Abstract.–*Caranx hippos* spawn at subtropical and tropical latitudes, but some of their propagules are dispersed hundreds of kilometers north of Cape Hatteras into temperate waters of the western North Atlantic. The effect that this northward dispersal pattern has upon the population depends on whether these juveniles return south during autumn to overwinter or whether they become expatriated from the spawning population and die from hypothermal winter conditions at temperate latitudes. We evaluated whether repatriation was possible by comparing *C. hippos* seasonal abundance and size-structure from New York to Florida. Young-of-the-year *C. hippos* occurred annually during summer and autumn but were uncommon in relation to other species in subtropical and temperate estuaries. Sizes of *C. hippos* at temperate latitudes were as large as conspecifics at subtropical latitudes and juveniles of other species that are known to migrate during autumn from temperate nursery grounds to subtropical latitudes. As *C. hippos* disappeared from estuaries of the middle Atlantic states in autumn, similar-size fish appeared on the inner continental shelf. We postulate that at least some of the *C. hippos* observed migrating from temperate estuaries during the autumn eventually overwinter at subtropical latitudes, where they can return to the spawning population. This is unusual, because individuals of many other species whose larvae are transported north of Cape Hatteras do not appear to successfully migrate back to subtropical overwintering habitats. This life-history pattern, in which fish begin their first year in the Carolinian biogeographic province, are dispersed to the Virginian province, and return to the Carolinian province before their first winter, has been demonstrated for only one other western North Atlantic finfish species: bluefish (*Pomatomus saltatrix*). A few other species are likely to occupy and reproduce within such large-scale oceanographic systems because they have a combination of spawning, larval, and juvenile traits that is similar to that of *P. saltatrix* and *C. hippos*.

Consequences of dispersal of subtropically spawned crevalle jacks, *Caranx hippos*, to temperate estuaries*

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In the western North Atlantic, many species spawn at tropical and subtropical latitudes, and their larvae are dispersed to temperate and even boreal regions (e.g. Gill, 1904; Markle et al., 1979; Curran, 1989). This transport of larvae occurs in association with the Gulf Stream (Wroblewski and Cheney, 1984; Hare and Cowen, 1991, 1996) and disperses propagules from the Carolinian to the Virginian biogeographic province (Briggs, 1974, 1996). This process, which involves the entrainment of eggs and larvae into oceanographic currents and the dispersal of propagules to various water masses, is understood for only a few species and may vary considerably between species. Perhaps the most famous example is that of catadromous freshwater eels (*Anguilla anguilla* and *A. rostrata*), which spawn in the Sargasso Sea and whose larvae are transported to coastal nurseries in North America and Europe (McCleave et al., 1987). Larval *A. rostrata* drift for up to one year (Kleckner and McCleave, 1985) through gyres in the southwestern Sargasso Sea, the Antilles Current, and the Florida Current and its Gulf Stream extension before moving into coastal waters (McCleave, 1993). In the case of a wrasse, *Xyrichtys novacula*, northward transport across hundreds of kilometers occurs in as little as eight days, and cross-shelf transport in the

northern portion of the Carolinian province is aided by interactions between western-edge, warm-core eddies and the Gulf Stream itself (Hare and Cowen, 1991). Similar northward transport in association with the Gulf Stream occurs for "spring-spawned" bluefish, *Pomatomus saltatrix*, except that for this species dispersal time is longer—about 2 months (McBride and Conover, 1991)—and its juveniles may actively swim out of the Gulf Stream system (Hare and Cowen, 1996). Although some species are transported annually in this manner (e.g. *Pomatomus*), others are transported less regularly (*Xyrichtys*, *Bothus*, *Syacium*), and still other species do not move between slope and shelf water masses (Cowen et al., 1993).

Those individuals dispersed across biogeographic boundaries become expatriated, in terms of passing on their genes if they do not return to spawning grounds to reproduce. *Anguilla* species remain in coastal habitats for several years before migrating back to the Sargasso Sea (Tesch, 1977), but many species that spawn at subtropical latitudes are physiologically incapable of overwintering at temperate latitudes. To our knowledge, only *P. saltatrix* spawns at

subtropical latitudes and its propagules, once dispersed to temperate latitudes, are known to migrate south within the same year. This species is successful largely because it spawns early in the year in the subtropics and juveniles enter temperate estuaries at a time when their principal prey is becoming available (Juanes et al., 1994). Direct evidence of a successful autumn migration by young-of-the-year *P. saltatrix* is available from recaptures of tagged individuals and size-frequency analyses (Lund and Maltezos, 1970; McBride et al., 1993). This "spring-spawned" cohort of *P. saltatrix* was more abundant than other intraspecific cohorts in the western North Atlantic during the 1980s and early 1990s (Chiarella and Conover, 1990; McBride et al., 1993), and this species repeats this life-history pattern in several oceanographic systems worldwide (Juanes et al., 1996).

The effects of this transport process, from the Carolinian province to the Virginian province, is known for few other species and these examples suggest a different fate for these species than for *P. saltatrix*. Moss (1973) concluded that the "sluggish" swimming ability and the critical thermal minimum of 8.7°C for planehead filefish, *Monocanthus hispidus*, prevented individuals of this species from surviving once they had been dispersed to temperate latitudes. Hare and Cowen (1991) observed a wrasse, *Xyrichtys novacula*, settling on the continental shelf at temperate latitudes, but successive cruises could not find survivors from the initially observed cohort. And McBride and Able (1998) reported on the annual appearance of butterflyfishes (*Chaetodon* spp.) at temperate latitudes, but field collections and laboratory experiments led them to conclude that none of these individuals survived through their first winter. Sinclair (1988) would categorize these unfortunate individuals as "vagrants" from, as opposed to "members" of, a population.

