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Efforts to understand stock structure of summer flounder (*Paralichthys dentatus*) in North Carolina, USA

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Abstract

Understanding the stock structure of the summer flounder is critical to attempts to manage this species. Currently such research is particularly urgent due to increased interest in commercial culture and stock enhancement of summer flounder as this creates pressure to transplant fish among geographic areas. Studies of summer flounder in the coastal waters of North Carolina are of particular relevance to the stock structure due to the existence of a zoogeographic boundary at Cape Hatteras, NC. The importance of this boundary is being investigated through mark–recapture studies of adults, field sampling of larvae and laboratory experiments on larvae and juveniles originating from different brood stocks. Twenty-three thousand summer flounder were marked in coastal waters and movement of recaptured animals relative to season and the zoogeographic boundary analysed. Seasonal occurrence of larvae relative to this boundary was compared and animals were characterised in terms of fin ray numbers and size and developmental stage at arrival at the coast. In the laboratory we reared larvae from two brood stocks; one originating from the northern portion of the summer flounders range, and the other from North Carolina. These animals were used to determine the importance of temperature to fin ray formation and to compare growth of the two groups of larvae relative to temperature. Additional laboratory experiments include comparisons of salinity tolerance of larvae during the settlement period. Our results support the existence of different groups relative to this zoogeographic barrier and suggest that extensive movement of summer flounder from one region to another for stock enhancement or culture should be prohibited. Published by Elsevier Science B.V.

Keywords: mark recapture; larval immigration; salinity tolerance; zoogeographic barrier

1. Introduction

The range of the summer flounder (*Paralichthys dentatus*) extends from the southern edge of the boreal zone to the subtropics of the Atlantic coast of the United States. Included within this range is the well-known zoogeographic boundary that exists at Cape Hatteras, North Carolina. This boundary forms in association with divergence of the Gulf Stream current from the coast at Cape Hatteras. North of the Cape, coastal waters are temperate and generally flow south with the North West Atlantic Coastal Current while to the south, coastal waters are subtropical, warmed by the Gulf Stream, and direction of flow is more variable. This strong environmental

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discontinuity results in clear northern and southern fish distributions (Schwartz, 1989). Early investigations of summer flounder suggested the existence of at least two stocks relative to this boundary based on meristics (Ginsburg, 1952; Smith and Daiber, 1977), adult movements, distribution of eggs, larvae and landings (Smith, 1973), morphology (Wilk et al., 1980), and apparent geographical differences in growth patterns (Able et al., 1990). A recent physiological study indicated that juvenile summer flounder from North Carolina had higher growth rates and gross growth efficiencies than juveniles from Delaware Bay while the later were significantly more tolerant of decreasing temperatures than North Carolina juveniles (Malloy and Targett, 1994). Despite these findings, recent genetic research on summer flounder in relation to Cape Hatteras revealed no significant population subdivision relative to this zoogeographic boundary (Jones and Quattro, 1999). Genetic similarity over wide sea areas appears to be typical of marine species unless a hydrological or topographical feature acts as a barrier to dispersal (Smith et al., 1990). The presence of a major hydrological feature at Cape Hatteras and the observed physiological and morphological differences suggest that if the summer flounder population is continuously distributed, a clinal difference may exist and genetic isolation may be achieved by distance.

The question of whether the summer flounder should be divided into substocks for management is particularly important at this time. This species is currently considered over-fished and catch is regulated based on the assumption that a single functional stock exists over the species range. This could result in a variety of negative consequences (Bailey, 1997) if the population is divided into sub-stocks with independent dynamics regardless of whether these stocks are genetically independent. The question of genetic structure is also critical as the species is currently being considered a candidate for stock enhancement efforts. Clearly extensive stocking of flounder with exotic genes could have a negative impact on viability of a local population if local adaptations are genetically based (Tanaka et al., 1997). We tested the hypothesis that a single phenotypic group of summer flounder exists relative to Cape Hatteras based on mark recapture data, studies of larval immigration and physiological laboratory experiments.

