of an internal wave (Ewing 1950; LaFond 1959). The currents over the internal waves generate slicks by both perturbing small surface waves and concentrating the organic surface film (Ewing 1950; Gargett 1976). Buoyant flotsam will be carried into the convergence zone by the surface currents, but because of the particle's buoyancy they will not follow the water as it is downwelled; the flotsam will be trapped at the surface in the convergence and as the convergence zone moves onshore so will the flotsam. The proposed mechanism of larval transport suggests that any organism which can remain at the surface in the convergence zone either by swimming or other behaviors (Shanks 1985) will, like flotsam, remain in the slick and be transported onshore (Shanks 1983).

The conditions necessary for the production of tidally generated internal waves (tides, sharp bottom relief, and some water column density stratification) are present in the waters adjacent to nearly all land masses, and the surface manifestations of internal waves have been observed from both ships and satellites in numerous locations (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Evidence that internal waves may be capable of transporting planktonic larvae onshore has been collected in the Pacific Ocean off Southern California (Shanks 1983, 1985, 1986), in the San Juan Archipelago (Shanks and Wright 1987), and in the waters off the North

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and South Islands of New Zealand (Zeldis and Jillett 1982; Jillett and Zeldis 1985; Kingsford and Choat 1986). These areas are characterized by mesotides, i.e., tidal range 2 to 4 m (Davis 1964). The first purpose of the research reported in this paper was to test if transport occurred in the Atlantic Ocean and in an area of microtides (tidal range <2 m, Davis 1964), the South Atlantic Bight.

To date researchers have compared the density (no./m^2) of larvae in the convergence zones (slicks) over internal waves to the density present in the divergence zone (ripples). Cases where the densities of larvae were significantly higher in slicks than the ripples were used as evidence for the proposed hypothesis. Higher density in the convergence implies that larvae tend to spend more time in the slick than in the water between slicks. Because of the speed at which internal waves are propagating, even a brief residence in an internal-wave-slick could cause appreciable shoreward transport. For example, if a larvae spent an hour in a slick it could be carried about 2 km (assuming an average internal wave speed of 56 cm/s, Sawyer 1983).

Higher larval densities in the convergence zone is only one of several predictions which should be true if internal waves are transporting larvae shoreward. The second purpose of this research was to test several additional predictions. As an internal wave moves shoreward, larvae from in front of the wave will be swept by the currents associated with the wave into the convergence zone. If these larvae can remain at the surface in the convergence, they will be carried shoreward. Predictions include 1) larval density in the waters in front of the set of internal waves should be significantly higher than in the waters behind the set; 2) because larvae will accumulate in the convergence, the observed density of larvae over an internal wave will be significantly higher than the density in the waters in front of the set of internal waves; and 3) a rare larval type may be carried into an area from a distant source in which case these particular larvae may only be present in the waters over the internal wave and will be concentrated in the slicks. To test these predictions, replicate neuston net samples were collected in the convergence and divergence zones over a set of internal waves, and in the waters immediately in front and behind this set of internal waves.

METHODS

The study was confined to the ocean waters at the northern end of Onslow Bay within about 20 km of Beaufort Inlet, NC, U.S.A. (long. 34°40′W, lat. 76°40′N; Fig. 1). Surface plankton tows from the waters over internal waves were collected during the summer of 1985 on 4 and 24 June, 14 and 20 July, and 21 August. On 24 June 1985 surface plankton tows were also collected from immediately in front and behind a set of internal waves. On 14 June 1985 and 9 and 19 June 1986 samples were collected at the surface and in the water column to determine which taxa were exclusively neustonic in distribution.

Winds stronger than 10 to 15 knots obliterate the slicks, which delineate the convergence zones over internal waves. Searches for internal-wave-slicks and sampling of the associated plankton were limited to periods with winds less than a moderate breeze (Beaufort scale 4). The procedure for locating internal-wave-slicks was to proceed along shore until the estuarine front associated with Beaufort Inlet was crossed and thence perpendicular to shore until we found a set consisting of at least three large (at least 30 m wide by about 500 m long) linear slicks separated by one to several hundred meters of rippled water. Sets of large slicks separated by rippled water are a unique surface signature of large, usually tidally generated internal waves (Ewing 1950; LaFond 1959; Apel et al. 1975; Gargett 1976; Fu and Holt 1982; Chereskin 1983; Sawyer 1983).

To test if a set of internal waves was capable of transporting flotsam, surface drifters (weighted Styrofoam cups) were released in a line perpendicular to and in front of the set of internal-wave-slicks (Shanks 1983). Prior to the release of the surface drifters and immediately after all sampling was completed the position of the first slick in the set was determined by either compass bearings on landmarks or with loran. From these measurements we were able to determine the distance that the set of waves propagated during the period of observation.

