

Comparison of average larval fish vertical distributions among species exhibiting different transport pathways on the southeast United States continental shelf

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Water currents are vertically structured in many marine systems and as a result, vertical movements by fish larvae and zooplankton affect horizontal transport (Power, 1984). In estuaries, the vertical movements of larvae with tidal periods can result in their retention or ingress (Fortier and Leggett, 1983; Rijnsdorp et al., 1985; Cronin and Forward, 1986; Forward et al., 1999). On the continental shelf, the vertical movements of organisms interact daily and ontogenetically with depth-varying currents to affect horizontal transport (Pillar et al., 1989; Barange and Pillar, 1992; Cowen et al., 1993, 2000; Batchelder et al., 2002).

A suite of fish species, which use estuaries during the juvenile stage, spawn during winter on the mid- and outer continental shelf of the southeast United States (Fig. 1A): *Brevoortia tyrannus* (Atlantic menhaden), *Leiostomus xanthurus* (spot), *Micropogonias undulatus* (Atlantic croaker), *Paralichthys albigutta* (Gulf flounder), *P. dentatus* (summer flounder), and *P. lethostigma* (southern flounder). Vertically structured flow is a major part of proposed larval transport mechanisms for these species from offshore spawning areas to estuarine nursery habitats (Govoni and Pietrafesa, 1994; Hare et al., 1999). *Brevoortia tyrannus*, however, is found higher in the water column on average than the other species that use estuaries

during their juvenile stage (Miller et al., 1984; Govoni and Pietrafesa, 1994; Govoni and Hoss, 2001). Further, larvae of *B. tyrannus* apparently exhibit a difference in horizontal transport compared to other winter-spawning species that use estuarine habitats as juveniles; *B. tyrannus* larvae spawned on the southeast U.S. shelf may be transported to estuarine nursery habitats along the northeast U.S. shelf (Warlen et al., 2002). The effects of differences in vertical larval distribution on cross-shelf larval transport are unknown, and the transport pathways from shelf spawning areas to estuarine nursery areas remain unclear.

Other species also spawn during winter on the southeast United States continental shelf. Some species settle to benthic habitats on the shelf (e.g., *Etropus cyclosquamus* [shelf flounder], *E. microstomus* [smallmouth flounder], and *E. rimosus* [grayflounder], Leslie and Stewart, 1986) or remain on the shelf in pelagic habitats (e.g., *Etrumeus teres* [round herring], Crawford, 1981; Schwartz, 1989). However, some species are regularly advected offshore, entrained into the Gulf Stream, and exported northwards (e.g., *Bothus* spp. [peacock, eyed, and spotted flounders], *Peprius triacanthus* [butterfish], *Syacium papillosum* [dusky flounder], *Xyrichtys novacula* [pearly razorfish]; Hare and Cowen, 1991; Cowen et al., 1993;

Rotunno and Cowen, 1997; Grothues and Cowen, 1999).

The purpose of our study was to examine associations between average larval fish vertical distributions and general larval transport pathways on the southeast United States continental shelf during winter. Our goal was to determine if larval vertical distributions differed among species that exhibit different outcomes of larval transport: export from the local shelf, arrival at local estuaries, and retention on the shelf. Our approach, however, was unconventional. Rather than couple detailed descriptions of the flow field with detailed descriptions of larval vertical distributions (including diel variation), we chose to compare average vertical distributions among species that exhibit overall differences in larval transport. Vertical distribution data were collected in three separate years, over periods of time ranging from 24 to 96 hours. If average larval vertical distributions are different among species, and these differences occur consistently among the various sampling times and in concordance with the general outcome of transport, then we conclude that larval vertical distributions are an important part of larval transport on the southeast U.S. shelf.