2. Materials and methods

Life history parameters of summer flounder from north and south of Cape Hatteras were evaluated by examining data from the peer reviewed literature (Morse, 1981; Dery, 1988) and governmental agency reports (Monaghan, 1992; NOAA, 1998; USDC, 1986; Wenner et al., 1990). Mortality rates were calculated from these data using the methods of Pauly (1980) and Hoenig (1983). To evaluate movement of summer flounder relative to Cape Hatteras we combined data from mark recapture studies conducted by the North Carolina Division of Marine Fisheries between 1973 and 1996. In these studies 22 878 summer flounder were fitted with anchor tags and released in estuarine and near-shore ocean waters from Cape Henry, Virginia to the Cape Fear River in southeastern North Carolina. Length, date and location were recorded for each fish at the time of release and recapture. Fish that were recovered in the same location where they were tagged were excluded from the analysis. Release and recapture data were categorised as to area tagged (north or south of Cape Hatteras), latitudinal direction moved (north or south), and season (winter: January–March; spring: April–June; summer: July–September; fall: October–December) for analysis. The Chi-square analysis was used to test whether directional movement was independent of area tagged.

From October 1994 to April 1995, immigration of pelagic fish larvae was investigated using a sampling series at Oregon Inlet to the north of Cape Hatteras and to the south at Beaufort Inlet (Fig. 1). Although details of sampling procedure differed at the two inlets (Hettler, 1998) both studies were designed to determine temporal patterns of the abundance and size of fish larvae immigrating to estuarine nursery grounds during the season. Sampling was conducted at weekly intervals at night during the time of predicted flood tide. A flow meter was used to estimate the volumes of water sampled. No correction was made for gear efficiency, and the catch was standardised as the number 100 m^{-3}. At Oregon Inlet, 12 surface to bottom tows were made into the tidal current with a 1 m conical net of 800 μm mesh. At Beaufort Inlet four samples were taken with a 2 m^2 neuston net of 999 μm mesh. Samples were preserved in 70% ethanol, summer flounder sorted