While the currents acted on these surface drifters, 3 or 4 replicate 5- to 10-min surface (<20 cm depth) plankton tows were made in the slicks and rippled water between slicks. These 1985 samples were collected on 4 and 24 June, 14 and 20 July, and 21 August 1985. In addition, on 24 June 1985 replicate surface plankton samples were also collected from the water immediately in front and behind the set of internal waves (within 200 m of the internal wave set). Plankton samples were collected using a manta net (Brown and Cheng 1981) with a mouth opening of 0.95 × 0.26 m and a net mesh of 0.333 mm. A flow meter mounted in the mouth of the net measured the volume of water filtered. Between tows

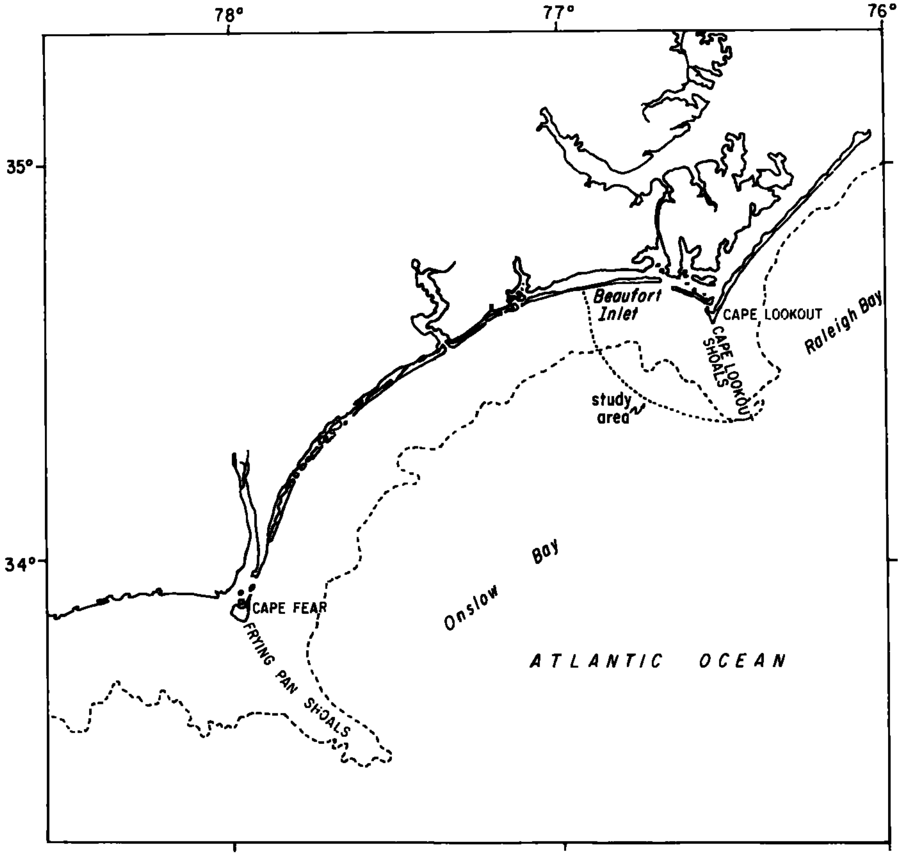

FIGURE 1.—Map of the study area. The dashed line running along shore is the 20 m contour and the dashed line running from just to the left of Beaufort Inlet to the tip of Cape Lookout Shoals encloses the study area.

in the different habitats the manta net was cleaned by towing for 5 to 10 minutes with the cod end removed. Most of the plankton was washed from the net by this procedure. For convenience and in order to more accurately sample the relatively small environments studied these plankton tows were made from a 6 m motor boat. Plankton samples were preserved in 5% formalin.

To assess the vertical distribution of larval types, surface and oblique plankton tows were made on 14 June 1985 and 9 June 1986. On 19 June 1986 replicate (n = 3) surface, oblique, and bottom tows were made. The dimensions of the oblique and bottom sled nets were 0.55 × 0.55 m and 0.80 × 0.45 m respectively. Both nets had mesh of 0.333 mm, and flow meters on the nets were used to measure the volume of water filtered. The procedure for the oblique tows was as follows: with the boat moving slowly forward the net was lowered rapidly to near the bottom (about 10 to 20 m) and then, maintaining a wire angle of about 60°, the net was hauled slowly to the surface. The bottom tows were made by lowering the sled straight to the bottom with the boat stationary; as the boat moved slowly forward, the line was paid out until a scope of 1 to 3 was achieved; tows lasted 5 to 10 minutes; at the end of the tow the boat was backed down onto the net; and the net was pulled vertically back to the surface. Both the oblique and bottom nets were open when they passed through the surface and were thus contaminated by some surface plankton.

Organisms were sorted and identified with the aid of a dissecting microscope. A variety of sources were used to identify larval fish (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978; Fahay 1983). Larval fish were also sorted by developmental stage which were defined following the terminology and descriptions in Ahlstrom et al.

(1976) and Moser and Ahlstrom (1970). Megalopae were identified from references sited in Williams (1984). *Portunus* spp. and *Callinectes* spp. megalopae were separated using the characters suggested by Smyth (1980). Penaeids were identified using Cook (1966). No attempt was made to precisely identify the other groups of organisms counted.

Statistical comparisons of the density of larvae and flotsam in the different sampled habitats were made using Wilcoxon's two-sample test (Sokal and Rohlf 1969). Densities were considered to be significantly different when $P \leqslant 0.05$.