Our specific objectives were two-fold: 1) to test the null hypothesis that there are no differences in larval fish vertical distributions between species, and 2) to evaluate significant differences in larval depth distribution in relation to the *a priori* classification of the outcome of transport. Vertically discrete data from six sampling times were analyzed, and owing to differences in protocols among sampling times, comparisons of larval vertical distributions were made within sampling times only. The results of these comparisons were then combined to evaluate whether there were consistent differences in larval vertical distributions among sampling times related to the outcome of larval transport.

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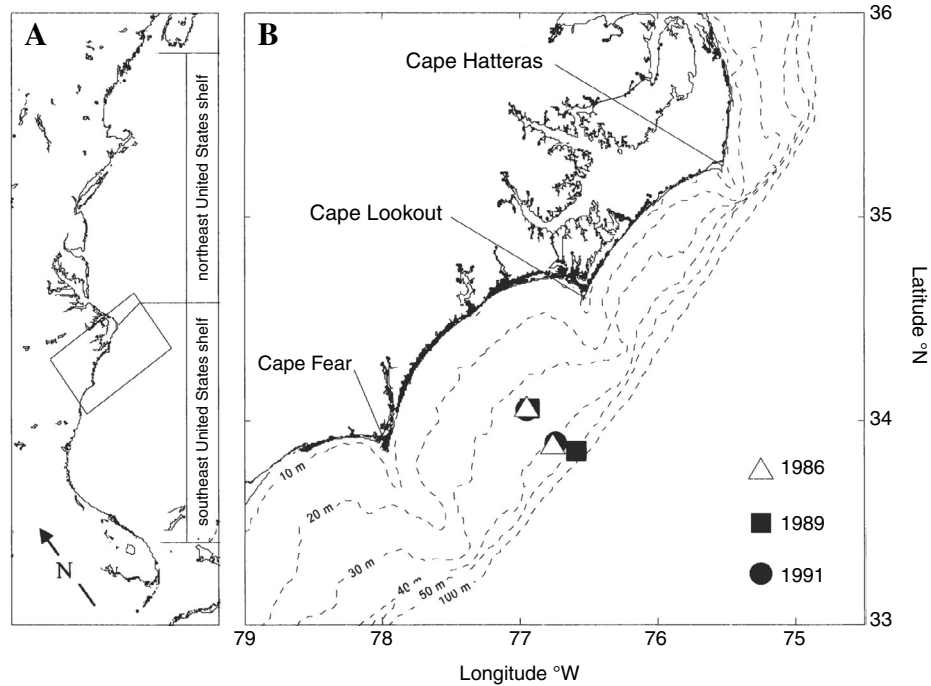


Figure 1

(A) Map of the east coast of the United States rotated 18° counter-clockwise. The spatial extent of the northeast and southeast United States continental shelves is indicated by each rectangle. The area of panel B is shown as a trapezoid. (B) The northern portion of the southeast United States continental shelf showing the coastline, the 10-m, 20-m, 30-m, 40-m, 50-m, and 100-m isobaths. The three prominent capes are identified and locations of stations sampled in this study are shown.

Material and methods

Data collection

Larval fish were collected every six hours (0600, 1200, 1800, and 2400) at an offshore and an inshore station during three winters: 21–26 February 1986, 26 January–1 February 1989, and 5–7 February 1991 (Fig. 1B). Offshore stations were located on approximately the 50-m isobath, and inshore stations were located on approximately the 35-m isobath. In 1986, offshore and onshore stations were occupied for 102 and 48 h, respectively. Collections were taken horizontally at 1, 18, and 32 m at the offshore station and 1, 13, and 25 m at the inshore station with a 60-cm opening-closing bongo net (Weibe and Benfield, 2003) with 333- μ m mesh and a 1-m² Tucker trawl (Weibe and Benfield, 2003) with 202- μ m mesh. In 1989, offshore and inshore stations were occupied for 78 and 72 hours, respectively. Collections were taken horizontally at 1, 22, and 45 m at the offshore station and 1, 13, and 30 m at the inshore station with a 1-m² Tucker trawl with 333- μ m mesh. In 1991, offshore and inshore stations were occupied for 24 and 30 h, respectively. Collections were made with 1-m² MOCNESS (Wiebe et al., 1976) with 333- μ m mesh. Oblique samples were collected within 5-m intervals from 35 m

