

Abstract—Summer flounder (*Paralichthys dentatus*) is one of the most economically and ecologically important estuarine-dependent species in the northeastern United States. The status of the population is currently a topic of controversy. Our goal was to assess the potential of using larval abundance at ingress as another fishery independent measure of spawning stock biomass or recruitment. Weekly long-term ichthyoplankton time series were analyzed from Little Egg Inlet, New Jersey (1989–2006) and Beaufort Inlet, North Carolina (1986–2004). Mean size-at-ingress and stage were similar between sites, whereas timing of ingress and abundance at ingress were not similar. Ingress primarily occurred during the fall at Little Egg Inlet and the winter at Beaufort Inlet. These findings agree with those from earlier studies in which at least two stocks (one north and one south of Cape Hatteras) were identified with different spawning periods. Larval abundance at Little Egg Inlet has increased since the late 1990s and most individuals now enter the estuary earlier during the season of ingress. Abundance at Little Egg Inlet was correlated with an increase in spawning stock biomass, presumably because spawning by larger, more abundant fish during the late 1990s and early 2000s provided increased larval supply, at least in some years. Larval abundance at ingress at Beaufort Inlet was not correlated with spawning stock biomass or with larval abundance at ingress at Little Egg Inlet, further supporting the hypothesis of at least two stocks. Larval abundance at Little Egg Inlet could be used as a fishery-independent index of spawning stock size north of Cape Hatteras in future stock assessments. Larval occurrence at Beaufort Inlet may provide information on the abundance of the stock south of Cape Hatteras, but additional stock assessment work is required.

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Larval abundance of summer flounder (*Paralichthys dentatus*) as a measure of recruitment and stock status

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Summer flounder (*Paralichthys dentatus*) is one of the most economically important species in the northeastern United States because of the central role it plays in both commercial and recreational fisheries (Collette and Klein-McPhee, 2002). There was considerable concern over this species in the late 1980s when landings and spawning stock biomass declined precipitously (Kraus and Musick, 2001; Terceiro, 2002). In recent years, summer flounder has started to recover, but there is continued controversy over the rate of recovery relative to established benchmarks and recruitment success based on recent stock assessments (NRC, 2000; NEFSC¹).

Two major issues contribute to this controversy. First, there are differing opinions as to the number of stocks present off of the U.S. east coast. Summer flounder is managed as a unit from the southern border of North Carolina to the U.S.-Canada border (Terceiro, 2002) based on stock-definition research (Wilk et al., 1980) and a population genetics study (Jones and Quattro, 1999). The assessment unit, from which catch and survey data are obtained, however, is an area from Cape Hatteras, North Carolina, to the U.S.-Canada border, consistent with a recent review of stock definition (Kraus and Musick, 2001). A coastal North Carolina stock (extending from Cape Hatteras southward) has been hypothesized (Burke et al., 2000; Kraus and Musick, 2001), but this unit is not subject to a separate assessment (Terceiro, 2002). Second, recruitment processes in summer flounder are unclear, particularly the relationship between spawning stock

¹ NEFSC (Northeast Fisheries Science Center). 2008. 47th northeast regional stock assessment workshop (47th SAW) assessment report. NMFS NEFSC Ref. Doc. 08–12a, 335 p. NEFSC, Woods Hole, MA

size and larval and juvenile abundance. Brodziak and O'Brien (2005) found that summer flounder recruitment lagged after the North Atlantic Oscillation (NAO) index by two years (i.e., recruitment in 1990 was related to the NAO in 1988). Analyses conducted during a recent stock assessment confirmed this relationship (NEFSC¹), but a mechanistic recruitment hypothesis has yet to be developed. Recruitment is the result of the integration of survival from spawning through the juvenile stage, whereas the stage at which recruitment is determined can be inferred by examining the abundance indices at successive life stages (Nash and Dickey-Collas, 2005).

In an attempt to resolve these issues, we examined the relationship between two long-term time series of summer flounder larval abundance at ingress, recruitment, and spawning stock biomass over the period of presumed stock recovery. We evaluated whether these data sets 1) contribute to an improved understanding of stock identification; and 2) result in indices that correlate with patterns of abundance relative to spawning-stock biomass and recruitment. In prior studies of the abundance of larval summer flounder at ingress, the timing, size, and developmental stage of inlet samples at the New Jersey (Able et al., 1990; Szedlmayer et al., 1992; Keefe and Able, 1993, 1994) and North Carolina (Williams and Deubler, 1968; Burke et al., 2000; Taylor et al., 2009) sites were determined from a shorter time series. A combined analysis has not been attempted until now.

Materials and methods

General life history of summer flounder and study sites

Summer flounder spawn during an offshore migration from estuaries and bays to the outer continental shelf. This spawning event occurs during fall and early winter and the larvae are transported inshore from where they enter estuaries, settle to the bottom, and grow quickly. Most fish are sexually mature by age 2 and it is about this time that they begin to be caught in the commercial fishery.

The locations of data collections were Little Egg Inlet (New Jersey) and Beaufort Inlet (North Carolina) from the northeast and southeast United States continental shelf ecosystems, respectively (Fig. 1). Little Egg Inlet is the primary source of Atlantic Ocean water that enters the Great Bay–Little Egg Harbor estuarine system, which is polyhaline and shallow (average water depth 1.7 m). The system is composed of a drowned river valley (Mullica River), an embayment (Great Bay), and an adjacent barrier beach estuary (Little Egg Harbor). This estuary has a broad, seasonal temperature range (-2° to 28° C) and a moderate tidal range (~ 1 m; Kennish, 2004). Sampling was conducted from a bridge over Little Sheepshead Creek (water depth ~ 3 m), a thoroughfare connecting Great Bay and Little Egg Harbor, located 3 rkm from the creek mouth and 2.5 km from Little Egg Inlet. Atlantic Ocean water flows into the

estuary through Little Egg Inlet during flood tides, and portions are diverted into the mouth of Little Sheepshead Creek (Charlesworth, 1968; Chant et al., 2000). Recent work has shown that ichthyoplankton samples collected from this location are representative of dynamics occurring in the estuary proper (e.g., Witting et al., 1999; Chant et al., 2000; Neuman et al., 2002; Able and Fahay, 2010).

Beaufort Inlet connects several estuarine systems and two sounds, Back Sound and Bogue Sound, to the Atlantic Ocean (Churchill et al., 1999). The area around the inlet shares many characteristics with other estuarine systems in the southeast United States. Seasonal temperature variation (8° to 30° C) is more moderate than that at Little Egg Inlet, whereas tidal range is similar (~ 1 m). Sampling is performed from a bridge (~ 1.5 km inside of Beaufort Inlet) that spans a 40-m wide channel between Radio Island and Pivers Island (water depth ~ 4 m). Atlantic Ocean water flows into the estuary through Beaufort Inlet and approximately 10% moves up the channel that provides water to the Radio Island–Pivers Island channel (Churchill et al., 1999). Species composition and abundance of samples taken from Beaufort Inlet are also characteristic of collections from surrounding sounds and have potential value as predictive measures of year-class strength of estuarine-dependent fishes (Lewis and Mann, 1971; Hettler et al., 1997; Hettler and Hare, 1998; Forward et al., 1999; Rice et al., 1999; Taylor et al., 2009).