RESULTS

During the summer of 1985 searches for internal-wave-slicks were made on eight occasions. On three days, despite favorable wind and sea conditions, no internal-wave-slicks were observed. On 4 and 24 June, the observed sets of slicks were oriented parallel to shore and the bottom topography while on 14 and 20 July sets were oriented nearly perpendicular to shore. On 21 August a set of slicks aligned nearly perpendicular to shore was observed about 5 km offshore, and at about 9 km offshore a second set of slicks was found oriented parallel to the bottom topography. Both types of slicks, perpendicular and parallel orientation, possessed all of the usual characteristics of internal waves. Slicks were about 30 to 50 m wide, they were separated by one to several hundred meters of rippled water, and the sets moved (the parallel-to-shore slicks moved onshore while the perpendicular-to-shore slicks moved north).

The surface drifters released in front of sets of slicks oriented parallel to shore on 4 June and 21 August could not be located following the plankton tows. On 24 June, all of the drifters located at the end of the plankton tows (48 of 50 released) were found in the first two slicks of the set of internal waves. The drifters, which had been released in a 250 m long line in front of the set of internal waves, had been caught, concentrated, and carried about 4 km shoreward by the internal waves. Clearly this set of internal waves was capable of carrying buoyant flotsam shoreward.

Sargassum floats were abundant in the plankton tows. The floats are buoyant, do not extend above the water (i.e., are not blown directly by the wind), and, hence, the floats should act much like the released surface drifters. On all three dates when the internal-wave-slicks were oriented parallel to shore, the density of Sargassum floats was significantly higher (14- to 300-fold higher; Tables 1, 2) in the convergence than divergence zones. These data indicate that not only was the set of internal waves sampled on 24 June capable of carrying flotsam shoreward, but the sets oriented parallel to shore on 4 June and 21 August were also capable of carrying buoyant flotsam shoreward.

In contrast, on those days when the slicks were oriented roughly perpendicular to shore (14 July, 20 July, and 21 August, Table 1) released surface drifters were about equally distributed between slick and rippled water and, despite the fact that the slicks moved northward during the observation period, the drifters were not carried along with the waves. The density of Sargassum floats was not significantly higher in the slicks than the rippled water between the slicks. These data suggest that these internal waves were not transporting flotsam.

Before larval densities can be interpreted, it is first necessary to determine which larval types are found exclusively in the neuston. An increase in the neustonic density of organisms, which inhabit both the neuston and the water column, could be due to forces concentrating just the neustonic portion of the population, or it could be due to animals from the water column augmenting the population in the neuston. Given the sampling regime of this study it was impossible to differentiate between these two possibilities. Because of this limitation a series of tows were made in the neuston, the water column, and bottom water to determine which organisms exclusively inhabited the neuston.

There was a distinct assemblage of megalopae and larval fish that were caught in the oblique water column and bottom plankton tows but were nearly absent from the neuston tows (Table 3). Unfortunately, organisms that were common in the neuston tows made over or around internal waves were abundant on only one of the three dates when the vertical distribution samples were collected. On this one date (19 June 1986, Table 3) there was a group of larval fish and crabs that were only present in the neuston tows. This latter group included the megalopae of *Portunus* spp. and *Callinectes* spp., juvenile *Monacanthus hispidus*, and juvenile and larval *Hyporhamphus unifasciatus* and *Sphoeroides maculatus*. Previous research also suggests that these larvae and postlarvae as well as others are inhabitants of the surface waters. Both the behavior (Sulkin andVan Heukelem 1981) and the vertical distribution (Smyth 1980; Johnson 1985a) of *Callinectes* spp. megalopae suggest that they are usually neustonic. The megalopae of *Portunus* spp. and

TABLE 1—The density of larval fish and invertebrates (mean no./100 m^2 ± SE) in the slicks (convergence zones) and ripples (divergence zones) over internal waves and the relative concentration of these organisms in the slicks (i.e., the ratio of slicks/ripples) over internal waves oriented parallel (data in upper section of table) and perpendicular (data in lower section of table) to shore.

	Dates when slicks were oriented parallel to shore[1]					
	4 June 1985			21 August 1985		
	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]
Total fish	12 ± 2.9	4.2 ± 0.9	3*	1.7 ± 0.9	0.8 ± 0.3	2
Hypsoblennius hentzi	6.0 ± 2.1	3.1 ± 0.2	2	0.1 ± 0.1	0.4 ± 0.1	0.3
Membras martinica	1.7 ± 1.1	0.3 ± 0.1	5	0	0	—
Hyporhamphus unifasciatus	0.7 ± 0.7	0.6 ± 0.4	1	0	0	—
Brevootia tyrannus	1.6–0.8	0	—	0	0	—
Monacanthus hispidus	0.9 ± 0.6	0	—	0.8 ± 0.6	0	—
Cheilopogen heterurus	0	0	—	0.2 ± 0.1	0	—
Miscellaneous	1.1 ± 0.3	0.3 ± 0.2	4	0.4 ± 0.4	0.2 ± 0.1	2
Total Brachyura	41 ± 12	1.7 ± 0.6	24*	12 ± 3.9	0.5 ± 0.4	22*
Callinectes spp.						
Megalopa	0.2 ± 0.2	0	—	3.9 ± 1.7	0.2 ± 0.1	19*
First crab	1.5 ± 0.6	0	—*	0.2 ± 0.2	0	—
Portunus spp.						
Megalopa	36 ± 11	1.6 ± 0.8	23*	7.5 ± 21	0.3 ± 0.3	24*
First crab	1.2 ± 0.6	0	—	0	0	—
Miscellaneous	2.0 ± 1.1	0.1 ± 0.1	15*	0.3 ± 0.2	0	—
Amphipods	40 ± 16	1.2 ± 0.1	33*	2.2 ± 1.5	0	—
Polychaete larvae	5.2 ± 1.7	0.7 ± 0.5	8*	0	0	—
Stomatopod larvae	0	0	—	32 ± 8.8	8.1 ± 2.6	4*
Cnidaria	0	0	—	9.9 ± 2.9	18 ± 6.2	1
Salpa	0	0	—	15 ± 2.6	60 ± 2.9	0.3*
Sargassum floats	11 ± 6.8	0.8 ± 0.6	14*	8.8 ± 1.4	0.4 ± 0.3	21*