Although the ecological information about these tropical forms as they occur in temperate waters is limited, the common paradigm is that "[the] Gulf Stream has a profound effect upon the distribution of shore animals in the western Atlantic . . . many tropical forms are left stranded along the inhospitable shores of northeastern North America." (Briggs, 1996; p. 238). We believe that Briggs's conclusion can be applied to most of these species; nonetheless, juveniles of several "southern" species grow and survive well at temperate latitudes during the summer and, based on their size by autumn and their general mobility, may migrate successfully back to subtropical latitudes before winter (see also Hare and Cowen, 1993). We propose that at least one other species is capable of following a dispersal-migration pattern that links the temperate and subtropical latitudes during its first year. The crevalle jack, *Caranx hippos* (Linnaeus), is a migratory, coastal species that is distributed worldwide at subtropical and tropical latitudes (Briggs, 1960; Kwei, 1978; Grosslein and Azarovitz, 1982). In the western North Atlantic, it occurs primarily in the southeastern United States and the Gulf of Mexico (U.S. Department of Commerce, 1986), and spawning is known to occur only in the subtropical Straits of Florida (Berry, 1959; Fahay, 1975) and in the tropical Caribbean Sea (Montolio, 1978). Young-of-the-year (YOY) *C. hippos*

occur in subtropical estuaries of the south Atlantic states, and they use these habitats as nurseries before presumably migrating offshore in autumn (Berry, 1959). However, YOY *C. hippos* are also reported from many temperate estuaries north of Cape Hatteras (McBride[1]). Despite the broad geographic distribution of YOY *C. hippos*, little is known about their early life history at any latitude. From archived museum collections, recent field collections, and the literature, we assembled data about *C. hippos* in both southern and northern estuaries and postulate on the significance of dispersal of YOY *C. hippos* across two biogeographic provinces.

Materials and methods

Archival collections were examined at the New York State Museum, the American Museum of Natural History, and the Academy of Natural Sciences of Philadelphia, and collection dates, locations, and sizes of *C. hippos* from coastal habitats of New York and New Jersey were recorded (material examined is listed in McBride[1]). Similar data for *C. hippos* in subtropical estuaries (from Cape Hatteras, North Carolina, to Cape Sable, Florida) were taken from Berry (1959). Densities and size data from samples collected in Great South Bay (New York) and southern New Jersey embayments during 1987 and 1988 were also examined (see McBride and Conover [1991] for seine-survey design; weir-sample data from Rountree et al.[2]). Fish densities in these other estuaries and from the published literature were calculated as

$$CPUE = (Catch\ per\ unit\ of\ effort$$
$$[number\ of\ fish\ per\ seine\ haul])$$

for the period May–October unless stated otherwise. Field sampling (described below) of temperate coastal habitats was also completed, and abundance, habitats, seasonality, and sizes of *C. hippos* were examined. Unless noted otherwise, fish size is reported to the nearest cm fork length (FL). A Gompertz model was used to model growth:

$$FL = L_\infty \exp\left(-\exp\left\{-G[DOY - X_0]\right\}\right),$$

where FL = fork length in mm;
    L_∞ = asymptotic length;
    G = instantaneous rate of growth at age X_0;
  DOY = day of the year, and
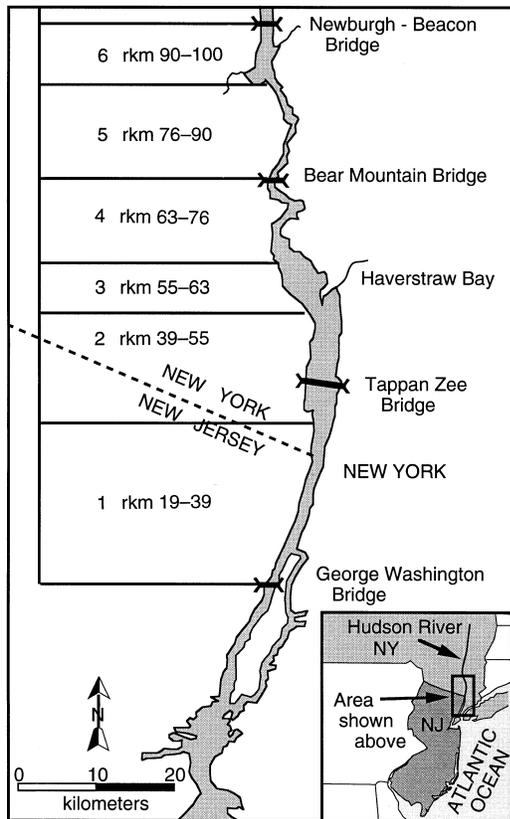 X_0 = inflection point of the curve.

Figure 1

Sampling strata (1–6) in the Hudson River region where *Caranx hippos* was common. Haverstraw Bay is within strata 2–4. Strata 7–12 (river kilometers 100–246) are not shown. Jamaica Bay is located just east of the mouth of the Hudson River.

Growth modeling and other statistical analyses were performed by using SAS (SAS, 1990).