Sampling of larvae at ingress

At Little Egg Inlet, larvae entering the estuary were collected with a 1-m diameter, circular plankton net (1-mm mesh) fitted with a flow meter. From August 1991 to 2006, three replicate 30-min sets were made weekly with the net deployed to a depth of 1.5 m during nighttime flood tides. From February 1989 to May 1990 (the first year of sampling), five 30-min sets of two concurrent plankton nets (one at the surface and one at the bottom) were made for a total of 10 sets per sampling date. From May 1990 to July 1991, three 30-min sets of two concurrent plankton nets (one at the surface and one at the bottom) were conducted. Weekly surface and bottom data from February 1989 to July 1991 were averaged and combined with weekly mid-water data from August 1991 to 2006 to develop a full time series of larval collections (Able and Fahay, 1998, 2010; Witting et al., 1999).

At Beaufort Inlet, larvae were collected with a 2-m² rectangular plankton net (1-mm mesh) fitted with a flow meter. The net was deployed during nighttime flood tides and larvae were sampled at the surface (0–1 m depth). Four replicate sets were made weekly from November to April, 1985–2001. Before 1998, tow duration was nearly constant (~ 5 min), resulting in a variable volume being filtered. Since 1998, tow volume has been standardized (~ 100 m³) with the use of an electronic flow meter.

The differences in sampling designs between locations resulted from the logistics of net deployment from the bridges and the abundance of fishes in the water col-

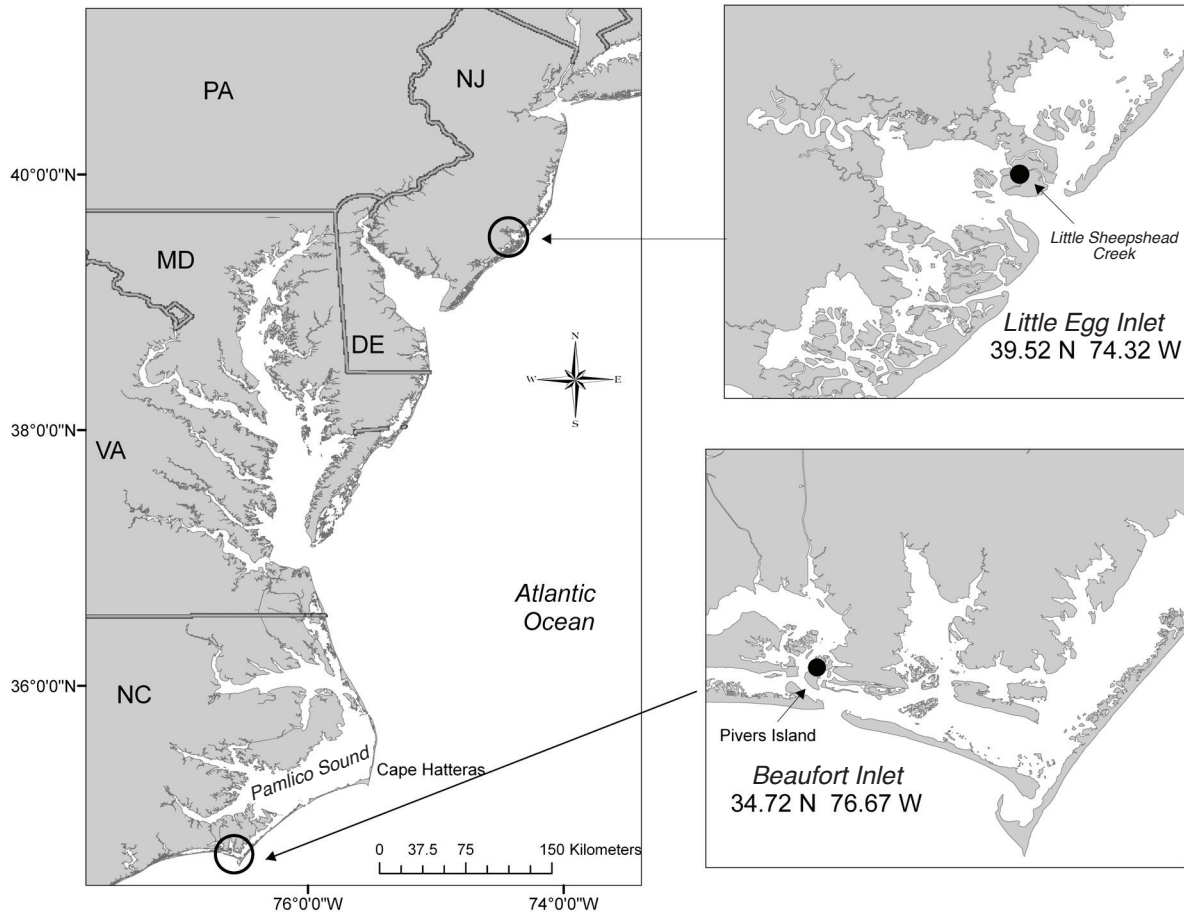


Figure 1

Location of larval summer flounder (*Paralichthys dentatus*) monitoring sites in the northeast and southeast United States shelf ecosystems during 1989–2006 (Little Egg Inlet) and 1986–2004 (Beaufort Inlet).

umn (Sullivan et al., 2006). Characteristics of the two sites and gears implied that the sampling programs were comparable: the environmental setting was similar (salinity ranges, proximity to respective inlets, presence of a well-mixed water column), and mesh-size (1 mm), and sampling time (nighttime and incoming flood tide) were identical.

Larval abundance at both collecting sites was standardized as the number of individuals per 1000 m³ of water that was filtered. Mean abundance for the replicate net sets on a given night was used as the estimate of summer flounder abundance at ingress during the flood tide. A maximum of 20 larvae per tow were preserved in 95% ethanol and then measured for standard length per tow and for developmental stage determination (after Keefe and Able, 1993).

Spawning stock biomass and recruitment data

Spawning stock biomass and recruitment data for summer flounder were obtained from the most recent stock assessment conducted by the Northeast Fisheries Science Center (NEFSC¹). In this assessment, indices

of spawning stock biomass and recruitment data were derived from the following surveys: Northeast Fisheries Science Center winter, spring, and autumn survey; Massachusetts spring and autumn survey; Rhode Island annual survey; Connecticut spring and autumn survey; New Jersey annual survey; and Delaware annual trawl survey. Recruitment indices were also developed from young-of-the-year surveys conducted by the states of North Carolina, Virginia, and Maryland. These indices were combined with catch-at-age information to estimate recruitment and spawning stock biomass by using the statistical catch at age model implemented in the Age Structured Assessment Program (NEFSC).