to the surface at the offshore station and from 30 m to the surface at the inshore station. The mid-point of each depth stratum was used as the depth of the collection. In 1986 and 1989, volume of water filtered was measured with a flowmeter (General Oceanics model 2030, Miami, FL) with a standard rotor. In 1991, volume filtered was measured with a flowmeter provided with the MOCNESS (BESS, Falmouth, MA).

Larval fish were sorted from collections and identified to the lowest taxon possible. The larvae of selected taxa were counted: *Bothus* spp., *Etropus* spp. (not including *E. crossotus*), *E. teres*, *Paralichthys* spp., *P. triacanthus*, *S. papillosum* and *X. novacula*. Counts of *B. tyrannus*, *L. xanthurus*, and *M. undulatus* were obtained from Govoni and Pietrafesa (1994) and Govoni and Spach (1999). Larval concentrations were calculated for each depth stratum (number of larvae/100 m³).

Comparisons of larval vertical distributions

Center of mass calculations are frequently used for comparison of fish larval depth distributions (e.g., Brodeur and Rugen, 1994), but Pearre (1979) raised valid criticisms of this approach; for example a uniform distribution still has a mean depth. To obviate these criticisms, larval depth distributions of each taxon were compared

by using a test of independence (Pearson chi-square, Sokal and Rohlf, 1981; McCleave et al. 1987). Depth distributions were averaged over each station. Comparisons were then made between all pairs of taxa within a station, and a Bonferoni correction was applied to assess the significance of the tests of independence. Comparisons were not made between stations, because sampling methods varied and depth distributions were not directly comparable. The following null hypothesis was evaluated: during each station occupation, average larval depth distributions were independent of species. Column and row variables were species and depth strata; cell values were the average proportion of the larvae captured in a depth stratum at a station. Comparisons of center of mass were also made and the results were very similar to the results of the test of independence reported in the present study.

The calculation of average proportion was made in two steps. First, the proportion of larvae (P) collected in each depth stratum (d) at each sampling time (i) during each station occupation (j) was calculated:

$$P_{dij} = \frac{C_{dij}}{\sum_d C_{dij}},$$

where C = larval concentration 100/m³.

Then the average proportion of larvae (\bar{P}) for each depth stratum (d) was calculated for each station (j):

$$\bar{P}_{dj} = \frac{\sum_i P_{dij}}{n_{ij}},$$

where n_{ij} = the number of sampling times (i) during station occupation (j).

Because the significance of a test of independence depends, in part, on the magnitude of the cell values (i.e., sample sizes), average larval concentration of each species during each station occupation (number of larvae/100 m³) was used as a weighting factor. The average proportion of larvae at depth during a station occupation (\bar{P}_{dj}) was multiplied by the weighting factor to derive the cell values for use in the test of independence. The weighting factor approximated the number of fish larvae collected, and incorporated the effect of variability in sampling volume.

Values of the standardized residuals, which are a result of the test of independence, were used to classify significant differences in depth distribution as follows: species A shallower (<) than species B, species A deeper (>) than species B, and species A distributed differently (< or >) than species B. This last category was assigned when one species was not clearly deeper or shallower than the other species, yet its depth distributions were significantly different.

To evaluate whether larval fish vertical distributions were associated with larval transport, the results of

the individual species comparisons were pooled across station by the *a priori* assigned outcome of transport. The number of significant differences found between species were then compared to the number of significant differences expected with a 5% error rate by using the G -statistic (Sokal and Rohlf 1981). For example, in a comparison of *B. tyrannus* to exported species, five pairwise comparisons of larval depth distributions were found to be significantly different and 12 were not significantly different. At $\alpha=0.05$, one significant and 16 nonsignificant differences are expected. The G -statistic demonstrates that more significant differences were found between *B. tyrannus* and exported species than expected by chance. The classifications of significant depth differences (shallower, deeper, different) were then examined to determine the relation between larval vertical distributions and the general outcome of larval transport.

