Circulation and larval fish transport within a tidally dominated estuary

JAMES H. CHURCHILL,[1] RICHARD B. FORWARD,[2] RICHARD A. LUETTICH,[3] JAMES L. HENCH,[3] WILLIAM F. HETTLER,[4] LARRY B. CROWDER[2] AND JACKSON O. BLANTON[5]

[1]*Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[2]*Duke University, Nicholas School of the Environment, Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA*
[3]*University of North Carolina at Chapel Hill, Institute of Marine Sciences, 3431 Arendell Street, Morehead City, NC 28557, USA*
[4]*National Marine Fisheries Service, NOAA, Southeast Fisheries Science Center, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516, USA*
[5]*Skidaway Institute of Oceanography, 10 Ocean Science Circle, Savannah, GA 31411, USA*

ABSTRACT

In March 1996 two surveys of larval fish abundance and water flow were carried out within the estuarine region near Beaufort Inlet, NC. Each survey extended over two full semidiurnal tidal cycles and included measurements of larvae concentration and velocity distribution at several locations. There was a large across-channel variation in the subtidal flow passing through Beaufort Inlet, with net inflow over the eastern and central portions of the inlet and net outflow on the western side of the inlet. This pattern was consistent with moored current meter measurements of a previous study, and was reproduced by a numerical model circulation forced only by the M_2 tide. A net ingress of larvae from the open ocean into the estuary was observed during both surveys. Most larvae entered the estuary over the eastern and central portions of the inlet, where the subtidal flow was up-estuary. However, the mean circulation played a minor role in the net movement of larvae into the estuary. Rather, net up-estuary transport of larvae was principally due to variation of larval abundance with tidal flow; with abundance during flood tide usually far exceeding ebb tide abundance. This mode of transport was likely driven by a behavioural response to tidal flow in which larvae tended to descend to the bottom on falling tides and reside throughout the water column on rising tides.

Key words: estuarine circulation, larval recruitment

INTRODUCTION

For several species of marine fish, recruitment to the adult population requires early life transport from open ocean spawning regions to estuarine nursery habitats. A critical, but poorly understood, stage of this journey is ingress into and retention within an estuary. This can be influenced by a number of elements of estuarine circulation. In estuaries with a strong two-layer gravitational circulation, outflow near the surface is partially balanced by net inflow in the bottom layer (e.g. Pritchard, 1967), allowing larvae in the lower water column to be carried up-estuary. As demonstrated in a theoretical analysis by Fisher (1972), the tendency for up-estuary transport can also depend strongly on lateral position across an estuary's axis. This has been confirmed by a number of observational studies which have found vertically and tidally averaged flows to be landward over some parts of an estuarine channel and seaward over other portions of the channel (e.g. Kjerfve and Proehl, 1979; Wong, 1994; Valle-Levinson and Lwiza, 1995). On relatively short time-scales (order days), wind forcing can result in massive influx of oceanic water to an estuary (e.g. Smith, 1977; Pietrafesa and Janowitz, 1988; Liu, 1992). All of these processes are modified by bathymetry, riverine outflow and tidal current strength (Pietrafesa and Janowitz, 1988).

Movement of larvae into an estuary can also be modified, and perhaps controlled, by larval behaviour. Larvae have been observed to migrate vertically through the water column in a manner which favours net up-estuary transport (e.g. Weinstein *et al.*, 1980; Boehlert and Mundy, 1988).

Gaining a better understanding of larval fish recruitment to the estuaries of the South Atlantic Bight (which extends from Cape Hatteras to the southern tip of Florida) was the principal goal of the

Correspondence: James H. Churchill, Woods Hole Oceanographic Institution, Department of Physical Oceanography, Woods Hole, MA 02543, USA.
Received for publication 1 June 1998 1999
Accepted for publication 19 February 1999
Copyright remains the property of the US government.

South Atlantic Bight Recruitment Experiment (SABRE). This study included an investigation of circulation and larval movement into a North Carolina estuary connected to the open ocean by Beaufort Inlet. As part of this effort, multivessel surveys of estuarine flows and larval abundance were carried out. Here we use the measurements acquired to examine: the flow structure and lateral exchange within the estuary ('Flow structure and volume transports'), the movement of larvae through the estuary ('Larval transports') and the possible impact of larval behaviour on the net ingress of larvae ('Evidence of behavioural influence on larval transport'). This is preceded by a brief description of the estuarine system ('Background') and details of the field measurement program ('Field measurements').

Companion papers in this issue deal with other aspects of circulation and larval distribution within the estuary onshore of Beaufort Inlet. Blanton *et al.* (1999) examine the influence of winds and fresh water inflow on estuarine water properties and dynamics. Details of the larval concentration fields observed in the estuary are presented by Forward *et al.* (1999). Luettich *et al.* (1999) examine estuarine flow and larval movement through modelling studies guided by the observational findings.

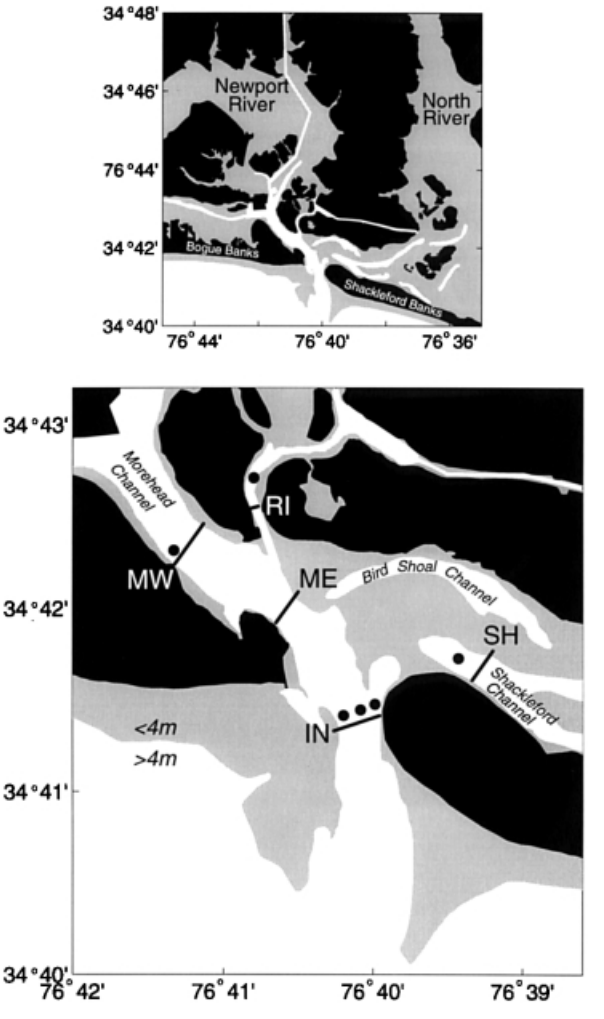
BACKGROUND

The area of our study, the estuary shoreward of Beaufort Inlet, NC, is located on the north-east portion of Onslow Bay (Fig. 1). The primary navigation passage of the estuary is Morehead Channel. This is a deep-draft channel, dredged to a minimum depth of 12 m, which extends north-westward from Beaufort Inlet to the Morehead City port facility. Branching off the Morehead Channel are three shallower channels: Shackleford Channel, which extends eastward from the inlet; Bird Shoal Channel, which also reaches eastward from the Morehead Channel; and Radio Island Channel which runs northward to the port of Beaufort. The Morehead Channel is also connected to the Newport River, which in turn is linked, via the Intracoastal Waterway, to the Neuse River. The fresh water input to the estuary is modest, resulting in an average salinity of roughly 34 psu near the inlet (Kirby-Smith and Costlow, 1989). The majority of fresh water appears to come from the Newport River, which has a drainage area of $\sim$340 km^2 and receives flow from the Neuse River. The largest drainage basin east of the Beaufort Inlet estuary is the North River, which has a drainage area of $\sim$260 km^2 (Kirby-Smith and Costlow, 1989).

Tidal motions within the estuarine channels shoreward of Beaufort Inlet have been examined by Klavans (1983) and Logan (1995). Based on data from an array of tide gauges and current meters, Klavans found that the tide advances through most of the estuary as a damped progressive wave. He also showed that the tide is dominated by the semidiurnal, M_2, constituent; but that other constituents, principally N_2, S_2, K_1, O_1 and M_4, tend to increase in relative strength going up-estuary. Both Klavans and Logan presented evidence of strong tidal asymmetries within the estuarine channels. These are characterized by stronger flood than ebb tide currents (flood dominance) on the right side (looking up-estuary) of the channels, and the reverse on the channels' left side.

Results of multiyear sampling of fish larvae within the Beaufort Inlet estuary have been reported by

Figure 1. Large and small scale views of the Beaufort Inlet estuarine system. Black areas represent land masses. Regions with water depth of < 4 m are shaded grey. Indicated in the lower panel are larval sampling locations (filled circles) and ADCP sampling transects (across channel lines).



Warlen and Burke (1990) and Warlen (1994). Analysis of the samples revealed that Atlantic menhaden larvae recruit to the estuary from mid-November through April, and are most abundant during February through April. March was chosen as the time of our study as this was found to be the month of greatest larval abundance within the estuary.