Statistical analysis

The following null hypotheses were examined with respect to the two overlapping time series: 1) there is no synchrony between inlets in annual abundance of summer flounder larvae and 2) there is no synchrony between annual abundance at each inlet, spawning stock biomass (SSB), and recruitment (REC). Using the overlapping time periods from each inlet, we determined syn-

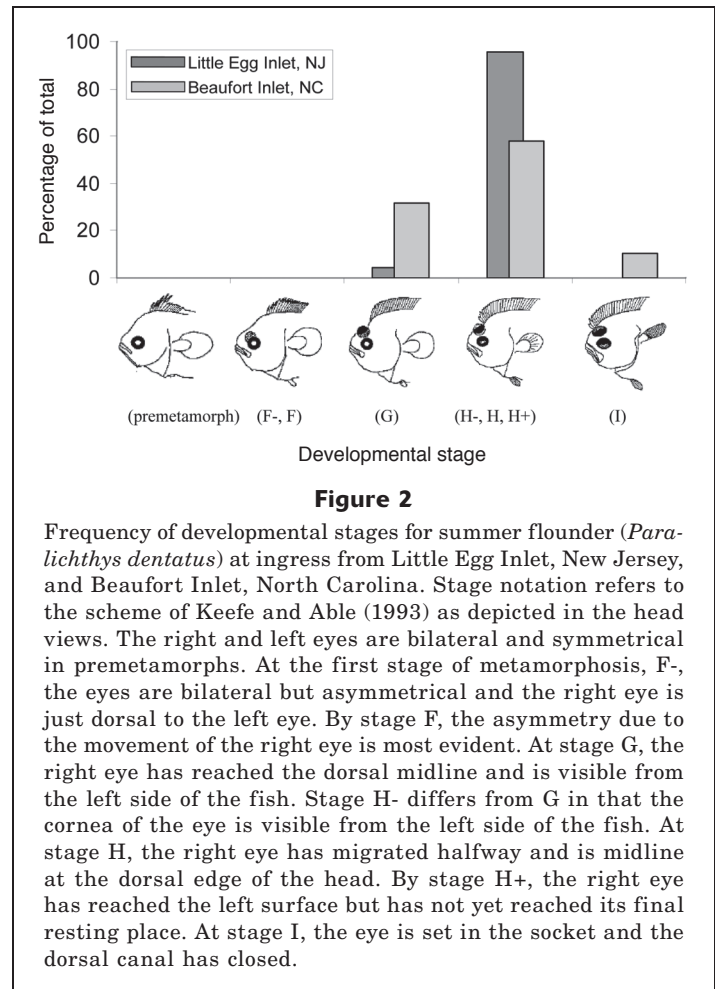
chrony in magnitude of abundance of ingressing summer flounder larvae between Little Egg and Beaufort inlets (and their respective relationship with SSB and REC) using two methods: 1) average cross-correlations of series values (r); and 2) measures based strictly on change (Buonaccorsi et al., 2001). For the latter method, the data consisted of n series, measured at T points in time, where x_{it} is the larval concentration at a given inlet, SSB, or REC. The relative direction of change was calculated as A_{ij} , where A_{ij} =(number of times series i and j move in same direction)/($T-1$). This expression was then modified into a correlative measure by using $\tau_{ij}=2A_{ij}-1$ (Buonaccorsi et al., 2001). For both methods, a large, positive value of r or τ signals strong synchrony in magnitude of abundance between populations (reject H_0), a value near zero corresponds with weak synchrony in magnitude of abundance (accept H_0), whereas a value below zero is indicative of populations consistently out of phase (accept H_0 ; Jones et al., 2003). In all cases, data were lagged to relate spawning stock biomass to subsequent larval abundance at ingress and recruitment. Spawning stock biomass in year y was related to larval abundance at ingress during the fall–winter of year y and the winter–spring of year $y+1$ and to recruitment in year $y+1$. All time series data on abundance were natural log transformed (\ln).

Results

Patterns of larval ingress

At both Little Egg Inlet and Beaufort Inlet, the larvae captured at ingress were in similar stages of development, i.e., transitional stages (stages F–I, based on Keefe and Able, 1993) nearing the completion of eye migration (Fig. 2). These same individuals had overlapping sizes from 10 to 17 mm standard length (SL) and most (90%) were between 12 and 15 mm SL in both inlets, but with slightly larger individuals at Beaufort Inlet (Fig. 3). Summer flounder larvae were consistently more abundant at Beaufort Inlet than Little Egg Inlet (average for all positive months, 8.18/1000 m³ compared to 4.95/1000 m³, respectively, Fig. 4).

The timing of ingress differed within and between inlets (Figs. 4 and 5). In the year-round collections at Little Egg Inlet, larvae were found from October through June over the study period (1989–2006). Before 1998, larvae were more abundant in the late winter and spring (January–March). The inconsistently late occurrence of the peak in 1993 is an artifact due to missed collections during the peak period of ingress. From 1998 onwards, larvae were typically more abundant in the fall and early winter (October–December; Fig. 5). From 1989 through 1998 fall and early winter larvae averaged 1.66/1000 m³, whereas from 1999 through 2006 they averaged 9.08/1000 m³. At Beaufort Inlet,



larvae occurred from December through the end of the sampling period in April or May, but individuals were most abundant from February through April. It is possible that larvae continued ingress but were undetected because sampling typically ended at the end of April or May (Fig. 4). Abundance at Beaufort Inlet varied annually, but seasonal patterns of ingress did not vary over the time series as strikingly as at Little Egg Inlet (Fig. 5). From 1989 through 1998, the late winter and spring larval abundance average (6.62/1000 m³) was similar for those from 1999 through 2006 (7.76/1000 m³).

Relationships between larval abundance at ingress, spawning stock biomass, and recruitment

Estimated spawning stock biomass of summer flounder has increased since the late 1990s and reached the highest values during 2000–06 (Fig. 6A). Estimated recruitment has been variable over the same period (Fig. 6B). A Beverton-Holt model has been used to describe the stock-recruitment relationship, but this model essentially predicts constant recruitment over the range of observed spawning stock biomass (NEFSC¹). Trends in larval abundance at Little Egg Inlet are similar to

trends in spawning stock biomass, with the highest values in the series occurring in 2003 and 2004 (Fig. 6C). Larval abundance at ingress into Little Egg Inlet and spawning stock biomass were significantly correlated (Fig. 7A, Table 1). This pattern was not evident at Beaufort Inlet where ingress values varied and had no long-term pattern (Fig. 6D), resulting in no significant correlation with spawning stock biomass (Fig. 7B, Table 1). Recruitment and larval abundance at ingress were not correlated (Fig. 7, A and B, Table 1). Abundance at ingress at the two sites did show a tendency to move in the same direction from year to year but were not correlated with overall abundance (Table 1).

Discussion

Stock identification

Annual patterns of summer flounder larval ingress (timing, abundance) between Little Egg Inlet, New Jersey, and Beaufort Inlet, North Carolina, were not synchronous. The strong differences in timing of ingress between the two inlets could be the result of different spawning times north and south of Cape Hatteras, North Carolina (Burke et al., 2000; Rogers and Van

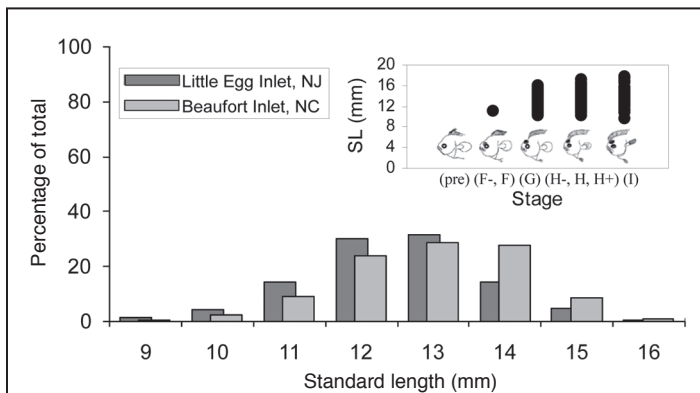


Figure 3

Frequency of standard lengths for summer flounder (*Paralichthys dentatus*) documented at ingress from Little Egg Inlet, New Jersey and Beaufort Inlet, North Carolina. Inset: relationship between standard length (SL) and developmental stages of summer flounder (after Keefe and Able, 1993). The right and left eyes are bilateral and symmetrical in premetamorphs. At the first stage of metamorphosis, F-, the eyes are bilateral but asymmetrical and the right eye is just dorsal to the left eye. By stage F, the asymmetry due to the movement of the right eye is most evident. At stage G, the right eye has reached the dorsal midline and is visible from the left side of the fish. Stage H- differs from stage G in that the cornea of the eye is visible from the left side of the fish. At stage H, the right eye has migrated halfway and is midline at the dorsal edge of the head. By stage H+, the right eye has reached the left surface but has not yet reached its final resting place. At stage I, the eye is set in the socket and the dorsal canal has closed.