Results

Comparison of larval vertical distributions indicated that *B. tyrannus* often had the shallowest larval vertical distribution. There were more significant differences than expected by chance between the vertical distributions of *B. tyrannus* and exported, estuarine, and shelf-resident taxa (Table 1). For all significant differences, the standard deviates from the test of independence indicated that *B. tyrannus* were found in shallower water than were other taxa (Appendix 1).

Exported taxa generally were higher in the water column than estuarine and shelf-resident taxa. There were more significant differences than expected by chance between the vertical distributions of exported taxa and estuarine and shelf-resident taxa (Table 1). Further, 9 of 12 significant differences between exported and estuarine taxa indicated that exported taxa were found in shallower water; 8 of 11 significant differences between exported and shelf resident taxa indicated that exported taxa were found in shallower water (Appendix 1).

The vertical distributions of estuarine and shelf-resident taxa were different more often than expected by chance, but taxa of neither group were consistently found in shallower water (Table 1). Significant differences in larval vertical distributions were distributed evenly among the three classifications of the direction of difference ($n=4$ shallower; $n=2$ deeper; $n=5$ different) (Appendix 1).

Discussion

The results indicate an overall hierarchy of larval vertical distributions; *B. tyrannus* was found in shallower water than were exported taxa, and exported taxa were shallower than estuarine and shelf-resident taxa. Although this general pattern emerged, considerable variability in larval vertical distributions was observed, which is a common result of many studies (e.g., Boehlert

Table 1

Summary of the pairwise comparisons of larval depth distributions between species classified by the *a priori* outcome of transport. In each table cell, the number to the left is the number of significant pairwise differences, the number to the right is the total number of comparisons across the six station occupations, and the number in parentheses is the *G*-statistic for evaluating the null hypothesis that the number of observed differences is as expected with a 5% error rate. The critical value at $\alpha=0.05$ is 5.99 and significant values are indicated in bold. Values greater than 5.99 indicate that there are more significant differences between species than expected by chance. Exported taxa are *Bothus* spp., *Peprilus triacanthus*, *Syacium papillosum*, *Xyrichtys novacula*. Estuarine taxa include *Leiostomus xanthurus*, *Micropogonias undulatus*, and *Paralichthys* spp. Shelf resident taxa include *Etropus* spp. and *Etrumeus teres*.

	<i>Brevoortia tyrannus</i>	<i>A priori</i> classification of the outcome of transport		
		Exported	Estuarine	Shelf resident
Exported	5 / 17 (10.29)	2 / 17 (1.17)		
Estuarine	12 / 15 (55.35)	12 / 43 (23.88)	5 / 13 (12.96)	
Shelf resident	9 / 12 (39.11)	11 / 34 (25.09)	11 / 30 (27.96)	2 / 6 (4.39)

and Mundy, 1994; Brodeur and Rugen, 1994). Variability in larval fish vertical distributions (and zooplankton) is related to processes that influence water column mixing (e.g., Heath et al., 1988; Ince et al., 2001) and to species-specific responses to diel cycles and gradients in turbulence, temperature, and salinity (DeVries et al. 1995; Olla et al., 1996; Gray and Kingsford, 2003). The approach used in the present study was to average over shorter-scale variability (hours) in larval vertical distributions to examine longer-time-scale patterns (days) in larval vertical distributions.