Field sampling—Hudson River

Recent data (1986–1993) were analyzed from an ongoing (since 1974) survey of the entire Hudson River (Fig. 1). Fish were collected during daylight over a 1-wk period every other week between mid-June and mid-November. During each sampling week, a 30.5-m × 2.4-m (max. mesh=10 mm) beach seine was set in an arc from a boat at approximately 100 stations. Station locations were selected in a stratified random design by using 12 strata between Manhattan and Albany, New York (from river kilometer [rkm] 19 to 246). The length of each stratum varied from 8 to 44 km, and typically 5–20 hauls were completed in each stratum during each biweekly period. Mean abundance, by month or stratum, was calculated from transformed values of the number of fish in each seine haul ($\log_e [n+1]$) and was expressed as a geometric mean (antilogged mean values of –1). Annual abundances were also calculated as geometric means but only for data from August to September (when *C. hippos* were consistently collected).

Field sampling—Haverstraw and Jamaica bays

Further analyses of the ecology of *Caranx hippos* in the Hudson River were based on data from an independent survey for the same 8-yr period (1986–1993) as the survey of the entire river. This additional survey focused on two subregions of the estuary: Haverstraw Bay and Jamaica Bay. Haverstraw Bay corresponds to strata numbers 2–4 of the Hudson River survey (Fig. 1); Jamaica Bay is a satellite embayment close to the mouth of the Hudson River.

Seining in Haverstraw Bay occurred biweekly from July to November (see also McKown and Young, 1992). Typically, 25 stations were sampled during daylight over a 2-d period; at each station, a single haul was made with a 61-m × 3-m beach seine (max. mesh=6.4 mm) set in an arc from a boat. This seine was used similarly in Jamaica Bay from May to November, but sampling frequency was generally monthly and only 4–5 stations were sampled each time. Temperature and salinity were measured with a hand-held thermometer and refractometer from surface-water samples after the net was hauled. Abundance of *C. hippos* was calculated as above (i.e. by geometric means).

Field sampling—the continental shelf

To determine seasonal abundance of *C. hippos* above the U.S. east coast continental shelf, we examined data collected during 1972–1996 in the National Marine Fisheries Service's bottom-trawling program. This program followed a stratified random statistical design to survey fish stocks of the continental shelf (9–366 m) from Cape Fear, North Carolina, to Nova Scotia, Canada. Standard methods were to tow a 24.4- or 30.5-m otter trawl (13-mm codend liner) for 30 min at randomly assigned stations within fixed strata (strata were delimited largely by depth and latitude). All samples combined covered all seasons, but sampling intensity was greatest during spring (March–May) and autumn (September–November), when about 350 stations were sampled during each 6–8 wk period. Fish were measured to the nearest cm. General survey design and its specific applications for other species can be found in many other studies (e.g. Grosslein and Azarovitz, 1982; Despres-Patanjo et al., 1988; McBride et al., 1998).

Results

Latitudinal comparisons

Young-of-the-year *C. hippos* occurred in subtropical estuaries between North Carolina and Florida from June to November and in temperate estuaries of New York and New Jersey during July–November (Fig. 2). On average, we observed only about one fish collected in three or more seine hauls, and these arithmetic mean densities were the same for temperate and subtropical estuaries (Fig. 3).

At subtropical latitudes, individuals <4.0 cm FL were present in all months, June–November (Fig. 2). Small individuals were also present for three months, July–September, at temperate latitudes. In both biogeographic regions,

some individuals had reached approximately 20 cm FL by October and November, suggesting that absolute growth could exceed 1 mm/d. The prolonged appearance of small fish in southern estuaries, in particular, and the lack of age-specific data precluded more detailed comparisons of growth rates.

Estuarine residency

In the Hudson River system, *C. hippos* occurred annually but its density varied by an order of magnitude among years (Table 1). This species occurred as far upstream as rkm 102 (i.e. lower part of stratum 7) but was most abundant in the upper portion of Haverstraw Bay (Fig. 4A). Seasonally, *C. hippos* resided in the Hudson River system from July to November and was most common from late July to early October (Figs. 4B, 5A). The median temperature for collections of *C. hippos* was 26°C in Haverstraw Bay and 24°C in Jamaica Bay (Fig. 6). Near Haverstraw Bay, where salinities were much lower than those of Jamaica Bay, *C. hippos* was capable of invading nearly freshwater regions of the Hudson River (Fig. 6). Abundance measured with a 61-m net, set in a comparable manner in both bays, showed that the abundance of *C. hippos* was much higher in Jamaica Bay than in Haverstraw Bay. Abundance in Great South Bay, New York, was also consistently higher than in Haverstraw Bay (Fig. 5A), even though a smaller, 30-m net was used.

Fork length of fish collected during 1986–1993 in the Hudson River estuary ranged from 2.9 to 17.6 cm. Growth rate was modeled by using data for New York and New Jersey estuaries (Fig. 5B; n=439), and the resulting equation,

$$FL = 136.6\exp\left(-\exp\{-0.0315\,[DOY - 211]\}\right), \quad (r^2=0.75),$$

predicted a peak instantaneous growth rate for July 30, after which growth slowed and fish reached a mean asymptotic length of 13.7 cm. The distribution of residuals for this growth model suggested that the asymptotic length was biased (i.e. lowered) by the presence of small, presumably young, juveniles in August–September; therefore we consider these growth estimates to be preliminary.

Continental shelf distributions

A total of 657 *C. hippos* were collected at 134 stations between 33°47'N and 41°00'N and at depths from 6 to 38 m (Fig. 7A). Although present in all but four years during 1972–1996, *C. hippos* were collected only in the months of July (1 of 134 stations=0.8%), September (84.3%), October (14.2%), and November (0.8%) during this period. Fish ranged in size from 3 to 29 cm FL, and modal size (17 cm) was the same for fish collected both north and south of 36°00'N (Fig. 7B).