Table 1

Pearson correlations r (right) and Kendall's tau (T, top) values for summer spawning stock biomass (SSB), recruitment (REC), larval abundance at Little Egg Inlet, NJ, and larval abundance of summer flounder at Beaufort Inlet, NC.

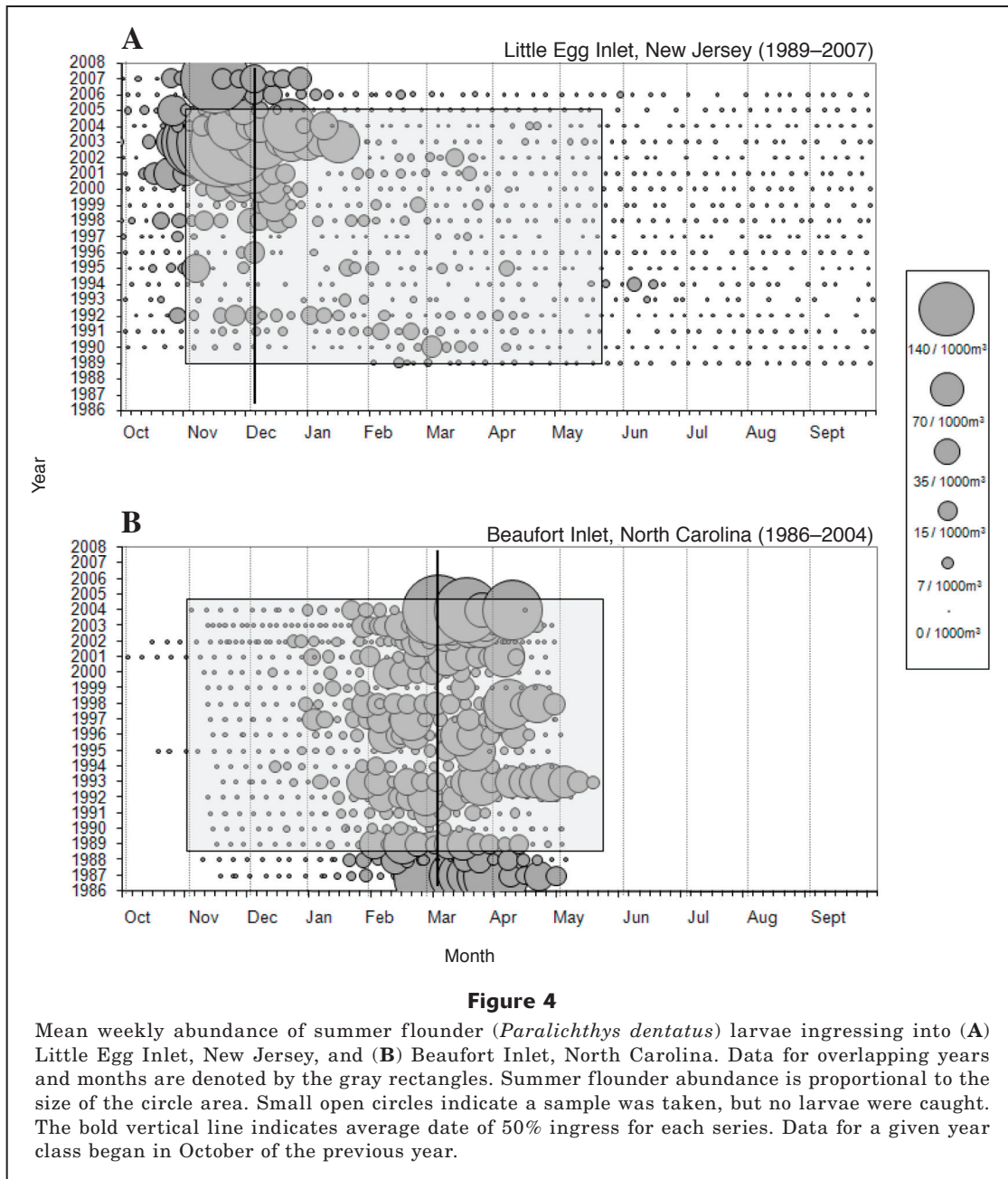
Magnitude of change (r)	Direction of change (T)			
	SSB	REC	NJ	NC
SSB	—	-0.20 ^{ns}	-0.18 ^{ns}	0.18 ^{ns}
REC	0.01 ^{ns}	—	0.06 ^{ns}	0.06 ^{ns}
NJ	0.49*	0.12 ^{ns}	—	0.47*
NC	0.33 ^{ns}	0.19 ^{ns}	0.29 ^{ns}	—

* $P < 0.05$; ns=not significant.

Den Avyle²). North of Cape Hatteras, spawning peaks in October–November based on gonad maturation (Morse, 1981; Wilk et al., 1990). A large peak in egg production is evident in October and November and a second, smaller peak occurs in April and May in the southern portion of the Bight. South of Cape Hatteras, a peak in summer flounder gonad development occurs during December and January (Powell, 1974). Other data on summer flounder eggs and larvae south of Cape Hatteras are relatively scarce, partly because identification has been complicated by the presence of other species of *Paralichthys* (Deubler, 1958; Williams and Deubler, 1968; Powles and Stender, 1976; Weinstein, 1979). Two separate spawning periods are also indicated by the occurrence of larvae just north of Cape Hatteras during the fall and again in the spring (Able and Kaiser, 1994; Burke et al., 2000), presumably representing contributions from spawning both from the north and south.

The two-stock hypothesis is supported by differences in timing of ingress at Little Egg Inlet and at Beaufort Inlet. Multiple studies indicate that summer flounder spawning (and subsequent ingress) throughout the area north of Cape Hatteras is most common in the fall (Able et al., 1990; Berrien and Sibunka, 1999; Burke et al., 2000). Similar trends in the timing of ingress are evident at other sites north of Cape Hatteras, including Chesapeake Bay, Virginia (Hare et al., 2005), and at Oregon Inlet, North Carolina (Hettler and Barker, 1993; Burke et al., 2000). For the area south of Cape Hatteras, winter spawning results in larval ingress in the late winter and early

² Rogers, S. G., and M. J. Van Den Avyle. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic): summer flounder, 14 p. U.S. Fish Wild. Serv. Biol. Serv. Prog. FWS/OBS 82(11.15).



spring only (Smith, 1973; Weinstein, 1979; Bozeman and Dean, 1980; Hettler and Chester, 1990; Burke et al., 2000; this study).