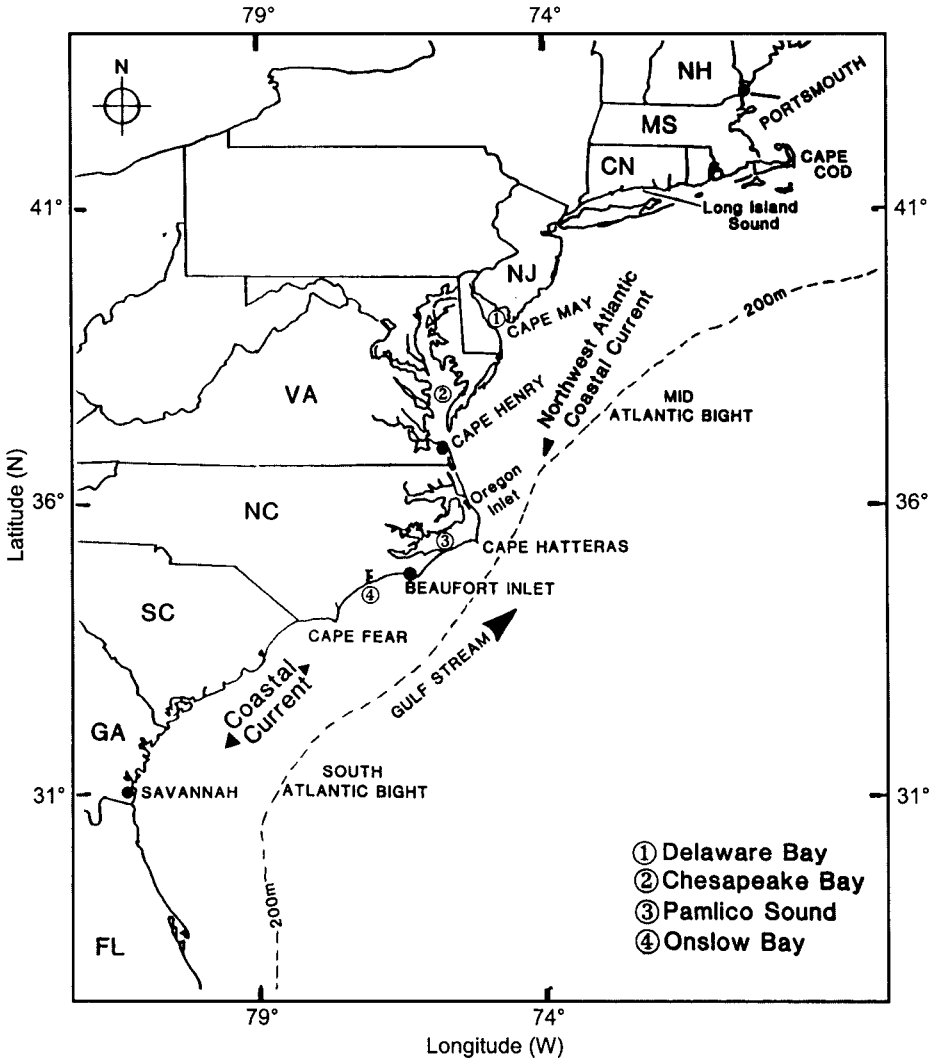


Fig. 1. Map of the Atlantic coast of the United States including geographic locations and areas mentioned in the text.

out, standard length determined to the nearest mm and developmental stage determined (Minami, 1982; Goto et al., 1989). Dorsal and anal fin rays were counted after relaxing them with a 1% solution of KOH. By G stage, the earliest developmental stage present in the samples, larvae have developed a full complement of fin rays. Relative abundance of summer flounder larvae at the two inlets is expressed as the arithmetic mean of volumetrically standardised catches from a given date.

Laboratory experiments were conducted on progeny originating from geographically distant broodstocks in 1998. One group originated from broodstock collected in Long Island Sound and maintained at the Great Bay Hatchery in Portsmouth, New Hampshire (Fig. 1). Yolk sack larvae shipped to the National Oceanic and Atmospheric Administration (NOAA) Beaufort Laboratory originated from eight females and five males that were strip spawned and their eggs incubated in a common hatching tank. The second group of progeny originated from broodstock collected from Onslow Bay, North Carolina and

Table 1
Life history parameters of summer flounder sampled north and south of Cape Hatteras, North Carolina

Location	Natural mortality (*M*)	Oldest fish aged	*L* infinity (mmTL)	TL at maturity L_{50} (female)	Age at maturity
North					
Mid-Atlantic Bight	0.27 Pauly[a] 0.28 Hoenig[a]	12[b]	827[c]	323[d]	2[e]
South					
South Carolina	0.48 Pauly[f] 0.87 Hoenig[f]	5[f]	402[f]	307[f]	1[f]

[a] Monaghan, 1992.
[b] Dery, 1988.
[c] USDC, 1986.
[d] Morse, 1981.
[e] NOAA, 1998.
[f] Wenner et al., 1990.

maintained at the NOAA Beaufort Laboratory. Eggs were collected from a volitionally spawning group that consisted of two females and three males. To remove the effects of mortality associated with early development and first feeding both groups of larvae were initially reared at a concentration of 30–60 dm^{-3}. When the larvae developed pigmented eyes and a functional mouth, rotifers (*Brachionus* sp., S-type) were introduced at a concentration of 5 cm^{-3}. The initial water temperature of 15°C was gradually raised to 18°C.