Discussion

Densities of *C. hippos* in Haverstraw Bay, where our study was focused, were generally low compared with other New
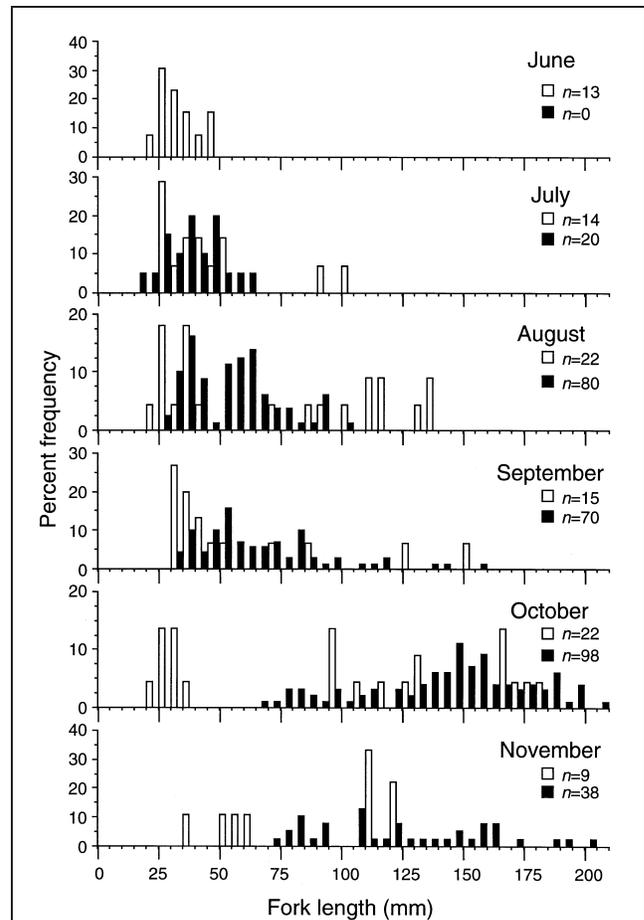

Figure 2

Monthly length frequencies of young-of-the-year *Caranx hippos* in estuaries from North Carolina to Florida (open bars) and New York or New Jersey (filled bars). Data for southern states are taken from Berry (1959; Table 23, Addenda, p: 534–535), and data for northern states are from material archived at the New York State Museum, Academy of Natural Sciences in Philadelphia, and American Museum of Natural History (listed in McBride[1]). n = number of fish measured.

York estuaries. We did observe considerable variation in densities of *C. hippos* between months, years, and estuaries, which we believe is at least partially the result of this species' relatively low density and shoaling (e.g. aggregating) behavior (Kwei, 1978). Larval dispersal processes or habitat may also affect juvenile *C. hippos* densities between temperate estuaries. This variability appears to have led to contradictory reports of *C. hippos* abundance at temperate latitudes: some investigators concluded that this species is "rare" or "scarce" (e.g. Bean, 1900; Greeley, 1937), whereas others have considered it to be "common" or "abundant" (DeKay, 1842; Smith, 1985).

Our review of seining data across a latitudinal range from 27°N to 41°N demonstrated that densities of *C. hippos* propagules transported to subtropical estuaries were not
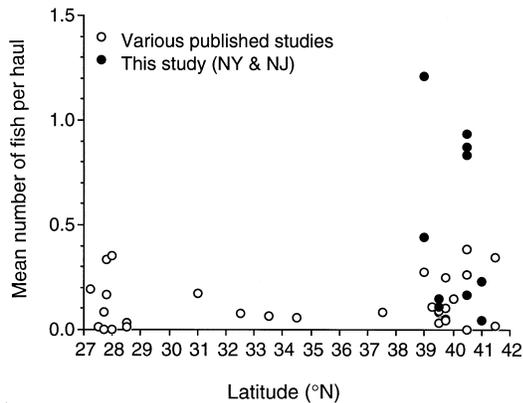
Figure 3

Densities (arithmetic mean number of fish caught per seine haul) of young-of-the-year *Caranx hippos* by sampling latitude (Rhode Island to Florida). Data were limited to seines from 10- to 90-m long, set during May–October and calculated per year if a study was conducted for multiple years. Data were taken from the following surveys (open circles), listed here by decreasing latitude (with seine length): Hoff and Ibara, 1977 (12 m); Briggs and O'Connor, 1971 (91 m); Briggs, 1975 (91 m); Ecological Analysts, Inc. 1981. Ecological studies at Oyster Creek Nuclear Generating Station. Feb. 1981 EA Report JCP91I3 Progress Report. September 1979–August 1980, prepared for Jersey Central Power and Light Company, Appendix D, E, unpaginated (46 m); Marcellus, 1972 (11 m); Thomas, D. L., and C. B. Milstein 1973. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the proposed site for the Atlantic generating station, NJ. Progress Report for January–December, 1972, vol. I: Fishes and volume II: Appendices, Ichthyological Associates, Inc. Absecon, NJ, 1065 p. (76 m); Thomas, D. L., C. B. Milstein, T. R. Tatham, R. C. Bieder, D. J. Danila, H. K. Hoff, D. P. Swiecicki, R. P. Smith, G. J. Miller, J. J. Gift, and M. C. Wyllie. 1975. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the proposed site for the Atlantic generating station, NJ. Progress Report for January–December, 1974. Volume I: Fishes, 490 p. Ichthyological Associates, Inc. Absecon, NJ. (76 m); de Sylva, D. P., F. A. Kalber, and C. N. Shuster. 1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary, with notes on other species collected in deeper water. University of Delaware Marine Laboratory. Information Series Publication 5. Technical Report to Delaware Board of Game and Fish Commissioners under Dingell-Johnson Federal Aid in Fish and Wildlife Restoration. Delaware Project F-13-R-1-2-3, 150 p. Contact senior Richard McBride (senior author) for data of this report (18 m); Richards and Castagna, 1970 (12 m); Tagatz and Dudley, 1961 (21 m); Ogburn et al., 1988 (15 m); Anderson et al., 1977 (20 m); Miller, G. L., and S. C. Jorgenson. 1969. Seasonal abundance and length frequency distribution of some marine fishes in coastal Georgia, 103 p. U. S. Fish Wildl. Ser. Data Rep. 35. Washington, D.C. (on two microfische) (21 m); Gilmore, 1988 (62 m); Schooley, 1977 (12 m); Peters, 1984 (9 m); Futch and Dwinell, 1977 (15 m); and Gunter and Hall, 1963 (15 m). Data from the present study, restricted to the years 1987 and 1988, are shown separately (filled circles) and include two southern New Jersey locales and Haverstraw, Jamaica, and Great South bays, New York (30 and 61 m seine nets). There was no significant relationship among the data (Spearman correlation coefficent, r_s=0.24, n=40; P=0.14).