Average larval vertical distributions of exported, estuarine-dependent, and shelf-resident taxa and the implied outcomes of their larval transport are consistent with the results of physical oceanographic models and observations of shelf circulation in the southeast United States continental shelf. The model of Janowitz and Pietrafesa (1980) (see also Miller et al., 1984) indicated a three-layered, cross-shelf flow during winter: surface and near-bottom offshore flow, and intermediate onshore flow. Similarly, the model of Werner et al. (1999) indicated a two-layered, cross-shelf flow during winter: an offshore flow near the surface and onshore flow throughout the rest of the water column. Surface flow in the study area during winter is typically offshore (Govoni and Pietrafesa, 1994). On the inner and middle shelf (water depths <40 m), average bottom flow is onshore; on the outer shelf (water depth 40–75 m), average intermediate flow is onshore, whereas bottom flow is offshore (Fig. 5b in Lee et al., 1989). Modeled and observed flow fields may indicate that larvae in the surface water will move offshore (exported taxa), where the probability of entrainment into the Gulf Stream is higher. Larvae that are in the middle or lower portion of the water column will move onshore (i.e., estuarine-dependent and shelf-resident taxa). Thus, the average larval vertical distributions, the general outcome of larval transport, and the generalized observed and modeled vertical flow fields are consistent.

Differences between vertical distributions of larval *B. tyrannus* and the other estuarine-dependent taxa (Fig. 2; see also Govoni and Pietrafesa, 1994) imply differences in cross-shelf transport. There are several possibilities, none mutually exclusive. 1) Onshore transport of larval *B. tyrannus* occurs with northeast wind events and onshore transport of other estuarine-dependent larvae occurs with southwest or northwest wind events. This possibility is supported by the model simulations of Hare et al. (1999). 2) Cross-shelf transport of *B. tyrannus* larvae occurs in surface Gulf Stream intrusions (Checkley et al., 1988; Stegmann and Yoder, 1996), whereas cross-shelf transport of other estuarine-dependent larvae occurs by wind-driven mechanisms. This possibility has not been adequately evaluated. 3) All estuarine-dependent larvae are transported across the shelf by the same mechanisms, but the rate of their transport differs. For example, southwest wind events cause onshore transport rates to be greater for the other estuarine-dependent taxa because *B. tyrannus* larvae spend less time in the intermediate portion of the water column. This possibility is also supported by Hare et al. (1999), who found that in modeled larval vertical distributions, the outcome of larval transport was modified by circulation. From these alternative hypotheses, it is clear that our understanding of the cross-shelf transport of larval fishes remains incomplete and that the effective physical and biological mechanisms are complex.

One approach to resolving the affect of vertical distribution on cross-shelf larval transport is to develop a specific hypothesis regarding supply of larvae to inlets that is based on the above possibilities and then to test these hypotheses using the long time-series of larval ingress collected at Beaufort Inlet (see Warlen, 1994). Three alternative patterns in ingress, based on the three possibilities presented above, could be evaluated by using ingress data collected at Beaufort Inlet: 1) ingress of *B. tyrannus* occurs during northeast winds, and