FIELD MEASUREMENTS

The data used in our study were acquired during two separate 25-h surveys: one on 13–14 March 1996 (survey 1) and the other on 25–26 March 1996 (survey 2). Both periods were times of neap tides. We had intended to conduct a spring tide survey, but were unable to do so because of harsh weather. Each survey began at close to slack water and continued throughout two semidiurnal tidal cycles.

During each survey, larvae were collected at six locations within primary channels of the estuary (Fig. 1). Three locations spanned Beaufort Inlet: one near the centre of the inlet channel and the other two over the eastern and western channel flanks. These stations were sampled at roughly hourly intervals by a 60-cm diameter bongo net towed obliquely through the water column. The other sampling sites were within primary estuarine channels: in Shackleford Channel (east of the inlet), in Morehead Channel (west of the inlet), and in Radio Island Channel (NNW of the inlet). Larval samples at the Morehead and Shackleford Channel sites were acquired from anchored vessels. At each site, surface samples were collected in a neuston net, and water column samples were acquired in a 60-cm diameter bongo net. The bongo net was lowered and raised from the surface to 0.5 m above bottom. The entrance of each net was equipped with a flow meter, and sampling times were adjusted so that 10 m^3 were sampled. In our study, we have used larval concentrations from the bongo net sampling only, which was done at hourly intervals. At the Radio Island Channel site, near-bottom and near-surface samples were acquired by towing two 1-m diameter nets. This was also done at roughly hourly intervals.

Net samples were counted for Atlantic menhaden (*Brevoortia tyrannus* Latrobe), spot (*Leiostomus xanthurus* Lacepede), pinfish [*Lagodon rhomboides* (Linnaeus)], Atlantic croaker [Micropogonias undulatus (Linnaeus)], gulf flounder (*Paralichthys albigutta*), summer flounder (*P. dentatus*), and southern flounder (*P. lethostigma*). For each sample, larval concentration (in larvae per m^3) was computed based on the larval abundance and the total flow through the net as measured by an attached current meter. In our study, we used a single concentration for flounder, determined from the combined abundance of all flounder species. This was justified because the temporal pattern of abundance was similar for all flounder species. Further details of the larval collection and treatment of the larval samples are given by Forward *et al.* (1999).

The velocity data used in our study were acquired with an acoustic Doppler current profiler (ADCP). This was mounted on a dedicated vessel which circuited the survey region and acquired velocity profiles along transects close to the larval sampling locations. Each transect extended perpendicularly across a channel. The ADCP returned velocity profiles over the depth and width of the transects, except within near-surface and near-bottom 'blanking bands' where acoustic reflections and reverberation precluded velocity measurements. The ADCP also produced a record of the total water depth along each transect. A full circuit of the survey region, with ADCP profiles acquired along each transect, was accomplished about once per hour.

Due to sea conditions and equipment capabilities, the set of ADCP transects covered during each survey differed. The first survey was conducted using a narrow-band 1200 kHz ADCP. This was programmed to give velocity profiles at 3-s intervals, with velocities averaged over 1-m bands. Velocity profiles were acquired over three transects. One cut across the inlet (labelled IN in Fig. 1). A second extended across Shackleford Channel, and the third cut across Morehead Channel slightly to the north-east (up-estuary) of the entrance to Radio Island Channel (respectively, SH and ME in Fig. 1). The inlet transect was actually covered twice, on eastward and westward ship tracks, during each circuit. No satisfactory profiles could be acquired across Radio Island Channel because the minimum depth at which the ADCP could return velocity data (due to the size of the blanking bands) exceeded the bottom depth over most of the channel.

During survey 2, velocity profiles were acquired with a broad-band ADCP with a centre frequency of 1200 kHz. Velocity profiles were obtained at a 2-s interval, with velocities averaged over 0.25-m bands. This had a much shallower minimum profiling depth than the narrow-band unit (roughly 2.4 m) and produced satisfactory profiles across the Radio Island Channel (over transect RI in Fig. 1). During this survey, velocity profiles were also acquired along the Shackleford and Morehead Channel transects of survey 1, and along a second Morehead Channel transect (MW in Fig. 1) located within 100 m of the Morehead Channel larval sampling site. Regular velocity profiling was not done at the inlet, however, due to rough seas.

The performance of both ADCP compasses were checked by comparing the orientation of the ship path

derived from the ADCP's bottom tracking to the orientation of the ship path determined from differential GPS locations. For all tracks examined, the orientations differed by less than 6°.

CTD data were also acquired from the ADCP survey vessel. The procedure was to perform a CTD lowering near the centre of each ADCP transect shortly after ADCP data were acquired along the transect. The resulting estuarine data set thus has nearly coincident profiles of temperature, salinity and velocity at each transect at roughly hourly intervals.

FLOW STRUCTURE AND VOLUME TRANSPORTS

Inlet currents

The ADCP measurements of survey 1 revealed a complex and rapidly changing structure of flow through Beaufort Inlet. This structure seldom conformed with the classical view of two-dimensional gravitational circulation through a partially mixed estuary, with stronger ebb and weaker flood currents near the surface. At most times, the velocities measured at the inlet were nearly vertically homogenous, varying by less than 20 cm s^{-1} over the vertical measurement range of the ADCP (Fig. 2). Relatively large vertical current shears were observed at the inlet only at times near slack low water: during late ebb and early flood tides. Reflecting a rapid change in near-bottom flow during these periods (by up to 1.2 m s^{-1} over 100 min), both late flood and early ebb tides significantly increased in strength approaching the bottom (Fig. 2).

Variations in currents in the across-inlet direction were often large. Along-channel current strength varied by as much as 80 cm s^{-1} across the inlet transect. As illustrated here by vectors of depth-averaged inlet velocity (Fig. 3), the lateral structure of current magnitude essentially reversed from flood to ebb tide. Ebb-tide velocities were significantly stronger on the western side of the inlet, whereas flood tide flows were much stronger on eastern side of the inlet.

Inlet volume transports

The velocities measured over each ADCP transect captured most of the flow passing through the channel which the transect spanned. The ADCP transect data thus enabled us to estimate the volume transport (in $m^3 s^{-1}$) through the inlet and the primary estuarine channels

The computation of volume transport was carried out using a software package supplied by the ADCP manufacturer (RD Instruments). This package first determined volume transport over the portion of the transect from which the ADCP velocities were acquired. This mid-layer transport, U_M, was computed by integrating the velocity component normal to the transect over the transect cross-section, i.e.

$$U_M = \int\int_A u \, da$$

where u is the velocity normal to the transect and the integration is over the transect area covered by ADCP measurements. Transports over the surface and bottom layers not covered by the ADCP measurements were determined by power law extrapolation of the mid-layer transport to the surface and bottom (see Simpson and Oltmann, 1990, and Chen, 1991). Total transport across a transect was taken as the sum of the individual layer transports. The transport obtained by extrapolation accounted for roughly 25% of the total transport across the inlet and Morehead Channel transects, and

Figure 2. Contours of along-channel velocity measured at the indicated tidal phase in Beaufort Inlet, NC during 13 March 1996. The view is looking shoreward. The dashed lines in the upper left panel depict the boundaries of the sectors over which along-channel volume transports were computed. The crosses in this panel show the mean depth of the inlet larval sampling sites.

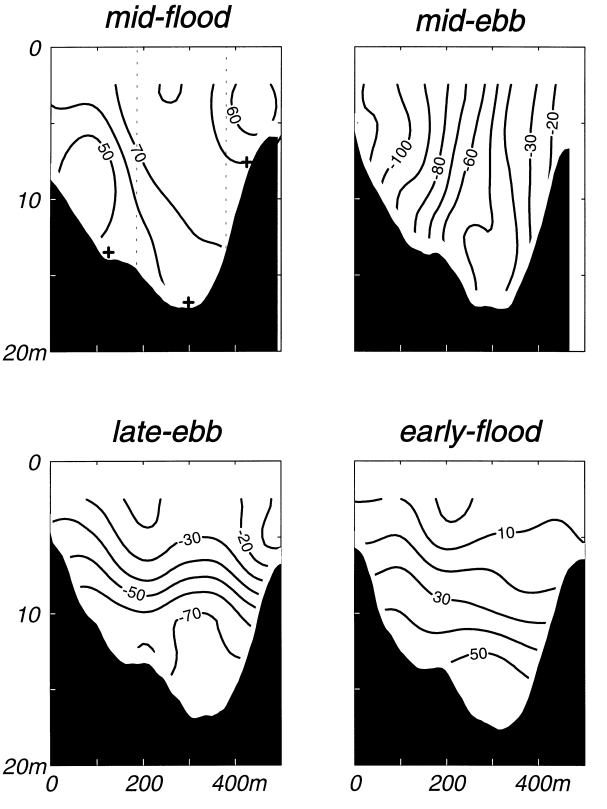
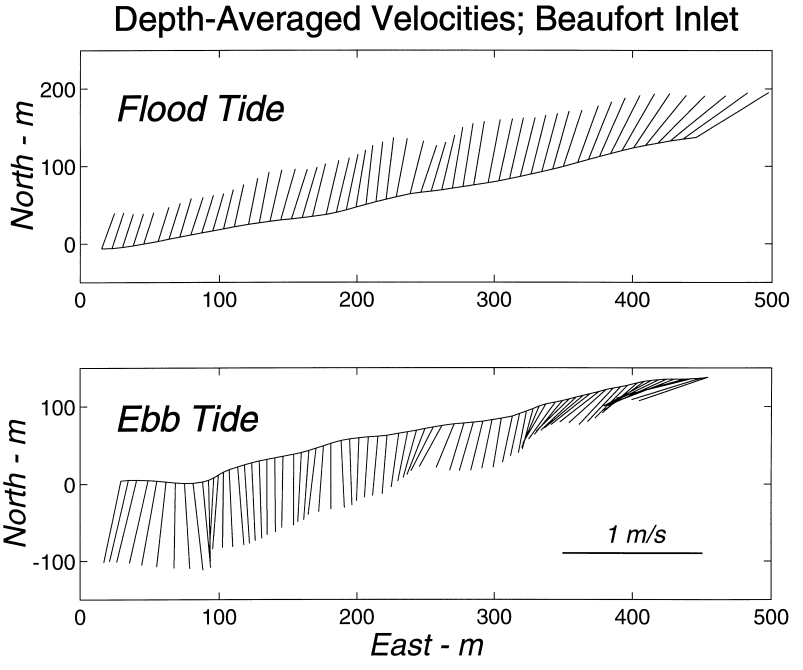


Figure 3. Vectors of depth-averaged velocity measured across Beaufort Inlet during mid-flood and mid-ebb tides.