higher, as would be expected for a "subtropical" species, than densities of those propagules transported to temperate estuaries. Not all CPUE values we examine in our study were directly comparable because of potential differences in deployment procedures, sampling habitats, and range of seine sizes. We hope that others will report more data for such comparative purposes in the future. We are also unaware of comparative data for tropical regions to determine if this species is more abundant in a more central portion of its latitudinal range. Young-of-the-year *C. hippos* abundance is generally low compared with other estuarine finfishes from Massachusetts to Florida (e.g. Ayvazian et al., 1992; Tremain and Adams, 1995; Able et al., 1996), and we conclude that this species is uncommon throughout this range.

Having found juvenile *C. hippos* in reasonable densities in temperate estuaries, we also observed them to occupy habitats similar to those of juvenile *C. hippos* in subtropical estuaries. In both temperate and subtropical regions, juveniles of this species appear to use estuaries as nurseries (see also Berry, 1959; Kwei, 1978). We observed individuals as far upstream as the freshwater interface (about 1 ppt), at about rkm 90–100 in the Hudson River during July–October (Cooper et al., 1988; Geoghegan et al., 1992). Several others have reported YOY *C. hippos* in oligohaline habitats (Christensen, 1965; Tagatz, 1968; Smith, 1985; Beebe and Savidge, 1988) but none in fresh water. The presence of *C. hippos* within the Hudson River was associated with warm temperatures; this species occurred in similarly warm temperatures in subtropical estuaries (18–33°C: Tagatz and Dudley, 1961; Christensen, 1965; Tagatz, 1968). The concentration of fish in and near Haverstraw Bay is probably due to this region's broad width and shallow bathymetry, which slows waterflow rates and responds rapidly to solar radiation (Cooper et al., 1988). In addition, three power plants that release heated effluent are located near Haverstraw Bay (Cooper et al., 1988). Temperature eventually becomes a very important parameter affecting YOY *C. hippos* distribution, and cold temperatures have been implicated in several cases of overwintering mortality for *C. hippos*. We know of no experimental study to document the lower lethal temperature for this species, but Bean (1903) noted that *C. hippos* could overwinter in aquarium conditions above 10°C, and Hoff (1971) observed dead *C. hippos* in waters colder than 9°C, whereas conspecifics in a downstream portion of the same Massachusetts river survived in waters above 9°C. Water temperatures fall below 10°C for at least the 4-mo. period of December–April near Haverstraw Bay and above the continental shelf of the middle Atlantic states (Cooper et al., 1988; Mountain and Holzwarth, 1989); therefore there is no suitable overwintering habitat for *C. hippos* north of Cape Hatteras. Yet although the predictability of the seasonal cycle may be an important determinant of a species' latitu-