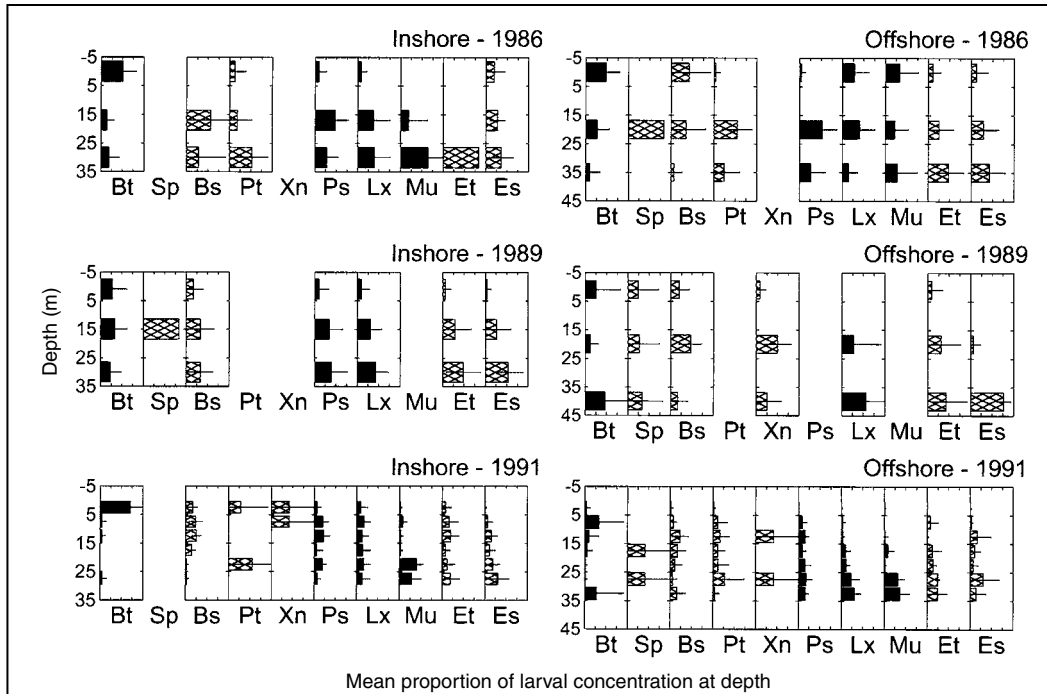


Figure 2

Mean proportions of larvae sampled at depths at six stations on the southeast United States shelf. Error bars indicate standard deviation of mean proportions calculated by using all the samples collected at a station. The x-axis of all panels is the same and ranges from 0 to 1.2. The species indicated in each figure is denoted by a two letter code (Bt=*Brevoortia tyrannus*, Sp=*Syacium papillosum*, Bs=*Bothus* spp., Pt=*Peprilus triacanthus*, Xn=*Xyrichtys novacula*, Ps=*Paralichthys* spp., Lx=*Leiostomus xanthurus*, Mu=*Micropogonias undulatus*, Et=*Etrumeus teres*, and Es=*Etropus* spp.). Species are grouped by an *a priori* assignment of their general outcome of transport.

the ingress of other species occurs during northwest, west, and southwest winds; 2) ingress of *B. tyrannus* is not related to wind, and ingress of the other species is related to northwest, west, and southwest winds; 3) and ingress of all estuarine-dependent species occurs during similar wind forcing. Other studies have established similar *a priori* predictions for relations between wind forcing and ingress, yet results have been equivocal (e.g., Blanton et al., 1995). One explanation is that cross-shelf larval transport and larval ingress occur through multiple steps (Boehlert and Mundy, 1988; Hettler and Hare, 1998), effectively decoupling wind-driven, cross-shelf larval transport from larval ingress.

Similarities in vertical distributions of larval *B. tyrannus* and exported larval taxa indicate that a greater proportion of *B. tyrannus* larvae may be entrained into the Gulf Stream than larvae of other species that use southeast estuaries as juvenile nurseries. Once entrained into the Gulf Stream, larvae are transported northeastward and they either continue to move in the Gulf Stream or are returned to the shelf edge north of Cape Hatteras by warm-core ring streamers or in discharges of Gulf Stream water (Hare and Cowen 1991, 1996; Churchill et al., 1993; Cowen et al., 1993; Hare

et al., 2002). Govoni and Spach (1999) reported offshore exchange of *B. tyrannus* larvae into the Gulf Stream, and Warlen et al. (2002) concluded that some *B. tyrannus* larvae spawned south of Cape Hatteras do enter estuaries north of Cape Hatteras in the spring. The mechanisms of northward transport of *B. tyrannus* have yet to be studied, but transport to the northeast United States shelf edge by the same mechanisms as those that drive exported taxa is possible.