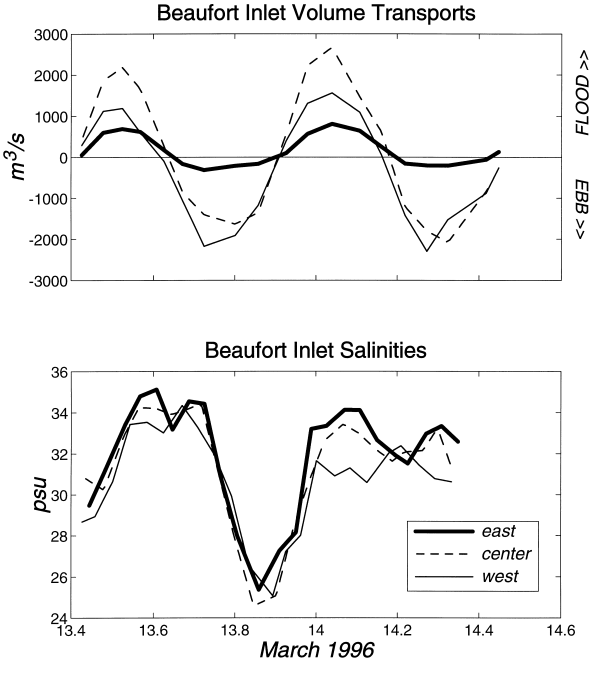
was 35–45% of the total transport through Shackleford and Radio Island Channel transects.

Volume transport through the inlet was partitioned into transports across three sectors: a central sector encompassing the navigation channel, and abutting sectors encompassing the channel flanks. Sector designation was based on bottom depth (Fig. 2), such that the mid-depth point of each sector was directly downstream (on the flood tide) of an inlet larval sampling site (Fig. 1).

The results (Fig. 4) showed large variation in volume transport across the inlet. Transports through the eastern and central sectors were flood-dominated, with much larger flood than ebb magnitudes; whereas transport through the western sector was strongly ebb-dominated. Transport also varied considerably in phase across the inlet. This was marked by 0.6-h transition periods between flood and ebb tides during which volume transport was seaward over the western sector and into the estuary over the central and eastern sectors.

CTD data from the inlet larval sampling stations (Fig. 1) revealed significant across-channel gradients in the properties of water traversing the inlet on the flood tides, with higher salinity and denser water entering on the east side of the inlet (Fig. 4). The salinity measured at the eastern inlet site exceeded the salinity measured at western inlet site by an average value of 1.5 psu over the survey's first flood and by 2.5 psu over the second

Figure 4. Top panel shows along-channel transport of water passing through the eastern (solid bold line), central (dashed line) and western (solid thin line) sectors of Beaufort Inlet (see Figure 2). Positive transport is up-estuary. Bottom panel shows vertically averaged (over 0.5–6 m) salinity measured at the inlet larval sampling stations.



flood tide. Apparently, water entering the western side of the inlet contained a higher proportion of the ebb–flow estuarine discharge. This pattern was likely related to the behaviour of the ebb tide discharge over the inner shelf. Data from repeated hydrographic surveying over 4 months have indicated that, in the absence of strong eastward winds, the plume of low-salinity water issuing from the inlet tends to flow to the west (Churchill *et al.*, 1999). In addition, drifter tracking studies have shown that the water entering the eastern side of the inlet tends to come from the area of higher-salinity water to the east of the inlet.

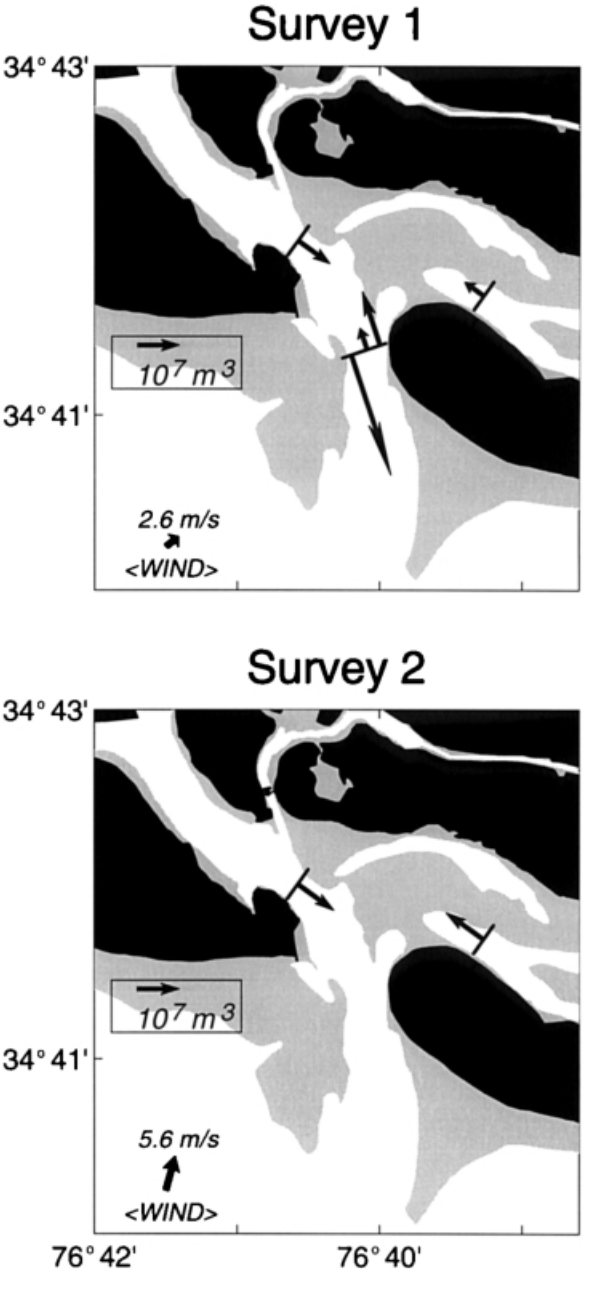
The total volume of water (in m^3) passing through each inlet sector over the course of the survey (referred to here as net volume transport) was determined by integrating the sector transport over the survey period. The period of each integration extended roughly from slack water to slack water, and was within 4% of two semidiurnal tidal cycles. Each integral thus very closely approximates the total volume passage over two full semidiurnal tides. The net transports (Fig. 5) revealed a large lateral exchange of water across the inlet, with 19×10^6 m^3 flowing into the estuary over the eastern and central sectors and 30×10^6 m^3 flowing out the estuary over the western sector.

To examine vertical exchange of water through the inlet, we partitioned the transport through the ADCP measurement layer of the central sector into 5 sublayer transports. Each sublayer spanned the width of the central sector and was 3 m in vertical extent. The time integrals of these sublayer transports revealed that vertical exchange of water through the inlet channel was small. Net transports of the upper three sublayers were up-estuary and summed to 5.3×10^6 m^3, whereas the net transports of the lower two sublayers were seaward and summed to only 0.4×10^6 m^3.