	Dates when slicks were oriented perpendicular to shore								
	14 July 1985			20 July 1985			21 August 1985		
	Slicks .$n = 3$	Ripples $n = 3$	Slicks ripples[2]	Slicks/ $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]	Slicks $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]
Total fish	2.6 ± 0.4	0.9 ± 0.5	3*	1.2 ± 0.3	1.0 ± 0.2	1	1.1 ± 0.1	1.8 ± 1.0	1
Hypsoblennius hentzi	0	0	—	0.6 ± 0.2	0.8 ± 0.1	1	0.3 ± 0.2	1.5 ± 0.9	0.2
Hyporhamphus unifasciatus	0.5 ± 0.3	0	—	0.4 ± 0.2	0	—	0	0	—
Monacanthus hispidus	0	0.2 ± 0.2	0	0	0	—	0.3 ± 0.2	0.2 ± 0.2	2
Cheilopogen heterurus	1.0 ± 0.4	0	—	0	0	—	0.2 ± 0.2	0	—
Miscellaneous	1.2 ± 0.4	0.4 ± 0.4	2	0.1 ± 0.1	0.2 ± 0.8	1	0.4 ± 0.3	0.2 ± 0.2	3
Total Brachyura	3.6 ± 1.3	5.2 ± 0.9	1	0.9 ± 0.3	0.3 ± 0.3	3	1.6 ± 0.5	0.6 ± 0.4	3
Callinectes spp.									
Megalopa	0.4 ± 0.3	0.6 ± 0.6	1	0.4 ± 0.2	0	—	0.2 ± 0.2	0	—
Portunus spp.									
Megalopa	0.9 ± 0.6	2.2 ± 0.6	0.4	0.2 ± 0.2	0.2 ± 0.2	3	0.1 ± 0.1	0.3 ± 0.3	0.5
Miscellaneous	1.8 ± 0.7	2.2 ± 0.1	1	0.1 ± 0.1	0.2 ± 0.2	1	1.4 ± 0.5	0.3 ± 0.2	5
Amphipods	5.7 ± 3.9	2.9 ± 0.6	2	4.4 ± 0.7	1.7 ± 0.8	3	0	0	—
Polychaete larvae	18 ± 7.3	8.1 ± 5.2	2	0	0	—	2.6 ± 1.3	0.3 ± 0.2	8
Stomatopod larvae	0	0	—	0	0	—	9.9 – 1.5	9.1 ± 2.6	1
Cnidaria	83 ± 15	126 ± 73	1	0	0	—	7.8 ± 1.2	4.9 ± 1.7	2
Salpa	91 ± 36	103 ± 78	1	0	0	—	239 ± 35	130 ± 38	2
Sargassum floats	22 ± 16	3.6 ± 1.7	6	0.4 ± 0.1	0.1 ± 0.1	5	5.2 ± 2.4	1.1 ± 0.3	5

[1] Also included in this category are the data from 24 June (Tables 2 and 4).

[2] The ratio of the abundance in the slick divided by the abundance in the rippled water. * = $P < 0.5$ Wilcoxon's two-sample test (Sokal and Rohlf 1969).

Ocypoda spp. are abundant in neuston net tows (Smyth 1980; Johnson 1985a). Juvenile filefish, *Monacanthus hispidus*, are abundant in neuston tows (Fahay 1975; Eldridge et al. 1977) and are commonly found associated with floating seaweeds (Dooley 1972). Larval *Hyporhamphus unifasciatus* and *Hypsoblennius hentz* are abundant in surface plankton tows (Fahay 1975; Eldridge et al. 1977; Fritzsche 1978). Both their behavior (Breder and Clark 1947) and abundance in neuston tows (Eldridge et al. 1977) suggest that larval *Sphoeroides maculatus* are also residents of the surface waters. These results suggest that there is an assemblage of larvae unique to the neuston and that tests of the internal-wave-mediated larval transport hypothesis outlined in the introduction can be made.

The distribution of organisms followed a pattern similar to that of Sargassum floats (Tables 1, 2, 4). In the tows from internal waves oriented perpendicular to shore there was only one instance in which the density of an organism was significantly higher in the convergence than the divergence zone (total larval fish, 14 July 1985, Table 1) indicating that these internal waves were not transporting larvae.

TABLE 2.—The density (mean no./100 m^2 ± SE) of invertebrates and Sargassum floats in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test.