In marine systems, larval fish interact with vertically structured flow with vertical motions and thereby affect their horizontal transport (Cowen et al., 1993, 2000; Grioche et al., 2000). Apart from specific transport mechanisms, the present study demonstrates an overall link between larval vertical distributions and transport for multiple species. Species that moved inshore or remained on the shelf were found deeper in the water column than species that were exported from the shelf. Cowen et al. (1993) indicated that as larvae on the northeast U.S. shelf edge move deeper, they become more susceptible to onshore flows. Similarly, Cowen et al. (2000) argued that pomacentrid larvae are distributed at mid-depths off Barbados, and these mid-depth distributions resulted in larval retention

closer to the island. Peterson (1998) proposed that in upwelling systems, copepods can affect retention on the shelf through ontogenetic vertical migrations, whereby younger stages inhabit the upper offshore-flowing water and older stages inhabit the lower onshore-flowing water (see also Peterson et al., 1979). Similar models were developed by Pillar et al. (1989) and Barange and Pillar (1992) for euphausiids in the Benguela upwelling zone. Additionally, Batchelder et al. (2002) indicated that copepods can be retained nearshore in upwelling systems through diel vertical migrations between offshore-flowing surface waters and onshore-flowing bottom waters. From these studies and the results from the present study, a general hypothesis emerges that in many marine systems, fish larvae and zooplankton can affect onshore transport by moving deeper in the water column. Thus, similar to selective tidal stream transport whereby larvae use predictable tidal flows to either remain in estuaries or enter estuaries (Forward and Tankersley, 2001), general features in circulation may exist across physical oceanographic systems that allow larvae to influence their cross-shelf transport through basic changes in their vertical distribution.

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Appendix 1

Significant pairwise differences between the average larval vertical distributions of 10 species on the southeast United States continental shelf. A total of 187 comparisons were made and the 69 significant differences are listed below. Significant differences between average depth distributions were determined by using a test of independence with the cell values as average proportion of larvae at depth, averaged over a station occupation and weighted by the mean larval concentration at the station. A Bonferroni correction was applied to significance tests within each station occupation. The direction of significant differences (shallower [<], deeper [>], and different [<>]) was determined from the standardized residuals from the test of independence.

Year	Station	Species A		Species B
1986	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Peprilus triacanthus</i>
1986	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Paralichthys</i> spp.
1986	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Leiostomus xanthurus</i>
1986	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Etopus</i> spp.
1986	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Etrumeus teres</i>
1986	Offshore	<i>Bothus</i> spp.	<	<i>Peprilus triacanthus</i>
1986	Offshore	<i>Bothus</i> spp.	<	<i>Paralichthys</i> spp.
1986	Offshore	<i>Bothus</i> spp.	<	<i>Etrumeus teres</i>
1986	Offshore	<i>Peprilus triacanthus</i>	>	<i>Leiostomus xanthurus</i>
1986	Offshore	<i>Peprilus triacanthus</i>	>	<i>Micropogonias undulatus</i>
1986	Offshore	<i>Peprilus triacanthus</i>	<>	<i>Etopus</i> spp.
1986	Offshore	<i>Peprilus triacanthus</i>	<>	<i>Etrumeus teres</i>
1986	Offshore	<i>Paralichthys</i> spp.	>	<i>Leiostomus xanthurus</i>
1986	Offshore	<i>Paralichthys</i> spp.	>	<i>Micropogonias undulatus</i>
1986	Offshore	<i>Paralichthys</i> spp.	<>	<i>Etopus</i> spp.
1986	Offshore	<i>Paralichthys</i> spp.	<>	<i>Etrumeus teres</i>
1986	Offshore	<i>Leiostomus xanthurus</i>	<	<i>Etopus</i> spp.
1986	Offshore	<i>Leiostomus xanthurus</i>	<	<i>Etrumeus teres</i>
1986	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Peprilus triacanthus</i>
1986	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Paralichthys</i> spp.
1986	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Leiostomus xanthurus</i>
1986	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Micropogonias undulatus</i>
1986	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Etrumeus teres</i>
1986	Inshore	<i>Peprilus triacanthus</i>	>	<i>Paralichthys</i> spp.
1986	Inshore	<i>Paralichthys</i> spp.	<>	<i>Etopus</i> spp.
1989	Offshore	<i>Bothus</i> spp.	<	<i>Etopus</i> spp.
1989	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Leiostomus xanthurus</i>
1989	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Etopus</i> spp.
1989	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Etrumeus teres</i>
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Bothus</i> spp.
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Peprilus triacanthus</i>
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Paralichthys</i> spp.
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Leiostomus xanthurus</i>
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Micropogonias undulatus</i>
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Etopus</i> spp.
1991	Offshore	<i>Brevoortia tyrannus</i>	<	<i>Etrumeus teres</i>
1991	Offshore	<i>Bothus</i> spp.	<	<i>Leiostomus xanthurus</i>
1991	Offshore	<i>Bothus</i> spp.	<	<i>Micropogonias undulatus</i>
1991	Offshore	<i>Bothus</i> spp.	<	<i>Etopus</i> spp.
1991	Offshore	<i>Bothus</i> spp.	<	<i>Etrumeus teres</i>
1991	Offshore	<i>Peprilus triacanthus</i>	<	<i>Leiostomus xanthurus</i>
1991	Offshore	<i>Peprilus triacanthus</i>	<	<i>Micropogonias undulatus</i>
1991	Offshore	<i>Peprilus triacanthus</i>	<	<i>Etrumeus teres</i>