Estuarine transports

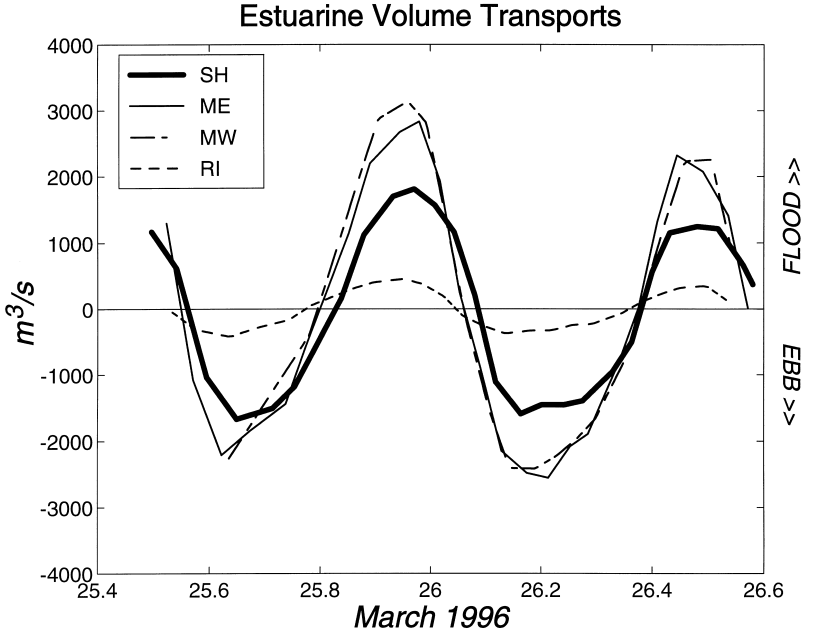
Transports measured across the estuarine transects (Fig. 6) gave an indication of the partitioning of flow entering Beaufort Inlet. They revealed that a sizable fraction of this flow turned eastward into Shackleford Channel. The amplitude of the transport measured through Shackleford Channel was roughly 60% of the amplitude of the transport measured across Morehead Channel. This was an unexpected result in view of the bathymetry of the system. Morehead Channel runs continuously to the inlet, whereas incoming flow must pass over a 3-m deep sill to enter Shackleford Channel, which is roughly half as deep as Morehead Channel (Fig. 1). In addition, the Shackleford Channel transport accounted for only a portion of the incoming flow which moved eastward. Missed were flows through Bird Shoal Channel to the north.

Figure 5. Computed net volume of water which passed the ADCP transects during surveys 1 and 2. The arrows show the direction (either up-or down-estuary) and magnitude of the transports. Magnitude scale is indicated on each panel. Survey-averaged wind velocity measured at the Cape Lookout meteorological station (15 km SE of Beaufort Inlet) is shown at the lower left of each panel.



All net volume transports of both surveys were directed down-estuary (Fig. 5), indicating a subtidal flow of water out of the estuary over the course of each survey. Analysis of wind and water pressure records by

Figure 6. Along-channel transport of water passing estuarine ADCP transects during survey 2. The transect designations in the legend match those shown in Figure 1.



Blanton *et al.* (1999) revealed that this outflow was largely a discharge of water which had accumulated in the estuary during times of strong wind-forced flows into the estuary prior to each survey.

Comparison with other observations and numerical model results

As part of a previous study described by Logan (1995), velocity measurements were acquired from two moored current meters set out over a 45-day period at the eastern side of Beaufort Inlet (at a water depth of 8 m). A net inflow of water at the eastern side of Beaufort Inlet, observed over two tidal cycles in our measurements, was also indicated by these longer-term velocity records. Mean velocities from these records were directed up-estuary with magnitudes in excess of 30 cm s^{-1}. The persistence of up-estuary flow at the eastern side of the inlet was revealed by the subtidal velocity signals from the current meters. These were directed seaward only on one occasion: a 1-day period in late March 1993 which followed a strong wind event, often referred to as the 'Storm of the Century' on the North Carolina coast. Logan argued that the anomalous seaward flow observed by the current meters during this time was due to a discharge of water driven into the estuary by the storm. Taken together, our findings and those of Logan indicate a strong and nearly continuous subtidal inflow of water over the eastern portion of Beaufort Inlet. It follows that the compensating outflow of water at the western side of the inlet, observed in our study, is also likely to be a persistent feature.

Bands of subtidal inflow and outflow across an estuary opening have been observed by a number of other investigators. However, the details have varied among the different estuaries studied. Currents measured in Delaware and Chesapeake Bays have shown mean inflow principally within a central channel and mean outflow over the adjacent shoals (Wong, 1994; Valle-Levinson and Lwiza, 1995). An opposite pattern, with mean ebb flow through the centre channel has been observed in North Inlet, South Carolina (Kjerfve, 1978). A flow pattern similar to that revealed by our observations, with mean inflow over the right side of an estuary opening (looking up-estuary) and mean outflow on the opposite side, has been observed in lower New York Harbor (Doyle and Wilson, 1978) and across the opening to the Cape Fear River (Pietrafesa and Janowitz, 1988). These observations suggest that the form of flow variation across an estuary opening depends strongly on local conditions.

The current meter measurements presented by Logan (1995), which spanned a large range of wind and freshwater inflow conditions, suggest that the persistent up-estuary flow observed over the eastern side of Beaufort Inlet may have been largely due to the combination of tides and inlet bathymetry. The tidally driven circulation in the Beaufort Inlet region has been examined in a companion modelling study by Luettich *et al.* (1999). As part of their study, they simulated estu-

arine flows using a two-dimensional, fully nonlinear, finite element numerical model. Forcing of model flows was limited to elevation changes at the model boundaries and did not include fresh water inflow. The model's mean circulation field (Fig. 6 in Luettich *et al.*, 1999) thus represents tidally driven residual flows. This field shows a mean flow pattern through the inlet similar to that determined from the ADCP observations, with net inflow on the eastern side of the inlet and net seaward flow on the western side of the inlet. This suggests that tidal rectification may have played a significant role in generating the mean flow pattern seen over the inlet. However, in view of the large density differences seen across the inlet (Fig. 3), the possibility that the mean flows were also strongly influenced by density differences cannot be discounted.

The modelled residual circulation field of Luettich *et al.* (1999) also gives an indication of the possible fate of the net inflow observed over the central and eastern inlet sectors. Our observations reveal that this did not extend far into the estuary as it was countered by net down-estuary volume transports over the Shackleford and Morehead Channel transects (Fig. 5). In the modelled mean circulation field, the inflow of water over the eastern side of the inlet is deflected into the Morehead Channel where it joins a down-estuary mean current and exits the estuary on the western side of the inlet.

LARVAL TRANSPORTS

The combination of ADCP transect data and measurements of larval concentration at locations close to the ADCP transects enabled us to estimate transports of individual larval species (in numbers of larvae per second) across each transect. Larval transport across estuarine transects was taken as the product of vertically averaged larval concentration and the transect's volume transport. For the Shackleford and Morehead Channel transects, vertically averaged larval concentrations were taken as the mean larval concentrations from the bongo net samples, which spanned most of the water column. Vertically averaged larval concentration of the Radio Island Channel site was computed by averaging the concentrations of the near-surface and near-bottom samples. Computation of the volume transport-larval concentration products required that the volume transport time-series be adjusted so that its points coincided with the times of larval sampling. This was accomplished by linear interpolation.

Transport of each species across the inlet transect was segregated into transports across the three inlet sectors described in 'Inlet volume transports' above. Larval transport for each sector was computed as the product of the sector's volume transport and vertically averaged larval concentration (from the inlet Bongo net samples).

The total number of a larval species passing a transect, or inlet sector, over the course of a survey was determined by integrating the species transport over time. This quantity is denoted here as net larval transport.

Inlet transports

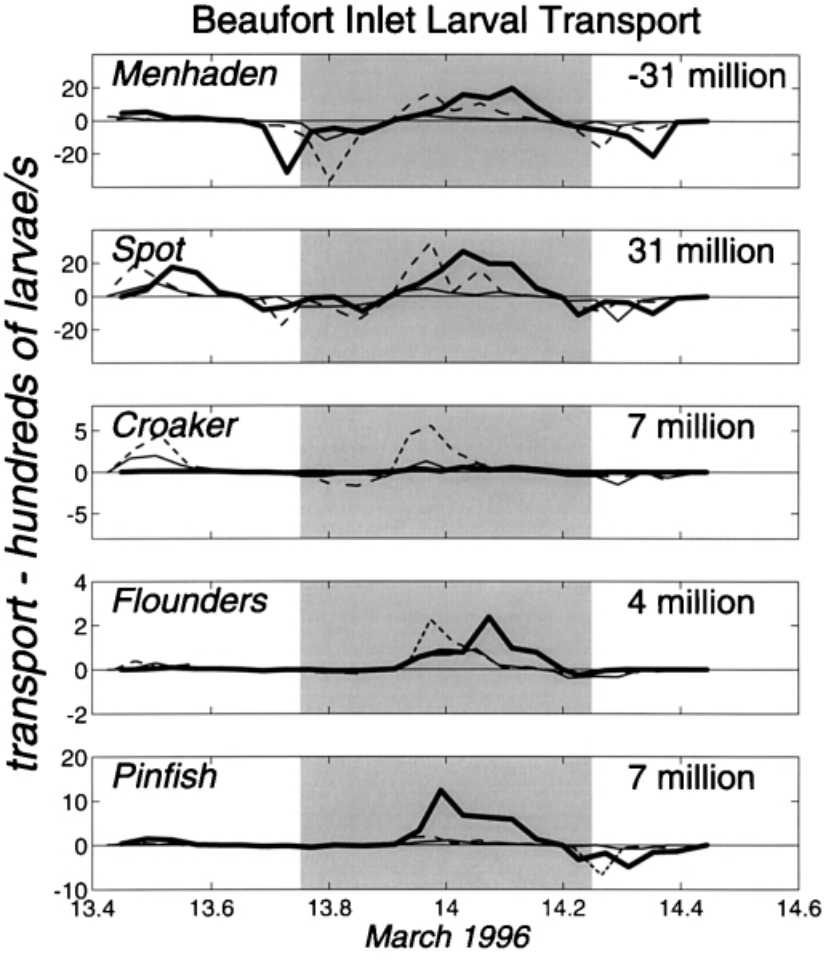
One of the most unexpected findings deduced from the larval collection data was the presence, during both surveys, of large gradients in larval concentration going across Beaufort Inlet. For all species except croaker, concentrations increased sharply going from west to east across the inlet. Croaker concentrations were slightly greater at the centre of the inlet than at either side. For menhaden, spot and pinfish larvae, the difference between the concentrations at the western and eastern sides of the inlet were particularly large, roughly a factor of 10 (based on time-averaged concentrations) favouring the eastern side concentration (see Forward *et al.*, 1999, for a more detailed discussion of the larval concentrations).