Table 1

Catch data for all Hudson River sampling sites; a 30.5-m seine or 61-m seine net was used. Geometric mean (GM) number of *C. hippos* per seine haul is calculated only from collections during peak abundance (August–September).
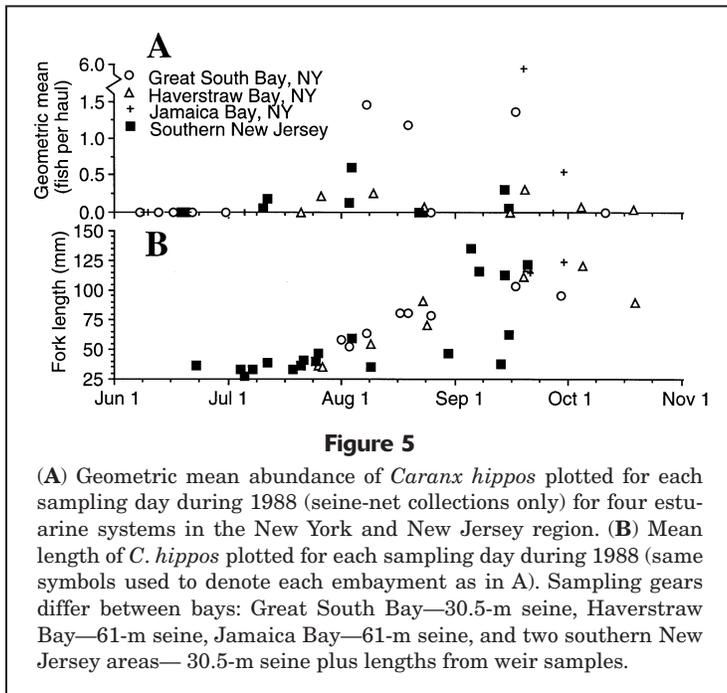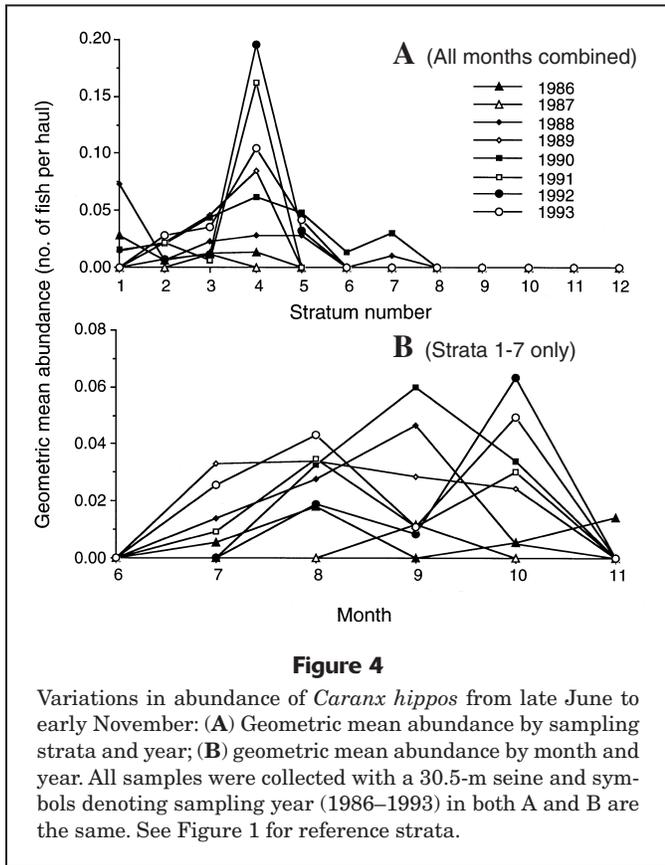
Year	Total no. of hauls	No. of hauls containing *C. hippos*	Total no. of *C. hippos* collected	GM	Total no. of hauls	No. of hauls containing *C. hippos*	Total no. of *C. hippos* collected	GM
Entire Hudson River (30.5-m seine)	All sampling strata				Haverstraw Bay (strata 2–4)			
1986	1000	6	10	0.0058	429	4	8	0.0135
1987	1101	2	3	0.0038	473	2	3	0.0089
1988	1100	12	22	0.0235	407	6	12	0.0344
1989	1100	15	40	0.0198	429	14	39	0.0468
1990	1000	19	32	0.0284	364	13	23	0.0395
1991	1000	11	58	0.0134	364	11	58	0.0341
1992	1000	9	53	0.0084	364	8	50	0.0130
1993	1000	17	30	0.0171	364	15	27	0.0403
Total	8301	91	248	—	3,194	73	220	—
Haverstraw and Jamaica bays (61-m seine)	Haverstraw Bay				Jamaica Bay			
1986	222	6	21	0.0398	38	2	10	0.732
1987	225	7	9	0.0406	56	4	14	0.468
1988	220	21	45	0.1578	42	4	54	1.151
1989	225	17	64	0.0730	49	2	2	0.000
1990	217	16	39	0.1274	48	7	11	0.475
1991	215	9	20	0.0649	58	4	6	0.000
1992	221	5	5	0.0140	44	2	3	0.292
1993	225	11	20	0.0437	43	3	11	0.000
Total	1770	92	223	—	378	28	111	—

dinal range, sudden and irregular freezes are more likely agents for actual hypothermal mortality, regardless of latitude (Storey, 1937). There are, for example, several instances of hypothermal mortality of *C. hippos* on Florida's Atlantic and Gulf coasts (Storey and Gudger, 1936; Miller, 1940; Galloway, 1941; Gilmore et al., 1978; Snelson and Bradley, 1978; Provancha et al., 1986). If individuals dispersed to temperate estuaries react in a similar manner to those dispersed to subtropical estuaries and emigrate from estuaries during autumn, then they may successfully migrate south to suitable overwintering habitats. We observed similar sizes of YOY *C. hippos* disappearing from estuaries and appearing on the continental shelf during September and October, which is strong circumstantial evidence of a migration pattern before hypothermal temperatures are reached.

During the summer, coastal water temperatures at temperate and subtropical latitudes are similar (e.g. Mountain and Holzwarth, 1989) and produce a favorable growth climate for *C. hippos* across a wide latitudinal range. Monthly sizes of YOY *C. hippos* were similar across latitudes, and the apparent growth rates were high in relation to other YOY estuarine fish species in temperate waters (Rountree and Able, 1992). Our comparative data suggested no size disadvantage for individuals dispersed to temperate estuaries.