continued

Appendix 1 (continued)

Year	Station	Species A		Species B
1991	Offshore	<i>Paralichthys</i> spp.	<	<i>Leiostomus xanthurus</i>
1991	Offshore	<i>Leiostomus xanthurus</i>	<>	<i>Etropus</i> spp.
1991	Offshore	<i>Leiostomus xanthurus</i>	<>	<i>Etrumeus teres</i>
1991	Offshore	<i>Etropus</i> spp.	<>	<i>Etrumeus teres</i>
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Bothus</i> spp.
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Paralichthys</i> spp.
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Leiostomus xanthurus</i>
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Micropogonias undulatus</i>
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Etropus</i> spp.
1991	Inshore	<i>Brevoortia tyrannus</i>	<	<i>Etrumeus teres</i>
1991	Inshore	<i>Bothus</i> spp.	<	<i>Peprilus triacanthus</i>
1991	Inshore	<i>Bothus</i> spp.	<	<i>Paralichthys</i> spp.
1991	Inshore	<i>Bothus</i> spp.	<	<i>Leiostomus xanthurus</i>
1991	Inshore	<i>Bothus</i> spp.	<	<i>Micropogonias undulatus</i>
1991	Inshore	<i>Bothus</i> spp.	<	<i>Etropus</i> spp.
1991	Inshore	<i>Bothus</i> spp.	<	<i>Etrumeus teres</i>
1991	Inshore	<i>Peprilus triacanthus</i>	<>	<i>Etropus</i> spp.
1991	Inshore	<i>Xyrichthys novacula</i>	<	<i>Micropogonias undulatus</i>
1991	Inshore	<i>Xyrichthys novacula</i>	<	<i>Etropus</i> spp.
1991	Inshore	<i>Paralichthys</i> spp.	<	<i>Micropogonias undulatus</i>
1991	Inshore	<i>Paralichthys</i> spp.	<	<i>Etropus</i> spp.
1991	Inshore	<i>Leiostomus xanthurus</i>	<	<i>Micropogonias undulatus</i>
1991	Inshore	<i>Leiostomus xanthurus</i>	<	<i>Etropus</i> spp.
1991	Inshore	<i>Micropogonias undulatus</i>	>	<i>Etropus</i> spp.
1991	Inshore	<i>Micropogonias undulatus</i>	>	<i>Etrumeus teres</i>
1991	Inshore	<i>Etropus</i> spp.	>	<i>Etrumeus teres</i>