Estimated transports of the individual larval species through the inlet sectors (Fig. 7) also exhibited appreciable across-inlet gradients. For example, the transport magnitudes of spot across the eastern and central inlet sectors were roughly equivalent and exceeded transport magnitudes across the western sector by an order of magnitude.

The transport estimates further revealed that the flood-tide ingress of larvae predominantly occurred over the eastern and central sectors. Integration of the computed transport time series of all larvae over the flood tides indicated that only about 10% of the survey 1 larval influx passed through the western sector. However, considerable species-to-species differences were exhibited in the details of the flood tide larval transports (e.g. timing of the peak transports and relative magnitudes of the different sector transports). Although we did not compute inlet transports of the second survey, owing to lack of ADCP data, examination of larval concentration time series indicated that flood-tide larval transports of this survey also predominantly occurred across the eastern and central sectors and varied greatly in detail from species to species. These observations suggest that the observed preponderance of larval ingress through the eastern and central inlet sectors was not a chance occurrence, due to the influx of a single highly concentrated larval patch, but likely reflected a common pattern of larval ingress.

The larval transports also revealed that most of the larval ingress through Beaufort Inlet during survey 1 occurred during the night flood tide of the survey.

Figure 7. Estimated transports of larvae passing through the eastern (solid bold line), central (dashed line) and western (solid thin line) sectors of Beaufort Inlet during survey 1. Up-estuary transports are positive. Shading encompasses the night period. Listed at the upper right of each panel is the estimated number of indicated species which passed the inlet transect over the survey (the sum of the individual net sector transports).



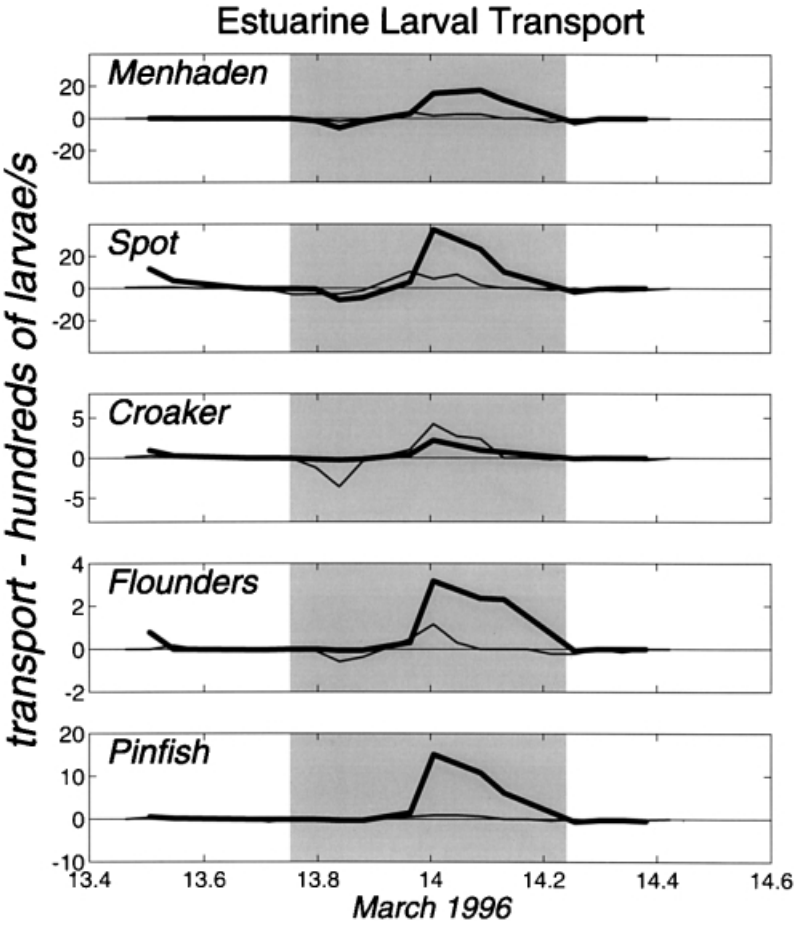
Appreciable daytime ingress of spot and croaker were measured, but they were considerably less than the nighttime influx of the species (Fig. 7). A preponderance of nighttime over daylight larval ingress was also deduced from the larval concentration time series of survey 2.

Estuarine transports

The dominance of nighttime transport observed at the inlet was even more pronounced over the estuarine transects. Estimated daylight larval transports over these transects were negligible for all species (Figs 8 and 9). The east-to-west variation in larval transport seen at the inlet was also observed within the estuary. For most species, computed transports through the Shackleford Channel transect (to the east of the inlet) were of appreciably greater magnitude than computed transports through the Morehead Channel transect (west of the inlet).

The combination of inlet and estuarine larval transport estimates of survey 1 (Figs 7 and 8) allowed us to deduce tentatively the paths followed by larvae entering the inlet sectors on the survey's night flood tide. A fairly well defined split of the incoming transport was revealed by the transports of menhaden, spot, flounders and pinfish. For these species, the observed flood-tide transport through the eastern inlet sector was remarkably similar, in magnitude and temporal variation, to the transport seen through the Shackleford Channel transect. Computed transports of these species through the western inlet sector and the Morehead Channel transect were also in close agreement. Apparently, the water and high larval concentrations entering the eastern inlet sector continued

Figure 8. Same as Figure 7, except showing the estimated transports of larvae passing through the Shackleford Channel (solid bold line) and Morehead Channel (solid thin line) transects during survey 1. To facilitate comparison with the estimated inlet transports, the concentration scales are identical to those of Figure 7.



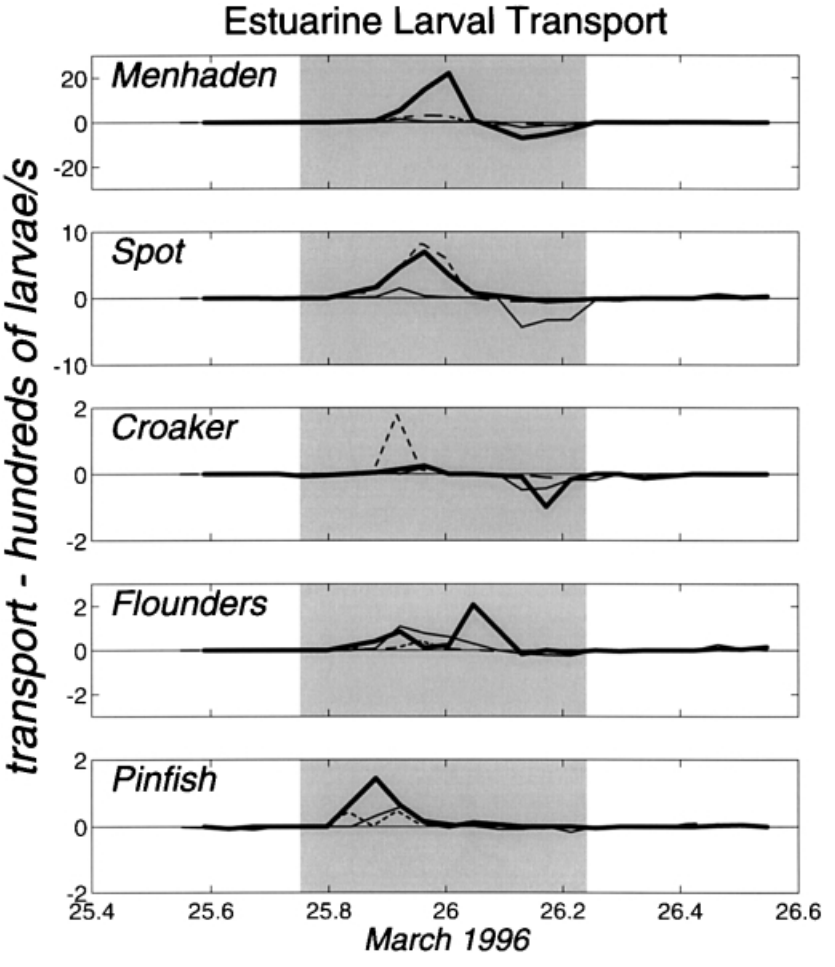
eastward through the Shackleford Channel, while the water and relatively low larval concentrations entering the western sector moved through the Morehead Channel.

An indication of the movement of larvae entering the central inlet sector was offered by the croaker transports. Observed croaker ingress during the night flood tide of survey 1 was predominantly through the central inlet sector (Fig. 7). This corresponded with observed up-estuary croaker transports at the Shackleford and Morehead Channel transects which were of nearly equal magnitude. The sum of these transports roughly equaled the incoming transport of croaker seen at the central inlet sector. A tentative conclusion is that the incoming flow through the inlet channel split into eastward and westward streams of comparable transport.