Overwintering mortality is size-dependent for some species that migrate offshore (Conover, 1990), so that if *C. hippos* in temperate waters were smaller by autumn than those in subtropical estuaries, then their overwinter survival could be lower. Nevertheless, individuals in temperate waters may be at a disadvantage to equal-size individuals in subtropical waters because the latter do not need to migrate as far to reach overwintering habitats. Our preliminary growth model was confounded by a prolonged (about 3 months) presence of small fish, and presumably there was considerable age variation within our late-summer samples. The continued presence of small fish into September confounded analysis of length frequencies and created the appearance of sudden shifts in average fish size in late summer. The discrepancy between predicted size in temperate estuaries during autumn and the modal size observed on the shelf (e.g. 14 vs. 17 cm FL) could be the result of smaller fish having a higher mortality rate during this habitat shift. Further work with growth modeling will improve with age-specific data. The growth and size data of our study, however, suggest that *C. hippos* emigrated from estuaries largely as YOY and at the same time and sizes across latitudes. These data suggest that the same behavioral cue to migrate operated on individuals dispersed to both biogeographic regions.
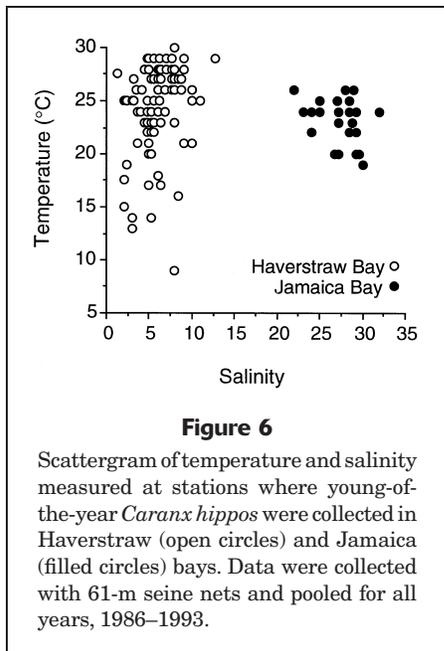
By the time YOY *C. hippos* reach shelf habitats during autumn, we postulate that they are of adequate size to continue south to subtropical latitudes. For example, YOY *C.*

Figure 4
Variations in abundance of *Caranx hippos* from late June to early November: (**A**) Geometric mean abundance by sampling strata and year; (**B**) geometric mean abundance by month and year. All samples were collected with a 30.5-m seine and symbols denoting sampling year (1986–1993) in both A and B are the same. See Figure 1 for reference strata.

Figure 5
(**A**) Geometric mean abundance of *Caranx hippos* plotted for each sampling day during 1988 (seine-net collections only) for four estuarine systems in the New York and New Jersey region. (**B**) Mean length of *C. hippos* plotted for each sampling day during 1988 (same symbols used to denote each embayment as in A). Sampling gears differ between bays: Great South Bay—30.5-m seine, Haverstraw Bay—61-m seine, Jamaica Bay—61-m seine, and two southern New Jersey areas— 30.5-m seine plus lengths from weir samples.

hippos are as large as "summer-spawned" YOY *P. saltatrix*; McBride et al. (1993) concluded the latter migrate from temperate nursery grounds to subtropical overwintering habitats at sizes of 10–15 cm FL. Moreover, several fish species have been tagged in temperate waters and recaptured in subtropical waters at sizes similar to those of *C. hippos* in autumn, including Atlantic croaker, *Micropogonias undulatus* (Pearson, 1932; Haven, 1959); spot, *Leiostomus xanthurus* (Pearson, 1932); weakfish, *Cynoscion regalis* (Nesbit, 1954); Atlantic thread herring, *Opisthonema oglinum* (Pristas and Cheek, 1973); bluefish, *P. saltatrix* (Lund and Maltezos, 1970); and Atlantic menhaden, *Brevoortia tyrannus* (Kroger and Guthrie, 1973). We reject the hypothesis that YOY *C. hippos* migrate offshore to the shelf edge, because they are distributed close to shore (<38 m) during autumn and they are not collected in winter or spring sampling out to 366 m depths by the National Marine Fisheries Service's trawling program. We similarly reject the hypothesis that the YOY *C. hippos* observed in coastal habitats during autumn have moved inshore from "offshore" nursery grounds. This cohort was not evident in summer trawl samples and such a hypothesis would require an alternative life history tactic for using shelf habitats as nurseries—a tactic that up until now has not been reported for this species.
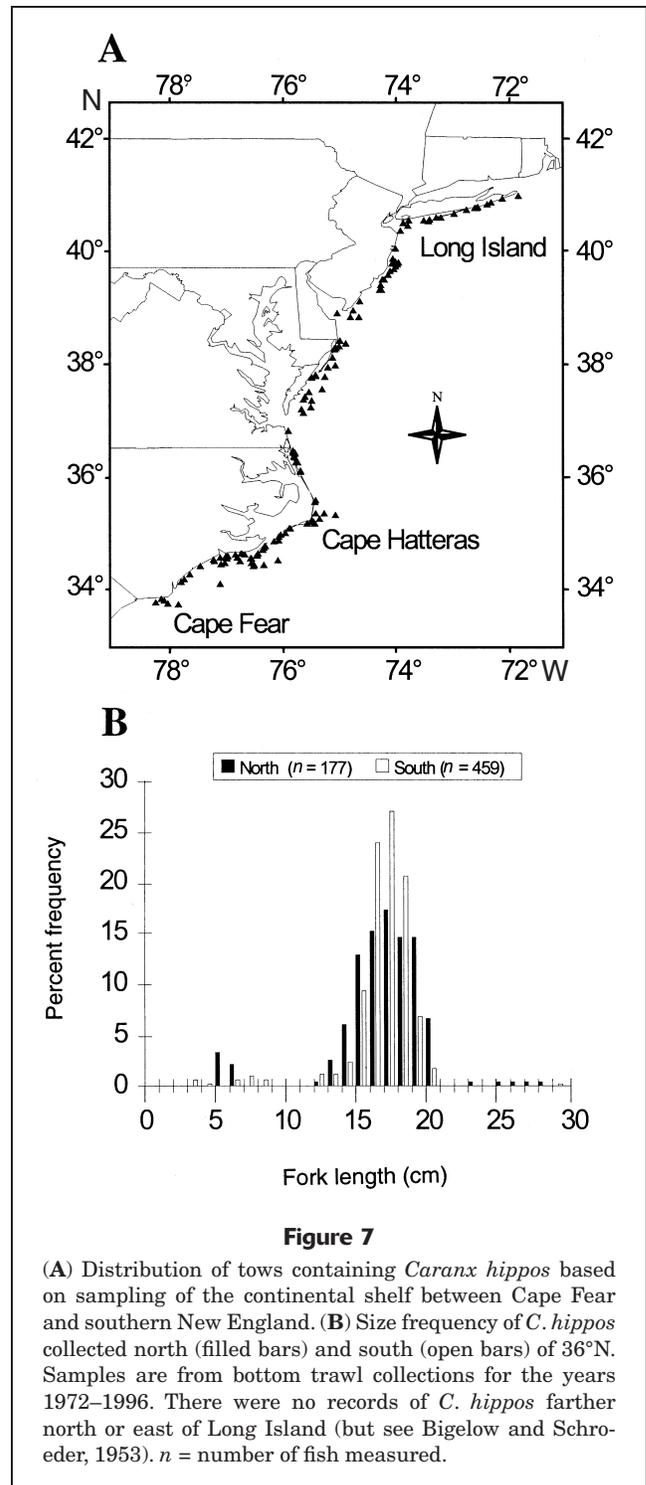
Direct evidence (e.g. mark-recapture) of successful migrations by marine fishes is rare, and the migration patterns of many species are inferred from seasonal changes in distribution (Leggett, 1977), as we have done in our study. In addition, we have examined growth rates and sizes to link the seasonal changes in geographic distribution to the YOY cohort. The above evidence indirectly links some YOY *C. hippos* that have dispersed to temperate estuaries back to suitable overwintering habitats and suggests that these individuals retain "membership" in the spawning population (*sensu* Sinclair, 1988). We do not, however, assume that all individuals leave temperate estuaries before hypothermal conditions can develop, nor that all individuals survive an autumn migration to subtropical latitudes. The relative importance of temperate estuaries over subtropical estuaries for YOY *C. hippos* depends on the relative contribution to future spawning by individuals dispersed to each biogeographic region, but this contribution can not be calculated without further study.