Although there are clear differences between Little Egg Inlet and Beaufort Inlet with respect to timing and abundance at ingress, size and developmental stage at ingress are similar (Keefe and Able, 1993; Forward et al., 1999; this study). The present analysis indicates that these trends are consistent over time and space and likely occur at other inlets along the east coast of the United States (e.g., Hare et al., 2005). These findings do not counter the multiple stock hypothesis, rather they suggest a narrow biological window (optimal

length and stage) exists for successful entry of summer flounder larvae into estuarine nursery habitats.

The possible existence of multiple summer flounder stocks is not new and has been frequently discussed and debated in the literature (see Burke et al., 2000; Kraus and Musick, 2001; Terceiro, 2002; Collette and Klein-McPhee, 2002, for reviews). The Beaufort Inlet site likely represents a winter spawning “southern stock” (or stocks)—also termed a coastal North Carolina stock. The Little Egg Inlet site likely represents a fall spawning “northern stock”—also termed a Mid-Atlantic stock. This interpretation is consistent with the stock hypothesis of Burke et al. (2000) and Kraus and Musick

(2001). Further, the examination of larval ingress immediately north (Oregon Inlet) and south (Beaufort Inlet) of Cape Hatteras indicates that this change occurs as a distinct step and not a smooth gradient (Burke et al., 2000).

To further resolve the identification of summer flounder stocks, it is necessary to understand population connectivity (e.g., larval dispersal, juvenile and adult movements) and associated vital rates (e.g., growth, mortality, recruitment) throughout their distribution range (Begg and Waldman, 1999; Hare, 2005). To complicate matters, Nye et al. (2009) documented changes in the latitude and depth of adult summer flounder from the late-1960s to the present, and these changes raise the possibility that stock boundaries are shifting over time. Identifying stocks and understanding their dynamic distribution remains a major issue for the management of U.S. east coast fisheries.

The ability to define the relationship between larval supply at ingress relative to spawning stock biomass and recruitment may be influenced by the scale of the different measures. Larval supply at ingress is measured at local inlets and it is assumed that they are representative of the separate stocks north and south of Cape Hatteras. This interpretation is supported by the

available literature. The measures of spawning stock biomass and recruitment used here were calculated for the portion of the population north of Cape Hatteras.

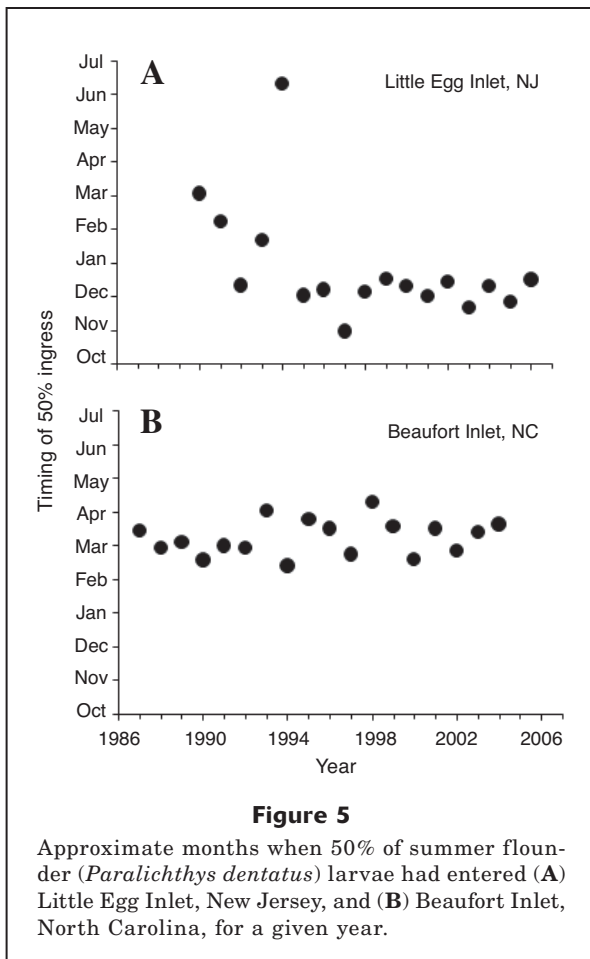
Larval abundance at ingress and spawning stock biomass

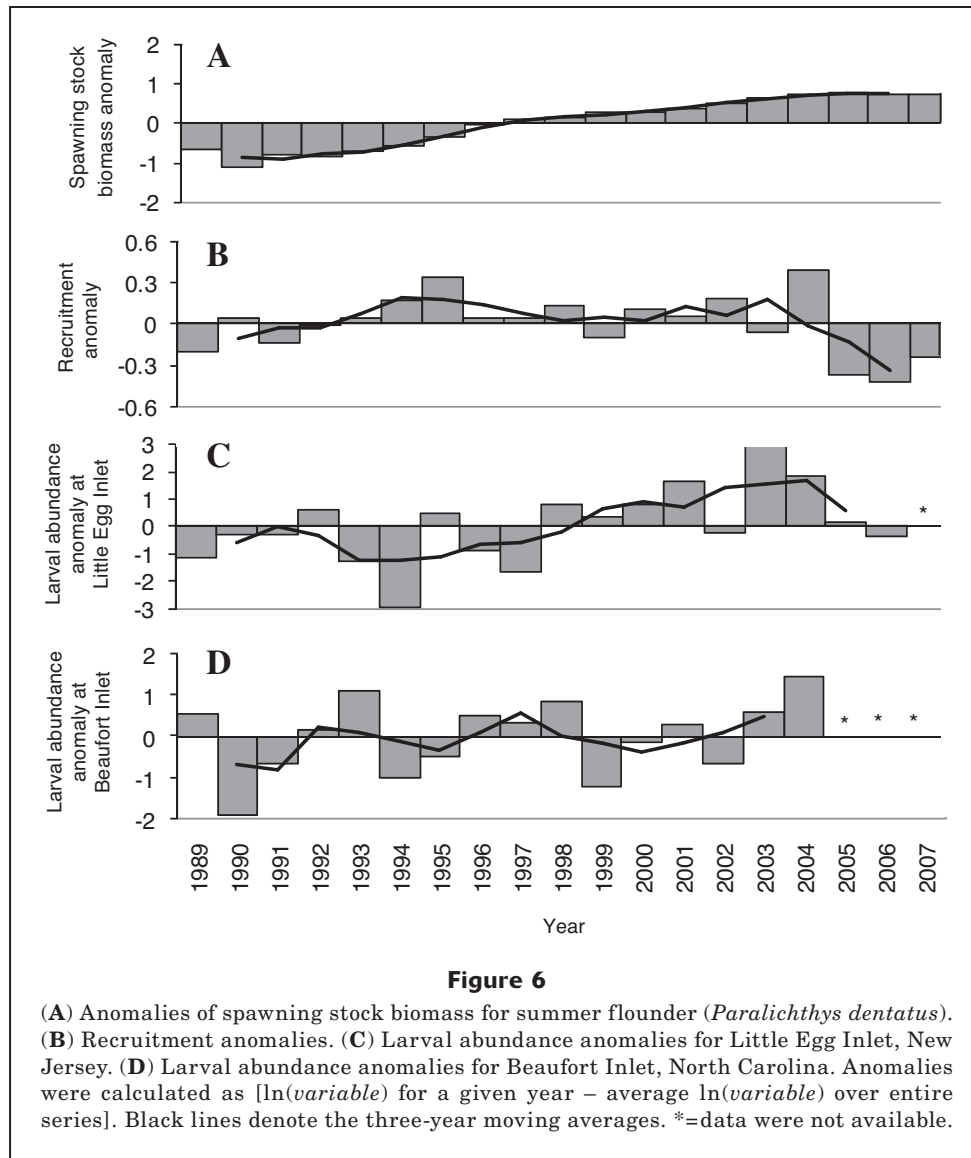
The long-term patterns of larval abundance at Little Egg Inlet and spawning stock biomass north of Cape Hatteras indicate that spawning and larval abundance at ingress are linked, presumably because increased spawning by larger, more abundant fish during the late 1990s and early 2000s resulted in increased larval abundance and survival and ultimately increased larval supply. Although the positive correlation may be biased by a few high values, we hypothesize that high spawning stock biomass is responsible for this increase in larval abundance at ingress. If a mechanistic link exists between these two data sets, data at ingress from Little Egg Inlet can be used as a fishery-independent index of spawning stock biomass for the "northern stock" of summer flounder. The lack of a relationship between spawning stock biomass and Beaufort Inlet larval abundance at ingress is not surprising because larvae entering Beaufort Inlet may be the result of a spawning event from a separate stock (see previous discussion). In a recent multispecies analysis of the Beaufort Inlet ichthyoplankton community, Taylor et al. (2009) concluded that the larval ingress from species spawning predominantly north of Cape Hatteras, including summer flounder, was not related to juvenile abundance in the Pamlico Sound system, but that ingress and juvenile abundance were related for species spawning predominantly south of Cape Hatteras. They proposed that larval supply to Pamlico Sound by northern spawning species is predominantly through inlets north of Cape Hatteras. The Beaufort Inlet site is south of Cape Hatteras.