The larval transport estimates of survey 2 (Fig. 9) revealed an appreciable flood-tide ingress of some species through Radio Island Channel. This was an unexpected result in view of the relatively small volume transports through the channel (Fig. 6). It was most likely an upshot of the eastward increase in larval abundance seen at the inlet. If this trend continued downstream through Morehead Channel, water with relatively high larval concentrations would have been passed along the northern side of the channel and likely entered Radio Island Channel (Fig. 1).

The eastward-westward split of flood tide inflow, deduced by the larval transports, was also indicated by the tracks of surface drifters released at various points across the inlet during early stages of the flood tide (Churchill *et al.*, 1999). Drifters released at the eastern and western sides of the of the inlet moved, respectively, down the Shackleford and Morehead Channels. Drifters released within the inlet's central channel followed paths down both Morehead and

Figure 9. Same as Figure 8, except showing the estimated transports of larvae passing through the Shackleford Channel (solid bold line), Radio Island Channel (dashed line) and Morehead Channel (solid thin line) transects during survey 2.



Shackleford channels. The drifter tracks also revealed a tendency for near-surface inflow through Morehead Channel to be diverted into Radio Island Channel. Of the six the drifters which were released at the channel centre and moved down Morehead Channel, four turned northward into the Radio Island Channel.

The comparison of inlet and estuarine larval transport estimates has provided a guarded measure of confidence in the accuracy of these estimates. A primary source of uncertainty in the larval transport estimates arose from the use of larval concentration at a single location to represent larval concentrations across a transect or inlet sector. If this produced significant errors in transport, they would likely be manifest by conspicuous differences between inlet and estuarine larval transports. For example, such a difference would be seen if a high concentration of larvae entering the estuary were sampled at an inlet station but missed at an estuarine station. The close correspondence of the magnitude and time variation of inlet and estuarine transports, discussed above, indicates that this sort of occurrence was rare and that our combination of larval concentration and velocity measurements produced reasonably accurate estimates of larval transport. The only notable exceptions were the computed ebb-tide menhaden transports of survey 1. Large ebb-tide transports of menhaden were seen at eastern and central inlet sectors, but not at any estuarine transects (Figs 7 and 8).

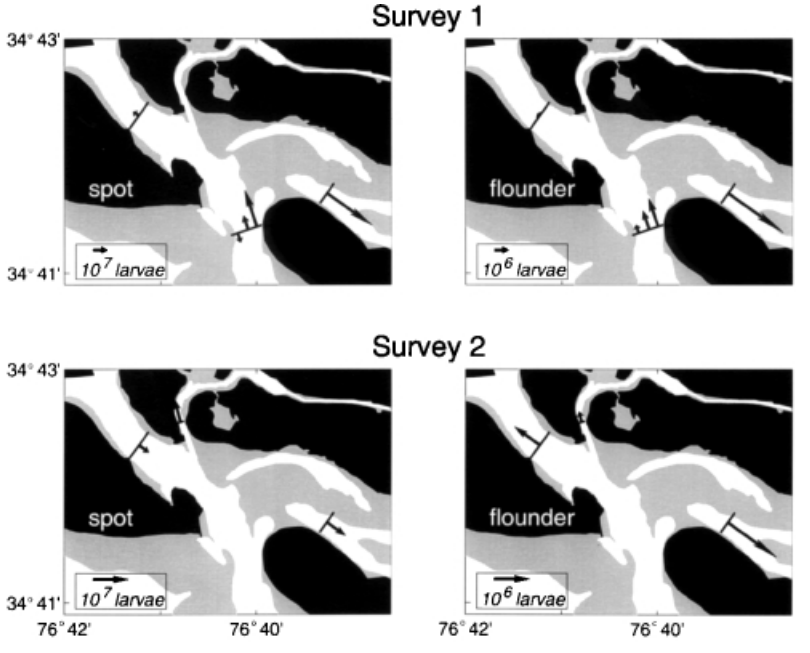
Net larval transports

The estimated net larval transports (Table 1, Fig. 10) indicated a widespread ingress of larvae during both surveys. Except for the estimated net seaward transports of menhaden through the inlet during survey 1, estimates of transport out of the estuary were rare and

Table 1. Net larval transports (in millions of fish) over the two tidal cycles of Surveys 1 and 2 (13–14 March and 25–26 March 1996). The values were computed by integrating larval transport over time. The larval transports were taken as a product of volume transport, derived from ADCP data, and larval concentration. Positive net transports are up-estuary

	Menhaden	Spot	Croaker	Flounder	Pinfish
Survey 1					
Inlet east	–6.4	27.2	0.7	2.1	8.5
Inlet centre	–17.7	10.4	5.1	1.4	–1.4
Inlet west	–7.3	–7.0	0.7	0.6	0.4
Inlet total	–31.4	30.6	6.5	4.2	7.5
Shackleford Channel	21.8	39.2	2.4	4.8	18.2
Morehead Channel	2.2	4.7	1.8	0.2	0.2
Survey 2					
Shackleford Channel	8.9	6.5	–0.4	1.7	1.1
Radio Island Channel	1.3	6.8	0.6	0.3	0.4
Morehead Channel	–1.1	–3.5	–0.4	0.9	0.3

Figure 10. Computed net spot and flounder transports of survey 1 and survey 2. The arrows show the direction (either up-or down-estuary) and magnitude of the transports according to the scale indicated on each panel. Note that net transport in the Morehead Channel is depicted at transect MW (Figure 1) but was computed using velocity data from transect ME and larval concentrations measured near transect MW.



relatively small. At the inlet, the bulk of the net ingress passed through the central and eastern sectors. During the first survey, a large fraction of this influx, of order 90%, was apparently diverted to the east through Shackleford Channel. Net larval transports of the second survey also showed a relatively large larval ingress through the Shackleford Channel. For some species, relatively large net transport was also indicated through Radio Island Channel.

The only net transports not clearly indicating larval ingress, the menhaden transports of survey 1, exhibited a conflicting pattern of net inflow and outflow. Net menhaden transports were directed up-estuary through Shackleford and Morehead Channels but were seaward over all inlet sectors (Table 1). From a larval budget viewpoint, the large ebb-tide menhaden transports observed at the central and eastern inlet sectors (Fig. 7) present the most serious inconsistency. The source of these transports is open to question as they were not matched by comparable flood-tide transports of menhaden through the inlet (indicating an oceanic source), or by comparable ebb-tide menhaden transports across

estuarine transects (indicating an estuarine source). They may have been balanced by incoming flood-tide transport missed by our inlet larval sampling. Given the eastward increase in larval concentrations seen at the inlet, it is possible that high, unsampled concentrations of larvae may have entered the estuary east of the eastern inlet sampling site. It is, however, less likely that high larval concentrations may have exited the inlet east of this site. Our ADCP measurements indicate that ebb currents at eastern side of the inlet tend to veer to the inlet centre (Fig. 3), which would tend to carry high larval concentrations to our inlet sampling sites.

EVIDENCE OF BEHAVIOURAL INFLUENCE ON LARVAL TRANSPORT

In areas with large temporal variations in flow and larval concentration, as observed at our measurements sites, it is reasonable to expect that net larval transports should depend on two factors. One is the net volume transport over the periods when larvae reside in the water column. The other is the variation of larval concentration with tidal flow. The second factor may be actively influenced by larval behaviour. Several investigators have found that larvae of a number of estuarine-dependent species may partially control their horizontal transport through an estuary by migrating vertically with tidal flow, tending to occupy near-bottom water during falling tides and reside throughout the water column during rising tides (Wood and Hargis, 1971; de Veen, 1978; Weinstein *et al.*, 1980; Johnson and Gonor, 1982; Epifanio *et al.*, 1984; Rijinsdorp *et al.*, 1985; Boehlert and Mundy, 1988; Tanaka *et al.*, 1989; De Vries *et al.*, 1994; Rowe and Epifanio, 1994). This allows a larval population to migrate up-estuary through 'selective tidal stream transport'. Forward *et al.* (1999) found that changes in larval concentration measured at our estuarine stations favoured up-estuary transport. In particular, the larval concentrations were generally highest during times of the strongest flood-tide currents. However, concentrations were highly variable and had nonzero values during ebb tides.

Determining the relative influence of the factors mentioned above on computed net larval transports can be done by mathematically separating the net transports into two components: one due solely to advection of larvae by the mean flow, and the other due to the covariation of larval concentration and flow. The separation is akin to Reynolds decomposition (e.g. Pond and Pickard, 1978), and is expressed as:

$$T = T_A + T_B$$

with

$$T = \int_{t_1}^{t_2} UC \, dt$$

and

$$T_A = \int_{t_1}^{t_2} \overline{U}\,\overline{C} \, dt = (t_2 - t_1)\overline{U}\,\overline{C},$$

$$T_B = \int_{t_1}^{t_2} (U - \overline{U})\,(C - \overline{C}) \, dt,$$

$$\overline{U} = \frac{1}{t_2 - t_1}\int_{t_1}^{t_2} U \, dt; \quad \overline{C} = \frac{1}{t_2 - t_1}\int_{t_1}^{t_2} C \, dt;$$

U and C are the volume transport and larval concentration, respectively. $\overline{U}$ and $\overline{C}$ are the averages of these quantities over the period from t_1 to t_2. T is the total net transport of larvae over the t_1 to t_2 period (in number of larvae). T_A is the advective component of this net transport, and is due to the mean volume transport from t_1 to t_2. T_B results from covariations in larval concentration and volume transport over this period. It is denoted here as the behavioural component of net larval transport, although we acknowledge that flow and larval abundance may covary due to factors other than larval behaviour.