At ten days post hatch, feeding, preflexion larvae were collected from rearing tanks and counted into replicate rearing tanks for temperature trials. Separate temperature trials were conducted on the two groups of summer flounder at three constant temperatures (16, 19 and 22°C). Larvae were reared at a common initial concentration (15 dm^{-3}) in 10-dm^3 containers. One third of the volume of the experimental containers was exchanged daily and larvae were fed ad libitum until all survivors had undergone metamorphosis and settled. In trial 1, four replicate containers/temperature were stocked with northern larvae; in trial 2, three replicate containers were stocked with southern larvae. Flounder in each tank were sampled at weekly intervals. Three to five flounder were captured from each tank, anaesthetised with MS222, measured for SL, developmental stage determined and preserved in 5% formalin. After all flounder had settled in a replicate, this sampling procedure was used to sample all remaining fish. Formalin-preserved juvenile specimens with completely developed fins from this final sample were used to make fin ray counts.

Salinity tolerance trials were designed to examine the tolerance of flounder from the two groups during the transition from planktonic to benthic life stages. For these trials, single, planktonic but metamorphosing larvae (G stage, Minami, 1982) were pipetted from 100-dm^3 rearing tanks (18°C, salinity 30‰) directly to 1-dm^3 beakers of low salinity water so that the treatment concentration was either 2.5 or 5‰. Temperature was maintained at 19°C, one third of the volume of each beaker was exchanged and larvae were fed *Artemia* nauplii daily. An individual trial was terminated when the flounder larvae died or completed the transition to benthic life. A series of 2 × 2 contingency tables were used to analyse flounder survival and mortality counts. We tested for differences in survival between the two groups and whether the salinity treatments affected overall and within group survival.

3. Results

Life history parameters calculated for summer flounder from South Carolina are quite different from those for flounder from the Mid Atlantic Bight (Table 1). Calculated natural mortality rates indicate that *M* is significantly more severe in the south

Table 2
Mark–recapture data for summer flounder tagged north and south of Cape Hatteras, North Carolina

Releases			Recaptures (fish that moved)				
Season	Area	Number	Season	Area	Number	Mean length	S.D.
Winter	North	3321	Winter	North	42	291	72
	South	1523		South	83	368	105
Spring	North	1535	Spring	North	40	369	77
	South	5373		South	33	274	46
Summer	North	1754	Summer	North	47	279	26
	South	4575		South	182	344	60
Fall	North	3043	Fall	North	139	345	84
	South	2230		South	105	310	46

resulting in a shorter life span, smaller maximum size and earlier sexual maturation.

In excess of 1500 fish were tagged for each area and season combination (Table 2). For fish that moved from the tagging location, recapture rate varied with season with greatest overall numbers recaptured in the fall. Size of recaptures varied with season and area. Largest fish in the north were recaptured in the spring and fall and largest fish in the south in the winter and summer (Table 2). Chi-squared tests to determine whether latitudinal movement was independent of area tagged (Table 3) indicated quite different patterns of movement in the two regions. Fish tagged in the north generally did not exhibit significant latitudinal movement with the exception of those, which were recaptured in the summer when significantly more fish moved north. In contrast, fish tagged in the south tended to move south in all seasons with the exception of the spring, when more fish moved north than south; however, this was not significant.

Timing of peak larval immigration differed by almost four months between Oregon and Beaufort inlets (Fig. 2). Immigration to the north of Cape Hatteras, at Oregon Inlet, rose rapidly to a peak in November and then declined. In contrast, south of Hatteras at Beaufort Inlet, summer flounder first appeared in late December and peaked in late February and March. Catch of summer flounder was higher

Table 3
Results of Chi-squared test for random latitudinal movement of summer flounder tagged north and south of Cape Hatteras

Season returned	Area tagged	Direction moved			Chi-square	p-Value
		North	South	Total		
Winter	North	23	19	42	0.381	0.827
	South[a]	12	71	83	41.940	0.000
Spring	North	25	15	40	2.500	0.287
	South	25	15	40	2.500	0.287
Summer	North[a]	35	12	47	11.255	0.004
	South[a]	27	155	182	90.022	0.000
Fall	North	65	74	139	0.583	0.747
	South[a]	30	75	105	19.286	0.000
Total		233	438	735		

[a] Non-random movement.