One alternative explanation for the relationship between spawning stock biomass and larval ingress is that general warming trends in the Mid-Atlantic Bight region (Nye et al., 2009) may be contributing to an increased availability of summer flounder larvae to Little Egg Inlet. Hare and Able (2007) suggested for another common estuarine dependent species (Atlantic croaker [*Micropogonias undulatus*]) that warmer water temperatures are allowing juveniles to survive critical developmental periods. Thus, there are multiple hypotheses to explain the concomitant increase in spawning stock biomass and abundance at ingress into Little Egg Inlet and these hypotheses should be explored. In the meantime, abundance at ingress into Little Egg Inlet can be used as a fishery-independent index of spawning stock biomass.

Recruitment

Many studies have shown that larval fish supply influences subsequent recruitment to adult populations (Powell and Steele, 1995; Myers and Barrowman, 1996; Hamer and Jenkins, 1996; Leggett and Frank, 1997;





Jenkins et al., 1998; Chapin et al., 2000). Thus, estimates of larval abundance at ingress could contribute to an improved understanding of the relationship between stock size and larval supply, and larval supply and recruitment (e.g., Quinlan and Crowder, 1999). For summer flounder there appears to be no direct relationship between larval supply and recruitment at Beaufort Inlet or Little Egg Inlet (Taylor et al., 2009; this study). This finding implies that recruitment strength may be determined by factors later in the life cycle, likely during the estuarine juvenile stage.

The complexity of habitats occupied by the early life history stages of fishes may be especially problematic for temperate species that encounter extended periods of low temperatures after ingress, which consequently result in suboptimal growth and potentially death, (Hurst, 2007; Able and Fahay, 2010). Slow growth may extend the period during which individuals are sus-

ceptible to abiotic and biotic size-dependent selection pressures (see Houde, 1987). The above scenario applies to summer flounder, which shows reduced growth and increased mortality at low temperatures (Malloy and Targett, 1991; Szedlmayer et al., 1992; Keefe and Able, 1994; Able and Fahay, 1998). Temperature effects may be most pronounced for those larvae that enter northern estuaries during the fall and are subsequently exposed to low winter temperatures, as is the case for summer flounder at Little Egg Inlet (Keefe and Able [1994] report 4°C as the lower lethal limit for summer flounder). In addition, during ingress and subsequent settlement, slow growing larvae may be more susceptible to predation by common invertebrate predators such as blue crabs (*Callinectes sapidus*) and the seven-spine bay shrimp (*Crangon septemspinosa*) (Witting and Able, 1995; Barbeau, 2000). If cold winters, combined with increased predation pressure, are relevant factors,

juvenile abundance would be reduced. At Little Egg Inlet, colder winters have become less frequent since the late 1990s (Able and Fahay, 2010), perhaps resulting in the release of early stage flounder from various sources of temperature-induced mortality. A similar hypothesis was proposed for Atlantic croaker (i.e., Hare and Able, 2007).

An improved understanding of the factors affecting the relationship between spawning stock biomass and larval supply, and larval supply and recruitment during the juvenile stage is likely to be critical to an improved management of year-class strength for summer flounder and other estuarine-dependent fishes (Myers and Barrowman, 1996). From a management stand-