A similar approach to that above is often employed to separate net estuarine salt transport into components due to mean advection and 'tidal pumping' of salt (e.g. Dyer, 1973; Lewis and Lewis, 1983; Uncles *et al.*, 1985; Geyer and Nepf, 1996). When determining the components of net larval transport from the above, careful attention must be given to properly choosing the integration period. It should be confined to the time when larvae are within the water column. This is necessary to ensure that the mean velocity used in computing the advective component is the average of the flow to which the larvae are actually exposed.

Evaluation of the above to determine net transport components over estuarine transects was carried out with the integration period restricted to the nighttime period of each survey. As noted in the previous section, larval transports observed at the estuarine transects were essentially confined to the night period. Advective net larval transport at these transects was thus principally due to the nighttime net volume transport, which was up-estuary during both surveys. Nevertheless, the

computed components of net larval transport (Table 2, Fig. 11) indicate that the covariation of larval abundance with flow was the dominant mechanism responsible for the up-estuary movement of larvae observed over the estuarine transects. For nearly all cases in which the estimated net nighttime transport of a species was up-estuary, the behavioural component was also up-estuary and far exceeded the advective component. For example, the behavioural components of the individual species net transports computed from the Shackleford Channel data of survey 1 were all up-estuary and exceeded the corresponding advective components by an average factor of 4.

We calculated two sets of net larval transport components through the inlet sectors. One set was determined by confining the integration indicated above to the nighttime period, and the other was computed by integration over the entire survey period. These differing integrations were carried out because daylight transports observed at the inlet were small but not negligible. Both sets of results led to the same conclusions regarding the relative importance of behavioural net transports through the inlet sectors. Here we list (Table 3) and discuss only the net transport components of the entire survey period.

Net transport components of all species except menhaden gave a reasonably coherent view of larval movement through the inlet. They indicated that the covariation of larval abundance with flow was the dominant mechanism responsible for larval ingress through the central and western sectors. The computed net up-estuary transports through these sectors each had an up-estuary behavioural component which far exceeded its companion advective component. Particularly noteworthy was that the computed net transports of croaker, flounder and pinfish through the western sector were directed up-estuary solely due to the behavioural net transport components. These were up-estuary and more than offset the corresponding seaward advective components of net transport. The only measurement location at which advection was indicated as the dominant mechanism of net up-estuary transport was the eastern inlet sector. The advective components of spot, croaker and pinfish net transport through the eastern sector were up-estuary and dwarfed the corresponding behavioural components. However, this was not true for flounder. Behavioural and advective components of the eastern sector's net flounder transport were comparable.

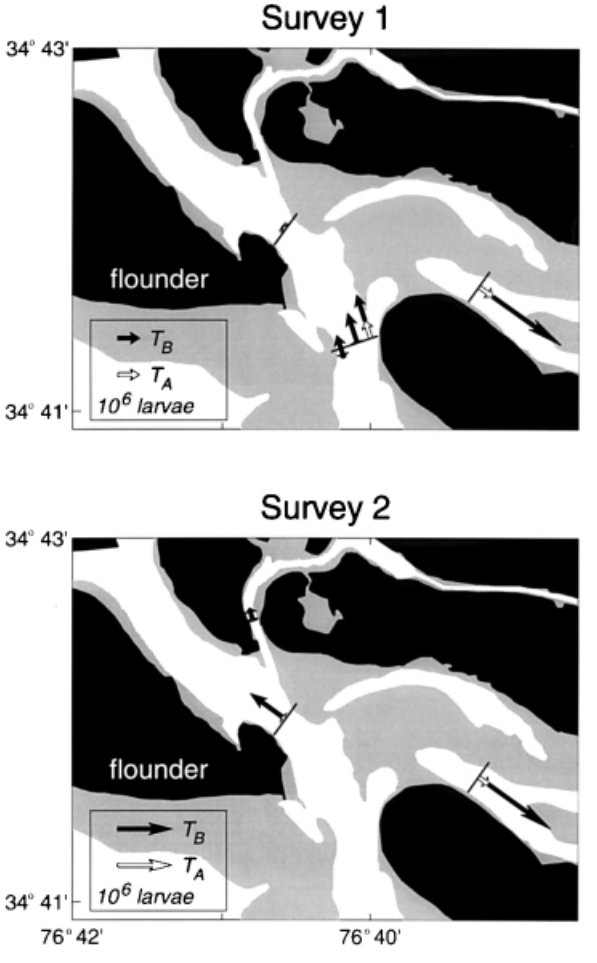
The relative size of the behavioural and advective components of net transport varied appreciably from species to species (Tables 2 and 3), suggesting that some species were more adept than others at taking advantage of flood-tide flows. To give a single indicator of this ability, we computed for each species the ratio of the sum of the behavioural components to the sum of advective components of the net transports across the estuarine transects. These spanned a range of 2.2–4.8. Based on these ratios, pinfish showed the greatest aptitude for selective flood-tide transport, followed by flounders, spot, menhaden and croaker.

To further evaluate the extent to which the T_B components of net larval transport were the result of larval behaviour, we computed the equivalents of the T_B and $T_A$components of net salt transport across the estuarine transects. These were as defined in the equation above, except with salt concentration (in kg m^{-3}) replacing larval concentration. The salt transport components may be viewed as benchmark indicators of the movement of a property with no behavioural influence. Computation of these components was carried out with the ADCP transect data and the CTD measurements taken near the centre of the ADCP

Table 2. Comparison of advective (T_A) and 'behavorial' (T_B) components of net larval transport (in millions of fish) measured during the night-time portions of Surveys 1 and 2. Positive net transports are up-estuary

		Menhaden	Spot	Croaker	Flounder	Pinfish
Survey 1						
Shacklef. Channel	T_B	16.47	25.86	1.62	3.84	15.16
	T_A	5.60	8.46	0.45	0.79	3.13
Morehead Channel	T_B	1.79	4.78	1.27	0.06	0.41
	T_A	0.74	1.68	0.57	0.15	0.18
Survey 2						
Shacklef. Channel	T_B	6.75	5.67	–0.40	1.40	0.98
	T_A	2.15	0.65	0.07	0.23	0.13
Radio Is. Channel	T_B	0.65	5.62	0.50	0.20	0.23
	T_A	0.69	1.01	0.09	0.04	0.07
Morehead Channel	T_B	–1.24	–3.41	–0.34	0.72	0.28
	T_A	0.18	0.32	0.03	0.08	0.04

Figure 11. Same as Figure 10 except showing advective (hollow arrow) and behavioural (solid arrow) components of net flounder transport. Note that the vectors representing the advective component at the inlet centre in survey 1, at Radio Island Channel in survey are too small to be seen with the chosen scaling. Also note that the vector representing the behavioural component at the western side of the inlet in survey 1 begins at the end of the advective component arrow, which is south of the transect line.



transects. The procedure was the same as that outlined above for computing the net larval transport components. The salt concentration across an ADCP transect was represented by averaged salt concentration of the companion CTD profile. The integration limits (t_1 and t_2) matched those of the computation of the net estuarine larval transport components and thus gave net salt transport components over the periods when larvae were observed within the water column. The results (Table 4) indicate that the covariation of vertically averaged salinity with flow made small contributions to the net salt transport over these periods (order 25% during survey 1 and 1.5% during survey 2). This contrasts sharply with the large $T_B$contributions to the net larval transports; a result which lends credence to the hypothesis that the $T_B$components of net larval transport were principally due to larval behaviour.

Taken together, our results indicate that the up-estuary net transport of larvae observed during our surveys was, with the possible exception of the net transport at the east of the inlet, predominantly due to the covariation of larval abundance and tidal flow. This finding strongly supports the notion that larvae were actively seeking up-estuary transport on the flood tide, and that this behaviour was the primary mechanism responsible for their retention within the estuary.