	Density Mean no./100 m^2 ± SE, n = 3					Significance[1]		
Species	In front	Internal wave[2]	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Total Brachyura	1.1±0.2	6.5±1.3	21±5.7	2.5±0.2	0.2±0.2	*	*	*
Portunus spp.								
Megalopa	0.3±0	3.8±0.9	14±4.2	0.8±0.2	0	*	*	*
First crab	0	1.2±0.7	4.7±2.5	0.1±0.1	0		*	*
Callinectes spp.								
Megalopa	0.2±0.2	0.2±0.1	0.9±0.2	0	0.1±0.1		*	
Miscellaneous								
Megalopa	0.6±0.3	1.7±0.3	1.8±0.7	1.7±0.2	0.1±0.1			
Amphipods	30±8.1	176±112	754±546	0.3±0.3	20±6.5		*	
Polychaete larvae	2.9±1.1	16±3.0	62±8.6	2.5±1.3	1.8±0.6		*	*
Penaeus spp.								
Postlarvae	1.8±1.3	34±6.5	94±6.5	16±4.4	0.4±0.4		*	*
Sargassum floats	0.9±0.1	42±29	182±122	0.6±0.3	0	*	*	*

[1] Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P \leq 0.05$.

[2] Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = $[(\text{slick no./m}^2 \times 30\ \text{m}^2) + (\text{ripples no./m}^2 \times 100\ \text{m}^2)/130\ \text{m}^2] \times 100$.

TABLE 3.—Comparison of the density of various types of megalopae and larval fish caught in neuston, oblique, and bottom plankton tows.

	Density, no./100 m^2						
	14 June 1985		9 June 1986		19 June 1986 Mean ± SE, n = 3		
Species	Neuston	Oblique	Neuston	Oblique	Neuston	Oblique	Bottom
Crab megalopa							
Portunus spp.	0	0	0	0	5.3±4.5	0	0
Callinectes spp.	0	0	0	0	3.1±2.4	0	0
Ocypoda quadrata	0	9.0	0	0	1.5±1.4	0	0
Pinnotheridae	0.4	9.0	0	9.0	0.1±0.1	310±160	18.7±9.2
Xanthidae	0	88.8	0	9.0	0	690±250	17.0±9.6
Cancer spp.	0	0	0	0	0	66.7±40.6	1.4±0.8
Unknown and misc.	2.0	239	0.2	90.0	1.3±0.8	194±89.2	11.4±3.6
Fish larvae							
Monacanthus hispidus[1]	0	0	1.1	0	0.1±0.1	0	0
Hyporhamphus unifasciatus[1]	0	0	0	0	0.3±0.2	0	0
Sphoeroides maculatus	0	0	0	0	0.3±0.1	0	0
Membras martinica	0.4	0	0	0	0	0	0
Hypsoblennius hentzi	0	0	0	0	0.3±0.3	6.0±6.0	0
Symphurus plagiusa	0	44.4	0	27.0	0	190±60	0.1±0.1
Prionotus evolans	0	18.0	0	136	0	510±210	15.1±6.0
Seriola spp.	0	0	0	27.0	0	46.0±17.8	0.3±0.3
Engraulidae	0	18.0	0	217	0	280±99	16.2±8.9
Unknown and misc.	0	9.0	2.2	63.0	0	150±110	3.9±3.0

[1] Juvenile or late postflexion stages only.

TABLE 4.—The density (mean no./100 m^2 ± SE) of larval fish in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test. J = Juvenile, LPF = Late Post Flexion, EPF = Early Post Flexion, F = Flexion, PF = Preflexion, and Total = Sum of all stages.

	Density Mean no./100 m^2 ± SE, $n = 3$					Significance[1]		
Species	In front	Internal wave	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Monacanthus hispidus	1.1±0.1	2.0±0.4	8.1±9.0	0.2±0.2	0.1±0.1		*	*
Hyporhamphus unifasciatus								
J	0	0.1±0.1	0.2±0.9	0	0			
LPF	0.1±0.1	0.9±0.5	4.2±2.3	0	0			*
EPF	0	0.5±0.2	1.8±0.6	0	0		*	*
F	0	0.1±0.1	0.2±0.2	0	0		*	
PF	0	—	0	0	0			
Total	0.1±0.1	1.5±0.6	6.5±2.6	0	0		*	*
Membras martinica								
J	0	0.1±0.1	0.4±0.4	0	0			
LPF	0	—	0	0	0			
EPF	0	—	0	0	0			
F	0	0.1±0.1	0.5±0.3	0	0			
PF	0.2±0.1	0.2±0.1	14±4.2	0.4±0.4	1.0±0.6		*	*
Total	0.2±0.1	0.2±0.1	15±44	0.4±0.4	1.0±0.6		*	*
Hypsoblennius hentzi								
J	0	0.2±0.2	0.8±0.8	0	0			
LPF	0	0.2±0.1	0.5±0.3	0	0		*	
EPF	0	0.2±0.0	0.7±0.1	0	0		*	*
F	0.3±0.9	0.2±0.1	0.9±0.4	0	0		*	
PF	14±2.4	4.5±1.8	16±6.0	0.9±0.5	2.6±0.2	*	*	
Total	14±2.0	5.2±1.6	19±5.5	0.9±0.5	2.6±0.2	*	*	
Brevootia tyrannus								
F	0.2±0.1	0.1±0.1	0.5±0.3	0	0.2±0.2			
PF	0.7±0.2	0.2±0.1	0.6±0.3	0	0.1±0.1			
Total	0.9±0.3	0.2±0.0	1.1±0.1	0	0.4±0.4			
Miscellaneous								
J	0	0.5±0.2	1.8±0.9	0	0		*	*
LPF	0	0.2±0.1	0.8±0.9	0	0.1±0.1		*	*
EPF	0	—	0	0	0			
F	0.1±0.1	0.1±0.1	0.4±0.4	0	0			
PF	0	0.1±0.1	0.4±0.4	0	0			
Total	0.1±0.1	0.8±0.2	3.4±1.0	0	0.1±0.1		*	*
Grand total	16±1.6	13±1.0	53±3.6	1.6±0.2	4.2±0.4	*	*	

[1] Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P < 0.05$.