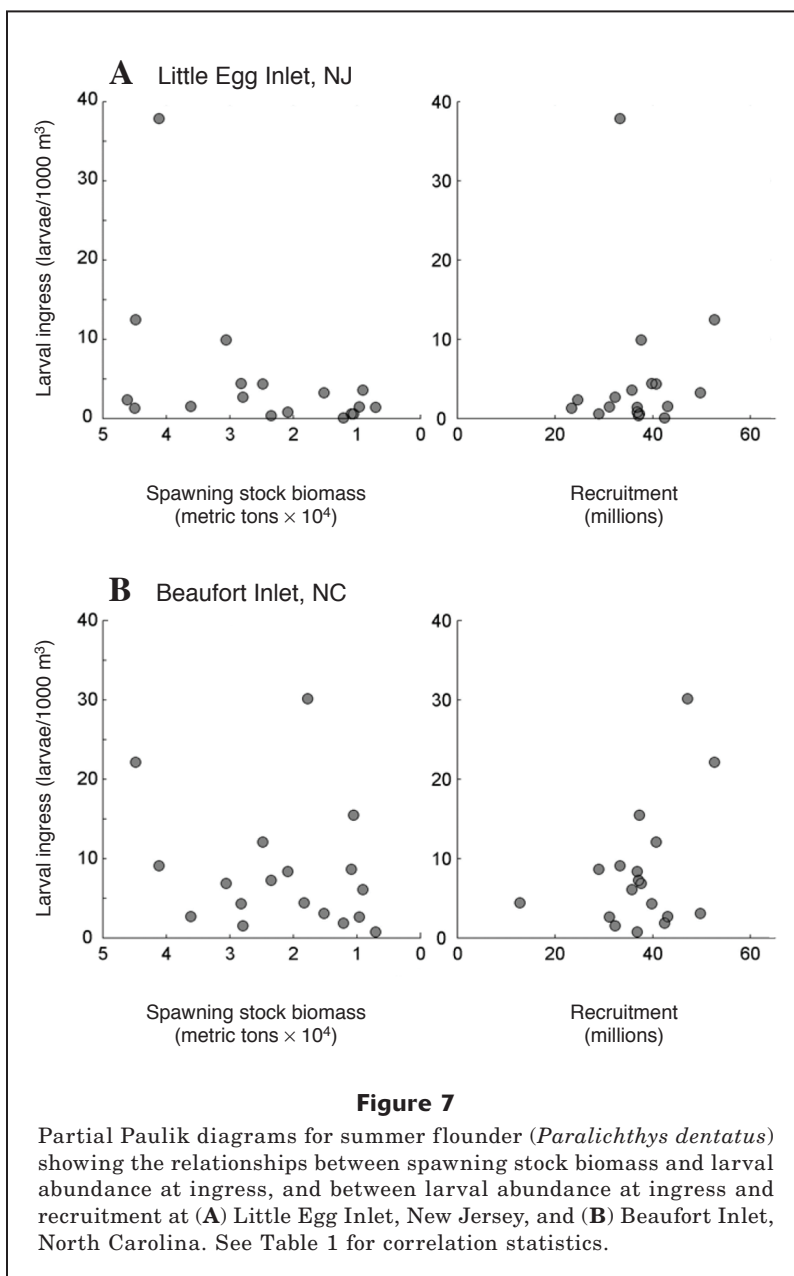
point, the continuation of larval collections at time of ingress into Little Egg Inlet would provide a fishery independent index for tracking spawning stock biomass for the stock north of Cape Hatteras, as well as data for continuing to explore the links between spawning, larval abundance at ingress, juvenile survival, and recruitment. Additionally, monitoring of larvae at ingress at Beaufort Inlet may provide an index of spawning stock biomass of the coastal North Carolina or "southern stock." The continuation and initiation of similar larval fish sampling programs at other estuarine inlets should provide an improved measure of stock status as well as help disentangle the complex relationships between biological and environmental factors affecting survival and ultimately recruitment for a number of species along the east coast of the United States.

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Literature cited

- Able, K. W., and M. P. Fahay.
1998. The first year in the life of estuarine fishes in the Middle Atlantic Bight, 342 p. Rutgers Univ. Press, Piscataway, NJ.
2010. Ecology of estuarine fishes: temperate waters of the western North Atlantic. Johns Hopkins Univ. Press, Baltimore, MD.
Able, K. W., and S. C. Kaiser.
1994. Synthesis of summer flounder habi-



- tat parameters. 68 p. NOAA Coastal Ocean Program Decision Analysis Series No. 1.
- Able, K. W., R. E. Matheson, W. W. Morse, M. P. Fahay, and G. Shepherd.
1990. Patterns of summer flounder *Paralichthys dentatus* early life history in the Mid-Atlantic Bight and New Jersey estuaries. *Fish. Bull.* 88:1–12.
- Barbeau, S.
2000. The influence of temperature-dependent growth of summer flounder, *Paralichthys dentatus*, on their period of vulnerability to two invertebrate predators. M.S. thesis, 70 p. Rutgers Univ., New Brunswick, NJ.
- Begg, G. A., and J. R. Waldman.
1999. A holistic approach to fish stock identification. *Fish. Res.* 43:35–44.
- Berrian, P., and J. Sibunka.
1999. Distribution patterns of fish eggs in the U.S. Northeast continental shelf ecosystem, 1977–1987. NOAA Tech. Rep. NMFS-145, 310 p.
- Bozeman, E. L., Jr., and J. M. Dean.
1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. *Estuaries* 3:89–97.
- Brodziak, J., and L. O'Brien.
2005. Do environmental factors affect recruits per spawner anomalies of New England groundfish? *ICES J. Mar. Sci.* 62:1394–1407.
- Buonaccorsi, J. P., J. S. Elkinton, S. R. Evans, and A. M. Leibhold.
2001. Measuring and testing for spatial synchrony. *Ecology* 82:1668–1679.
- Burke, J. S., J. P. Monaghan Jr., and S. Yokoyama.
2000. Efforts to understand stock structure of summer flounder (*Paralichthys dentatus*) in North Carolina, USA. *J. Sea Res.* 44:111–122.
- Chant, R. J., M. C. Curran, K. W. Able, and S. M. Glenn.
2000. Delivery of winter flounder (*Pseudopleuronectes americanus*) larvae to settlement habitats in coves near tidal inlets. *Estuar. Coast. Shelf Sci.* 51:529–541.
- Chapin, S. F., D. A. McGuire, J. Randerson, R. Pielke, D. Baldocchi, E. S. Hobbie, N. Roulet, W. Eugster, E. Kasischke, B. E. Rastetter, A. S. Zimov, and W. S. Running.
2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Glob. Change Biol.* 6:211–223.
- Charlesworth, L. J.
1968. Study of bay, inlet, and nearshore marine sedimentation: Beach Haven—Little Egg Inlet region, New Jersey. Ph.D. diss., 474 p. Univ. Michigan, Ann Arbor, MI.
- Churchill, J. H., J. L. Hench, R. A. Luettich Jr., J. O. Blanton, and F. E. Werner.
1999. Flood tide circulation near Beaufort Inlet, North Carolina: implications for larval recruitment. *Estuaries* 22:1057–1070.
- Collette, B. B., and G. Klein-MacPhee [eds].
2002. Bigelow and Schroeder's fishes of the Gulf of Maine. 3rd ed., 748 p. Smithsonian Institution Press, Washington, D.C.
- Deubler, E. E., Jr.
1958. A comparative study of the postlarvae of three flounders (*Paralichthys*) in North Carolina. *Copeia* 1958(2):112–116.
- Forward, R. B., Jr., K. A. Reinsel, D. S. Peters, R. A. Tankersley, J. H. Churchill, L. B. Crowder, W. F. Hettler, S. M. Warlen, and M. D. Greene.
1999. Transport of fish larvae through a tidal inlet. *Fish. Oceanogr.* 8:153–172.
- Hamer, P. A., and G. P. Jenkins.
1996. Larval supply and short-term recruitment of a temperate demersal fish, the King George whiting, *Sillaginodes punctata* Cuvier and Valenciennes, to an embayment in south-eastern Australia. *J. Exp. Mar. Biol. Ecol.* 208:197–214.
- Hare, J. A.
2005. The use of early life stages in stock identification studies. *In* Stock identification methods (S. Cardin, K. Friedland, and J. Waldman, eds.), p. 89–117. Academic Press, San Diego, CA.
- Hare, J. A., and K. W. Able.
2007. Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*). *Fish. Oceanogr.* 16:31–45.
- Hare, J. A., S. Thorrold, H. Walsh, C. Reiss, A. Valle-Levinson, and C. Jones.
2005. Biophysical mechanisms of larval fish ingress into Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 303:295–210.
- Hettler, W. F., Jr., and D. L. Barker.
1993. Distribution and abundance of larval fishes at two North Carolina inlets. *Estuar. Coast. Shelf Sci.* 37:161–179.
- Hettler, W. F., Jr., and A. J. Chester.
1990. Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. *Mar. Ecol. Prog. Ser.* 68:157–168.
- Hettler, W. F. Jr., and J. A. Hare.
1998. Abundance and size of larval fishes outside the entrance to Beaufort Inlet, North Carolina. *Estuaries* 21:476–499.
- Hettler, W. F., Jr., D. S. Peters, D. R. Colby, and E. H. Laban.
1997. Daily variability in abundance of larval fishes inside Beaufort Inlet. *Fish. Bull.* 95:477–493.
- Houde, E. D.
1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2:17–29.
- Hurst, T. P.
2007. Causes and consequence of winter mortality in fishes. *J. Fish Biol.* 71:315–345.
- Jenkins, G. P., M. J. Keough, and P. A. Hamer.
1998. The contributions of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. *J. Exp. Mar. Biol. Ecol.* 226:259–278.
- Jones, J., P. J. Doran, and R. T. Holmes.
2003. Climate and food synchronize regional bird abundances. *Ecology* 84:3024–3032.
- Jones, W. J., and J. M. Quattro.
1999. Genetic structure of summer flounder (*Paralichthys dentatus*) populations north and south of Cape Hatteras. *Mar. Biol.* 133:129–135.
- Keefe, M., and K. W. Able.
1993. Patterns of metamorphosis in summer flounder, *Paralichthys dentatus*. *J. Fish Biol.* 42:713–728.
1994. Contributions of abiotic and biotic factors to settlement in summer flounder, *Paralichthys dentatus*. *Copeia* 1994:458–465.
- Kennish, M. J.
2004. Jacques Cousteau National Estuarine Research Reserve. *In* Estuarine research, monitoring and resource protection (M. J. Kennish, ed.), p. 59–115. CRC Press, Boca Raton, FL.
- Kraus, R. T., and J. A. Musick.
2001. A brief interpretation of summer flounder, *Para-*