Table 4. Components of net night-time salt transport (in millions of kg) across interior ADCP transects due to advection (T_{AS}) and covariation of salinity with flow (T_{BS}). Positive transports are up-estuary

Survey 1	Shackleford Channel	T_{BS}	99
		T_{AS}	163
	Morehead Channel	T_{BS}	48
		T_{AS}	339
Survey 2	ShacklefordChannel	T_{BS}	3
		T_{AS}	192
	Radio Isand Channel	T_{BS}	4
		T_{AS}	255
	Morehead Channel	T_{BS}	1
		T_{AS}	66

Table 3. Same as Table 2, except comparing advective (T_A) and 'behavorial' (T_B) components of net larval transport measured at Beaufort Inlet during all of survey 1

		Menhaden	Spot	Croaker	Flounder	Pinfish
Inlet east	T_B	–42.94	–5.96	0.20	1.26	0.26
	T_A	36.52	33.18	0.49	0.85	8.28
Inlet centre	T_B	–19.66	7.97	4.65	1.36	–1.63
	T_A	1.96	2.42	0.45	0.08	0.21
Inlet west	T_B	–2.01	1.28	2.41	1.08	1.18
	T_A	–5.31	–8.33	–1.68	–0.45	–0.83

SUMMARY AND DISCUSSION

One of the most notable circulation features revealed by our measurements was the pattern of subtidal volume transport through the inlet. This was marked by net inflow over the eastern and central portions of the inlet, net outflow across the western side of the inlet, and by small vertical variations in net flow. Also noteworthy was the partitioning of flow entering the inlet. Flood-tide transport over the relatively shallow regions to the east of the inlet was comparable with the westward flood-tide transport through the main navigation channel. The general pattern of larval transport into the estuary appeared to have been tied to these characteristics of the flow. Most of the larvae carried into the estuary during our surveys entered over the central and eastern portions of the inlet. A large majority of these were advected eastward through Shackleford Channel. However, our measurements offered compelling evidence that retention of larvae within the estuary was principally due to their ability to selectively seek up-estuary transport on the flood tide. The proficiency of taking advantage of flood tide flows appeared to have varied from species to species, with pinfish and flounders demonstrating the greatest aptitude of the species examined. Nevertheless, our findings indicated that the movement of all these species depended on the details of both flow and larvae behaviour.

ACKNOWLEDGEMENTS

We are grateful to all those who participated in the larval transports surveys and worked in counting the larval samples acquired. They include: J. Amft, A. Crosby, L. Eby, D. Fuss, M. Greene, K. O'Malley, R. Robbins, L. Settle, H. Walsh and S. Warlen. Special thanks go to J. Welsh for round-the-clock work in acquiring the ADCP measurements, and to W. Spencer for supervision of the ADCP measurement effort. Our manuscript was greatly improved by implementing the suggestions of W. Geyer, J. Hare, A. Valle-Levinson and an anonymous reviewer. This work was supported by the Coastal Ocean Program of the U.S. National Oceanic and Atmospheric Administration through grant numbers *NA56RG0508, NA56RG0509 and NA66RG0250 and* by the North Carolina Sea Grant Program through grant *CF-92–07*.

REFERENCES

Blanton, J.O., Amft, J., Luettich, R.A., Hench, J.L. and Churchill, J.H. (1999) Tidal and subtidal fluctuations in temperature, salinity and pressure for the winter 1996 Larval Ingress Experiment—Beaufort Inlet, NC. *Fish. Oceanogr.* **8**(Suppl. 2)**:**134–152.

Boehlert, G.W. and Mundy, B.C. (1988) Roles of behavior and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *Am. Fish. Soc. Sym.* **3:**51–67.

Chen, C.-L. (1991) Unified theory on power laws for flow resistance. *J. Hydr. Eng.* **117:**371–389.

Churchill, J.A., Blanton, J.O., Hench, J.L., Luettich, R.A. and Wener, F.E. (1999) Flood tide circulation near Beaufort Inlet, North Carolina: implications for larval recruitment. *Estuaries* **22.** in press.

de Veen, J.F. (1978) On selective tidal transport in the migration of North Sea plaice (*Pleuronectes Platessa*) and other flatfish species. *Neth. J. Sea Res.* **12:**115–147.

De Vries, M.C., Tankersley, R.A., Forward, R.B., Kirby-Smith, W.W. and Luettich, R.A. (1994) Abundance of crab megalopae are associated with estuarine tidal hydrologic variables. *Mar. Biol.* **118:**403–413.

Doyle, B.E. and Wilson, R.E. (1978) Lateral dynamic balance in the Sandy Hook to Rockaway Point transect. *Est. Coast. Shelf Sci.* **6:**165–174.

Dyer, K.R. (1973). *Estuaries: a Physical Introduction*. New York: John Wiley.

Epifanio, C.E., Valent, C.C. and Pembroke, A.E. (1984) Dispersal and recruitment of blue crab larvae in the Delaware Bay, USA. *Estuarine Coastal Shelf Sci.* **18:**1–12.

Fisher, H.B. (1972) Mass transports mechanisms in partially stratified estuaries. *J. Fluid Mech.* **53:**671–687.

Forward, R.B., Reinsel, K.A., Peters, D., Tankersley, R.A., Churchill, J.H., Crowder, L., Hettler, W.F., Warlen, S.M. and Green, M. (1999) Transport of fish larvae through a tidal inlet. *Fish. Oceanogr.* **8**(Suppl. 2)**:**153–172.

Geyer, W.R. and Nepf, H. (1996) Tidal pumping of salt in a moderately stratified estuary. In: *Buoyancy Effects on Coastal and Estuarine Dynamics; Coastal and Estuarine Studies*, Vol. 53. D.G. Aubrey and C.T. Friedrichs, eds. Washington DC: American Geophysical Union, pp. 213–226.

Johnson, G.E. and Gonor, J.J. (1982) The tidal exchange of Callianassa californiensis (Crustacea, Decapoda) larvae between the ocean and the Salmon River estuary, Oregon. *Estuarine Coastal Shelf Sci.* **14:**501–516.

Kirby-Smith, W.W. and Costlow, J.D. (1989) The Newport River estuarine system. *UNC-Sea Grant Publication 89–04*.

Kjerfve, B. (1978) Bathymetry as an indicator of net circulation in well-mixed estuaries. *Limnol. Oceanogr.* **23:**816–821.

Kjerfve, B. and Proehl, J.A. (1979) Velocity variability in a cross-section of a well-mixed estuary. *J. Mar. Res.* **37:**409–418.

Klavans, A.S. (1983) Tidal hydrodynamics and sediment transport in Beaufort Inlet, North Carolina. *NOAA Technical Report NOS 100*.

Lewis, R.E. and Lewis, J.O. (1983) The principal factors contributing to the flux of salt in a narrow, partially stratified estuary. *Est. Coast. Shelf Sci.* **16:**599–626.

Logan, D.G. (1995) Oceanographic processes affecting larval transport in Beaufort Inlet, NC., MS Thesis, North Carolina State University, Raleigh, NC.

Luettich, R.A., Hench, J.L., Fulcher, C.W., Werner, F.E., Blanton, B.O. and Churchill, J.H. (1999) Barotropic tidal and wind driven larval transport in the vicinity of a barrier island inlet. *Fish. Oceanogr.* **8**(Suppl. 2)**:**190–209.

Liu, J.T. (1992) The influence of episodic weather events on tidal residual currents: a case study at Sebastian Inlet, Florida. *Estuaries* **15:**109–121.

Pietrafesa, L.J. and Janowitz, G.S. (1988) Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *Am. Fish. Soc. Sym.* **3:**34–50.

Pond, S. and Pickard, G.L. (1978). *Introductory Dynamic Oceanography*. New York: Pergamon Press.

Pritchard, D.W. (1967) Observations of circulation in coastal plain estuaries. In: *Estuaries*. G.H. Lauff, ed. Washington, DC: A.A.A.S. Publication 83, pp. 37–44.

Rijinsdorp, A.D., van Stralen, M. and van de Veer, H.W. (1985) Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. *Trans. Am. Fish. Soc.* **114:**461–470.

Rowe, P.M. and Epifanio, C.E. (1994) Tidal stream transport of weakfish larvae in Delaware Bay, USA. *Mar. Ecol. Prog. Ser.* **110:**105–114.

Simpson, M.R. and Oltmann, R.N. (1990) An acoustic Doppler discharge measurement system. *Proceedings 1990 Conf Hydraulic Engineering* **2:**903–908.

Smith, N.P. (1977) Meteorological and tidal exchanges between Corpus Christi Bay, Texas and the northwestern Gulf of Mexico. *Est. Coast. Mar. Sci.* **5:**511–530.

Tanaka, M., Goto, T., Tomiyana, M., Sudo, H. and Azuma, M. (1989) Lunar-phased immigration and settlement of metamorphosing Japanese flounder larvae into the nearshore nursery ground. *Rapp. P.-V. Reun. Con. Int. Explor. Mer.* **191**:303–310.

Uncles, R.J., Elliot, R.C.A. and Weston, S.A. (1985) Dispersion of salt and suspended sediment in a partially mixed estuary. *Estuaries* **8:**256–269.

Valle-Levinson, A. and Lwiza, K.M.M. (1995) The effects of channels and shoals on exchange between the Chesapeake Bay and the adjacent ocean. *J. Geophys. Res.* **100:**18 551–18563.

Warlen, S.M. (1994) Spawning time and recruitment dynamic of larval Atlantic menhaden, *Bevoortia tyrannus* in a North Carolina estuary. *Fish. Bull.* **92:**420–433.

Warlen, S.M. and Burke, J.S. (1990) Immigration of fall/winter spawning marine fishes into a North Carolina estuary. *Estuaries* **13:**453–461.

Weinstein, M.P., Weiss, S.L., Hodson, R.G. and Gerry, L.R. (1980) Retention of three taxa of post-larval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. *Fish. Bull.* **78:**419–436.

Wong, K.-C. (1994) On the nature of transverse variability in a coastal plain estuary. *J. Geophys. Res.* **99:**14 209–14 214 222.

Wood, L. and Hargis, W.J. (1971) Transport of bivalve larvae in a tidal estuary. In: *Proceeding of the Fourth European Marine Biological Symposium*, D. Crisp, ed. Cambridge, UK: University Press, pp. 29–44.