[2] Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = [(slick no./m^2 × 30 m^2) + (ripples no./m^2 × 100 m^2)/130 m^2] × 100.

In contrast, in tows from internal waves oriented parallel to shore there were numerous instances in which larval densities were significantly higher in the slicks (Tables 1, 2, 4); the densities observed in the slicks were 4- to >50-fold higher than those in the rippled waters. These data demonstrate that a variety of larval and postlarval invertebrates and fish were transported shoreward by these internal waves.

On 24 June 1985, surface plankton samples were collected in the first two slicks over a set of internal waves oriented parallel to the shore, in the rippled water between these slicks, and in front and behind the entire set of internal waves. Ninety-six percent of the surface drifters were caught by the first two convergence zones and carried shoreward about 4 km. The density of Sargassum floats was highest in the slicks (>100-fold, Table 2) and they were at significantly lower densities behind the set of internal waves than in front. There were 0.9 Sargassum floats/100 m^2 in the waters in front of the set of internal waves and none in the waters behind the waves (Table 2). The distribution of tar balls (spilled asphalt) over and around the internal waves was similar to the distribution of Sargassum floats (Shanks 1987). As these internal waves propagated shoreward, the currents over the waves swept buoyant flotsam from the waters in front of the set of waves into the convergence zone where the flotsam was caught and carried shoreward.

Calculation of the density of larvae or flotsam over the internal waves (i.e., density in the slicks plus the ripples) requires knowledge of the width of the slick and rippled waters over the internal waves. Unfortunately, in this initial study these measurements were not made, necessitating that these widths be approximated using values from the literature. Slicks were assumed to be 30 m wide and the rippled waters separating the slicks were assumed to be 100 m wide. These values are consistent with my experience and with published values (LaFond 1959; Sawyer 1983). The observed density over one internal wave was calculated as (slick no./m^2 × 30 m) + (ripples no./m^2 × 100 m)/130 m^2. The density over an internal wave was compared with the density in an equal area of water in front of the set of internal waves. Making these calculations for Sargassum floats gives an observed density of 42 floats/100 m^2 over the internal wave vs. 0.9 floats/100 m^2 in front of the set; the density over the internal wave is significantly larger (46-fold greater) than the density in front of the set (Table 2). Again the data indicate that Sargassum floats were carried shoreward by the internal waves.

None of the types of larval fish characteristic of water column samples (Table 3) were caught in any neuston tow. Present in the neuston tows were only those types of larval and juvenile fish which my samples and the descriptions in the literature suggest are characteristically neustonic.

The densities of larval and juvenile fish frequently were significantly higher in the slick samples than the samples from the rippled waters between slicks (Table 4). On 24 June 1985, most larval fish, especially juvenile and postflexion stage larvae, were rare in both the waters in front and behind the set of internal waves. On this date in 6 tows, 3 in front and 3 behind the set of internal waves, only 4 juvenile and postflexion larvae were caught as compared to 185 in the 3 tows made in the slicks. Probably because of the rarity of larval fish in both in front and behind tows there were only three cases, total and preflexion *Hypsoblennius hentz* and total larval fish, in which the density of fish in front of the set of internal waves was significantly higher than behind the set (Table 4). There are seven instances, however, in which the density over the internal wave of a larval or juvenile fish was significantly and at least 10-fold higher than the density in front of the set of internal waves (Table 4). In six of these instances the fishes were at the juvenile, late postflexion, or early postflexion stages of development.

Larval and juvenile fish were grouped by stage of development and the densities over and in front of the internal waves were calculated for each developmental stage (Fig. 2). The densities over the internal waves of the juvenile, late postflexion, and early postflexion developmental stages were significantly higher than the densities of these stages in front of the set. There was not a significant difference between the densities over and in front of the set of internal waves of flexion stage larvae and preflexion larvae were significantly more abundant in front of the set. These data suggest that internal