- lichthys dentatus*, movements and stock structure with new tagging data on juveniles. *Mar. Fish. Rev.* 63(3):1–6.
- Leggett, W. C., and K. T. Frank.
1997. A comparative analysis of recruitment variability in North Atlantic flatfishes: Testing the species range hypothesis. *J. Sea Res.* 37:281–299.
- Lewis, R. M., and W. C. Mann.
1971. Occurrence and abundance of larval Atlantic menhaden, *Brevoortia tyrannus*, at two North Carolina inlets with notes on associated species. *Trans. Am. Fish. Soc.* 100:296–301.
- Malloy, K. D., and T. E. Targett.
1991. Feeding, growth and survival of juvenile summer flounder *Paralichthys dentatus*: experimental analysis of the effects of temperature and salinity. *Mar. Ecol. Prog. Ser.* 72:213–223.
- Morse, W. W.
1981. Reproduction of the summer flounder, *Paralichthys dentatus* (L.). *J. Fish Biol.* 19:189–203.
- Myers, R. A., and N. J. Barrowman.
1996. Is fish recruitment related to spawner abundance? *Fish. Bull.* 94:707–724.
- Nash, R. D. M., and M. Dickey-Collas.
2005. The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.). *Fish. Oceanogr.* 14:279–291.
- (NRC) National Research Council.
2000. Improving the collection, management, and use of marine fisheries data, 222 p. Ocean Studies Board, Commission on Geosciences, Environment, and Resources. National Academy Press, Washington, D.C.
- Neuman, M. J., K. W. Able, and S. M. Glenn.
2002. The effects of upwelling on larval fish occurrence and abundance in the Jacques Cousteau National Estuarine Research Reserve at Mullica River—Great Bay (JCNERR). Jacques Cousteau Technical Report 100-17, 48 p. Institute of Marine and Coastal Sciences, Rutgers Univ., New Brunswick, NJ.
- Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz.
2009. Changing spatial distribution of fish stocks in relation to climate and stock size within the Northeast US continental shelf. *Mar. Ecol. Prog. Ser.* 393:111–129.
- Powell, A. B.
1974. Biology of the summer flounder, *Paralichthys dentatus*, in Pamlico Sound and adjacent waters, with comments on *P. lethostigma* and *P. albigutta*. M.S. thesis, 145 p. Univ. North Carolina, Chapel Hill, NC.
- Powell, T. M., and J. H. Steele.
1995. Ecological time series. Chapman & Hall, New York.
- Powles, H., and W. Stender.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. Technical Report 11, 46 p. South Carolina Marine Resources Center, Charleston, SC.
- Quinlan, J. A., and L. B. Crowder.
1999. Searching for sensitivity in the life history of Atlantic menhaden: inferences from a matrix model. *Fish. Oceanogr.* 8:124–133.
- Rice, J. A., J. A. Quinlan, S. W. Nixon, W. F. Hettler Jr., S. M. Warlen, and P. M. Stegmann.
1999. Spawning and transport dynamics of Atlantic menhaden: inferences from characteristics of immigrating larvae and predictions of a hydrodynamic model. *Fish. Oceanogr.* 8:93–110.
- Smith, W. G.
1973. The distribution of summer flounder, *Paralichthys dentatus*, eggs and larvae on the continental shelf between Cape Cod and Cape Lookout, 1965–66. *Fish. Bull.* 71:527–548.
- Sullivan, M. C., K. W. Able, J. A. Hare, and H. J. Walsh.
2006. *Anguilla rostrata* glass eel ingress into two U.S. east coast estuaries: patterns, processes and implications for adult abundance. *J. Fish Biol.* 69:1081–1101.
- Szedlmayer, S. T., K. W. Able, and R. A. Rountree.
1992. Growth and temperature-induced mortality of young of the year summer flounder (*Paralichthys dentatus*) in southern New Jersey. *Copeia* 1992(1):120–128.
- Taylor, J. C., W. A. Mitchell, J. A. Buckel, H. J. Walsh, K. W. Shertzer, G. B. Martin, and J. A. Hare.
2009. Relationships between larval and juvenile abundance of winter-spawned fishes in North Carolina, USA. *Mar. Coastal Fish.: Dynamics, Manag., Eco. Sci.* 1:12–21.
- Terceiro, M.
2002. The summer flounder chronicles: science, politics, and litigation, 1975–2000. *Rev. Fish Biol. Fish.* 11:125–168.
- Weinstein, M. P.
1979. Shallow marsh habitats as primary nurseries for fishes and shellfishes, Cape Fear River, North Carolina. *Fish. Bull.* 77:339–357.
- Wilk, S. J., W. W. Morse, and L. L. Stehlik.
1990. Annual cycles of gonad-somatic indices as indicators of spawning activity for selected species of finfish collected from the New York Bight. *Fish. Bull.* 88:775–786.
- Wilk, S. J., W. G. Smith, D. E. Ralph, and J. Sibunka.
1980. Population structure of summer flounder between New York and Florida based on linear discriminant analysis. *Trans. Am. Fish. Soc.* 109:265–271.
- Williams, A. B., and E. E. Deubler Jr.
1968. A ten year study of macroplankton in North Carolina estuaries: Assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. *Chesapeake Sci.* 9:27–41.
- Witting, D. A., and K. W. Able.
1995. Predation by sevenspine bay shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. *Mar. Ecol. Prog. Ser.* 123:23–31.
- Witting, D. A., K. W. Able, and M. P. Fahay.
1999. Larval fishes of a Middle Atlantic Bight estuary: assemblage structure and temporal stability. *Can. J. Fish. Aquat. Sci.* 56:222–230.