Cape Hatteras represents a major faunal (and floral) break along the U.S. east coast (Pielou, 1979; Briggs, 1996), but the larvae of many species that spawn in coastal habitats, particularly of those that broadcast their eggs into the water column and have moderate-to-long planktonic larval durations, are capable of being transported around this geographic barrier (e.g. Curran, 1989). Among these species, we postulate that there is a subset of species that have juvenile traits that allow them to exploit nursery habitats in both biogeographic provinces, and an additional subset of species for which some individuals can return

Figure 6

Scattergram of temperature and salinity measured at stations where young-of-the-year *Caranx hippos* were collected in Haverstraw (open circles) and Jamaica (filled circles) bays. Data were collected with 61-m seine nets and pooled for all years, 1986–1993.

from temperate estuaries to reproduce. Traits such as early spawning season (i.e. winter or spring), fast growth rate, large YOY body size, generalized habitat requirements, and fast swimming speeds are favorable traits for any species attempting to complete a life-history circuit within one year between subtropical and temperate waters of the western North Atlantic. These traits are found in several finfish species in the Carangidae, Scombridae, and Mugilidae. Grouping species by spawning, larval, and juvenile characteristics and comparing their fate in these large oceanographic systems will help define the appropriate spatial scale for sampling these populations in the western North Atlantic, as well as in other systems such as the Sea of Japan (Nishimura, 1965), the Agulhas Current (Beckley, 1985), and the East Australian Current (Miskiewicz, 1981) where similar dispersal patterns of subtropically spawned species to temperate waters have been described. An initial screening for such characters allows researchers to begin to evaluate whether a specific "subtropical" species can or cannot survive once dispersed to temperate habitats.

Some of these subtropically spawned species are dispersed to temperate waters during less favorable conditions (e.g. winter) and, presumably, others do not grow to a sufficient size or have the behavior characteristics to migrate in autumn. A nonadaptive outcome of dispersal for many species on an ecological timescale is not, however, necessarily surprising. An examination of the paleontological record, which is most complete for invertebrates, shows that biogeographic assemblages lag notably behind environmental changes at an evolutionary timescale (Briggs, 1974; Pielou, 1979). A modeling and theoretical method, such as that used by Hare and Cowen (1993), could help explain why the larvae of so many species are dispersed into large oceanographic systems even when expatriation

Figure 7

(**A**) Distribution of tows containing *Caranx hippos* based on sampling of the continental shelf between Cape Fear and southern New England. (**B**) Size frequency of *C. hippos* collected north (filled bars) and south (open bars) of 36°N. Samples are from bottom trawl collections for the years 1972–1996. There were no records of *C. hippos* farther north or east of Long Island (but see Bigelow and Schroeder, 1953). *n* = number of fish measured.

is likely, but more natural history data are necessary before such a method can be widely applied. A more complete record of which species are and are not expatriated within large-scale systems will contribute to understanding the processes underlying these biogeographic patterns, provide opportunities to examine further the evolution of

reproductive strategies, and help explain oceanographic effects on population dynamics.

Acknowledgments

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