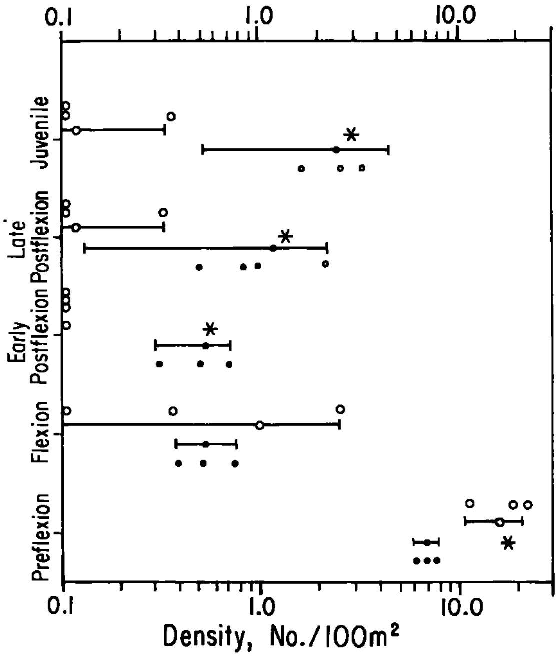

FIGURE 2.—Densities of larval fish by stage of development caught on 24 June 1985 in the waters in front of the set of internal waves (open circles) and over the internal waves (closed circles). Data are presented as the mean ±95% confidence interval with the points above or below this line being the actual observations. Asterisks indicate cases where the in front density was significantly different (Wilcoxon's two-sample test, $P \leq 0.05$) from the density over the internal waves. The method of calculating the densities is described in the text.

waves are capable of carrying fish larvae shoreward, but shoreward transport seems to be confined to postflexion stage larval or juvenile fish.

In the samples from 24 June 1985 there are a number of cases in which a fish species and/or stage of development was common in the tows from the convergence zones but was absent or very rare in the divergence zones, in front, or behind the set of waves (i.e., zero or one caught in the nine tows from these three habitats, Table 4). Either these larval fish are extremely rare in the waters surrounding the internal waves in which case the convergence zone must have accumulated larvae from a large volume of water or the internal waves transported the larvae into the study area from a distant source.

On 24 June 1985, the density of total Brachyura was significantly higher in the slicks over the internal waves than in any other area sampled (Table 2). *Portunus* spp., a group which previous data had demonstrated inhabited the neuston, made up the bulk of the Brachyura caught. The densities of *Portunus* were significantly higher in the slicks than the rippled water between slicks. The density of *Portunus* spp. megalopae differed significantly from 0.3/100 m^2 in front of the set of internal waves to 0/100 m^2 behind (Table 2). *Portunus* spp. first crabs were absent from both the waters in front and behind the set of internal waves; they were abundant in the waters over the internal wave (Table 2). The densities over the internal waves of *Portunus* spp. megalopae and first crabs were significantly higher than their densities in front of the set of waves (Table 2). *Callinectes* spp. were uncommon in the samples though their density was significantly higher in the slick than in the rippled waters. Included under the category of miscellaneous megalopae were the species *Uca* spp., *Sesarma* spp., and majid crabs, all forms which were found to be more abundant in the water column than in the neuston (Table 2). There was not a significant difference between their density in the slicks vs. the rippled waters, suggesting that these megalopae were not carried shoreward by the sampled set of internal waves. The data indicate that definitely *Portunus* spp. and possibly *Callinectes* spp. were carried onshore by the sampled set of internal waves.

Other organisms counted in the samples were adult amphipods, polychaete larvae, and *Penaeus* spp. postlarvae. Densities of these types of organisms were significantly higher in the slicks than the rippled waters (Table 2). While in each instance densities were lower behind the set of internal waves than in front, the differences were not statistically significant. The density of polychaete larvae and *Penaeus* spp. postlarvae over the internal waves were significantly higher than the density in front of the set. These data suggest that these invertebrate larvae were also transported onshore by the set of internal waves.

DISCUSSION

Tidally generated internal waves have been observed in many areas of the world (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Larvae may utilize internal waves as a mechanism of onshore migration along many coastlines. Testing this hypothesis would require the impossible task of making observations along all coastlines. An alternate technique is to test for internal wave transport in areas with different combinations of tidal range and shelf width. Previous work has been done in areas of mesotides (tidal range 2 to 4 m, Davis 1964) and either narrow (<6 km, Shanks 1983) or moderate (about 30 km, Kingsford and Choat 1986) shelf widths. The Atlantic adjacent to the Beaufort Inlet is characterized by microtides (tidal range <2 m, Davis 1964) and a wide shelf (about 80 km). The first purpose of this research was to test if onshore transport of larvae could occur in an area with these characteristics. On the three dates in which the internal-wave-slicks were oriented roughly parallel to shore the data suggest that internal waves were transporting larvae and flotsam onshore. If the waters around the Beaufort Inlet are representative of localities with microtides and wide shelves, then onshore migration of larvae via internal waves may occur in other similar areas of the world.

On three dates the internal-wave-slicks were oriented nearly perpendicular to shore and were propagating roughly northward. Over the continental shelf, internal waves oriented roughly perpendicular to shore have been observed in satellite photographs. These internal waves are invariably associated with submarine canyons (Apel et al. 1976). There are no submarine canyons in Onslow Bay. The internal waves causing these slicks may have been formed over Frying Pan Shoals (Fig. 1). These shoals extend about 50 km across the shelf from the end of Cape Fear and form the southern boundary of Onslow Bay. Just north of the study area, Cape Lookout and the Cape Lookout Shoals also extend out across the shelf (Fig. 1). On a flight over Cape Lookout numerous slicks oriented parallel to Cape Lookout Shoals were observed propagating northward into Rayleigh Bay (pers. obs.). The geography and oceanography of the Cape Lookout and Frying Pan Shoals are so similar that by analogy the internal waves oriented perpendicular to shore observed during this study may have been formed over Frying Pan Shoals and propagated northward into Onslow Bay. The mechanism for the formation of these internal waves is unknown.

As was observed in a previous study (Shanks 1983), only some sets of internal waves transported larvae or flotsam. In this study only those slicks aligned parallel to shore caused transport. It is not clear why some sets of waves cause transport while others do not. The physical characteristics of tidally generated internal waves are quite variable. The amplitude (Cairns 1968) and decay distance of internal waves varies over the fortnightly tidal cycle (Brink 1988). Further, the depth, wave length, and shape of the internal waves is dependent on the relative depths of the thermocline and the bottom and wave amplitude (LaFond 1959; Lee 1961; Cairns 1967, 1968). What is needed is simultaneous measurements of the physical characteristics of a set of internal waves much like those made by LaFond (1959) with measurements of the transport of flotsam or larvae.

The second purpose of this research was to test several new predictions derived from the hypothesis that internal waves can transport larvae. If transport was occurring, then one would predict that 1) due to the accumulation of larvae in the convergence zones as internal waves propagate shoreward, the density of larval types transported by the internal waves should be significantly lower behind than in front of the set, 2) the observed density of larvae over an internal wave should be significantly higher than in the waters in front of the set of waves, and 3) there may be types of larvae which are only present in the slicks, suggesting that they had been carried into the area from a distant source. The appropriate samples to test these three predictions were collected on 24 June 1985. The densities of several larval types were significantly higher in the waters in front of the internal wave set than behind. There were many instances in which the observed density over the internal waves of a type of larvae was significantly higher than in the waters in front of the set of internal waves. Lastly, there were a number of organisms that were only caught in the convergence zones over the internal waves. In this set of observations the three predictions were confirmed indicating that this set of internal waves was carrying larvae and flotsam shoreward.

The significant differences in larval densities observed on 24 June (i.e., in front vs. behind and over the internal waves vs. in the front of the set of waves) may have been due to fortuitous cross-shelf patchiness in larval density. Because conditions allowed only one opportunity to sample in front and behind a set of internal waves, this alternate explanation can not be rejected. Cross-shelf larval patchiness is, however, probably not an adequate explanation because of the very short distance over which large differences in larval abundances were observed. For example, the tows in front of the set and the tows in the slick and rippled water over the set were separated by at most 200 m, yet there were many cases (14, Tables 2, 4) where larval abundances were different by at least a factor of 10. Differences in plankton abundance of this magnitude and over this small a distance are almost always associated with oceanographic features (e.g., fronts: Boden 1952; Pingree et al. 1974; Owen 1981; Fogg et al. 1985). The only apparent oceanographic feature in the study area was the internal-wave-slicks. The observed differences in larval density were probably caused by the internal waves.

The data in Figure 2, the density of fish by stage of development over the internal waves vs. in front of the set of waves, suggest that only the later developmental stages of fish (juvenile through early postflexion) were transported onshore by the set of internal waves sampled on 24 June 1985. All five of the abundant fish species (Table 4) inhabit near shore or estuarine habitats as adults (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978). Flexion and preflexion larval fish are clearly not competent to adopt the adult or nursery habitat, and the data suggest that they were not carried onshore by the internal waves. There may be adaptive advantages to planktonic larvae avoiding estuarine waters during their development (Strathmann 1982). Juvenile fish and, perhaps, also postflexion larvae, are competent to recruit into the adult or nursery habitat. Transport onshore by internal waves may, therefore, be adaptively advantageous for those fish whose adult or nursery habitat is coastal or estuarine.

The larval development of the blue crab, *Callinectes sapidus*, occurs at sea (Smyth 1980; McConaugha et al. 1983; Johnson 1985b). The larvae are present in the waters over the continental shelf and out to the Gulf Stream (Smyth 1980). At the end of the larval period the megalopae must return to an estuarine habitat to continue its adult existence. How the megalopae make this migration is an open question (Johnson et al. 1984; Johnson

1985b). The behavior of the megalopae (Sulkin and Van Heukelem 1981) and their distribution in the plankton (Smyth 1980; Johnson 1985a) both suggest that these larvae are inhabitants of the neuston. Larvae that inhabit the neuston can be transported onshore by internal waves (Shanks 1985). On 4 and 24 June and 21 August the densities of *Callinectes* spp. megalopae and first crabs were significantly higher in the convergence zones over the internal waves than in the divergences, suggesting that *Callinectes* spp. were being transported onshore by the sampled internal waves. On 24 June, when *Callinectes* spp. were uncommon, there was not a significant difference in the density of *Callinectes* spp. in front vs. behind the internal wave nor was there a significant difference in the density of blue crabs over vs. in front of the set of waves. These results are mixed, but they do suggest that the megalopae of *Callinectes* spp. may be transported shoreward in the convergence zones over internal waves.

The megalopae of a variety of crab species were only caught in the water column (Table 3 and see Johnson 1985a). Some of these megalopae as adults occupy near shore and even estuarine habitats. If these megalopae migrate onshore they must be utilizing some mechanism of onshore transport other than slicks over internal waves.

In conclusion, the data presented in this paper indicate that in an area where the tides are of small amplitude and the continental shelf is wide, internal waves are nevertheless capable of transporting larval invertebrates and fish shoreward. The samples collected on 24 June 1985 more critically test the hypothesis that internal waves cause cross-shelf transport and the results support the hypothesis.

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