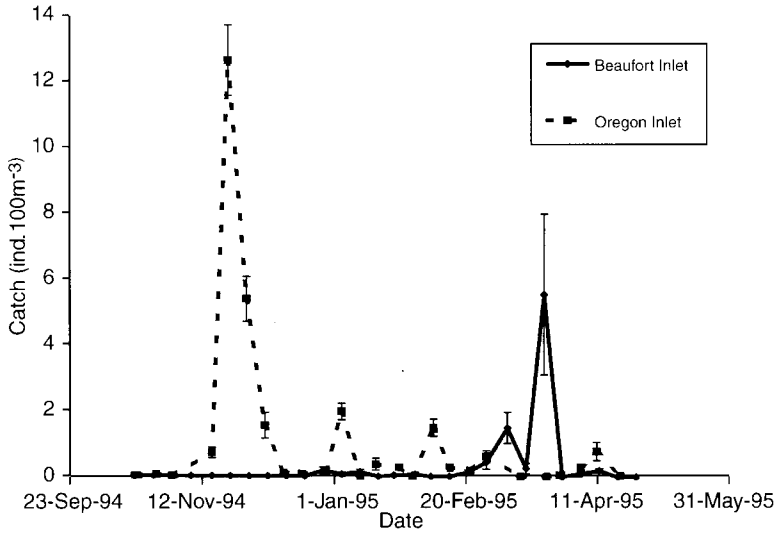


Fig. 2. Mean catch ± standard error (ind. 100 m^{-3}) of summer flounder, sampled weekly during the immigration season of 1994–1995 at Oregon and Beaufort Inlets.

at Oregon Inlet, where 329 larvae were captured, compared to 77 at Beaufort Inlet over the season. Patterns of length at immigration appeared to differ at the two inlets as regression analysis indicated a significantly positive slope ($p < 0.0001$) at Oregon Inlet while the slope was not significant at Beaufort ($p = 0.17$). The range in size at immigration also differed between the two inlets. Larger and smaller larvae occurred at Oregon Inlet, where range in length exceeded 6 mm, compared to 4 mm at Beaufort (Fig. 3a). Although mean numbers of fin rays were similar between the flounder entering the two inlets, temporal trends in fin ray number were different. Regression analysis indicated that at Beaufort Inlet the number of rays showed an increasing trend as the slope was positive and highly significant ($p < 0.001$), while at Oregon Inlet the slope was negative but not significant ($p = 0.44$) (Fig. 3b). At Beaufort inlet larvae tended to enter at a more advanced stage of development (Fig. 4). Analysis of the stage distributions with a 2 × 6 contingency table indicated that the distributions were significantly different ($p < 0.001$).

Performance of progeny from the northern and southern broodstocks in the rearing trials was similar at the high and low temperature but differed at 19°C. Regression analysis indicated that growth was highest at 22°C and that essentially identical linear equations best described growth of both groups (Standard length = 0.27 × Day + 1.7). At 16°C, growth of the two groups was also essentially the same and best described by the linear equation Standard length = 0.15 × Day + 2.4 (Fig. 5). Although growth of the two groups was the same at the high and low temperatures, a difference was apparent at the intermediate temperature. Regression analysis indicted that though linear models were the best fit for growth at 16 and 22°C, curves were required to describe growth at 19°C ($p < 0.05$). Interestingly, these curves described different growth trajectories. The southern group's growth rate increased over time while the northern group rate decreased (Fig. 5).

Settled juveniles from the growth study were used to compare fin ray development of the two groups, relative to temperature. Fin ray number showed a significant increase for both stocks with temperature ($p < 0.05$). The mean number of rays at a given temperature was consistently lower for fish from the northern group, but differences between groups at a given temperature were not significant (Fig. 6). Low salinity tolerance during settlement was different between the two groups (Fig. 7). Overall mortality differed between the two groups (Chi-squared, $p < 0.01$). Mortality of northern fish was higher

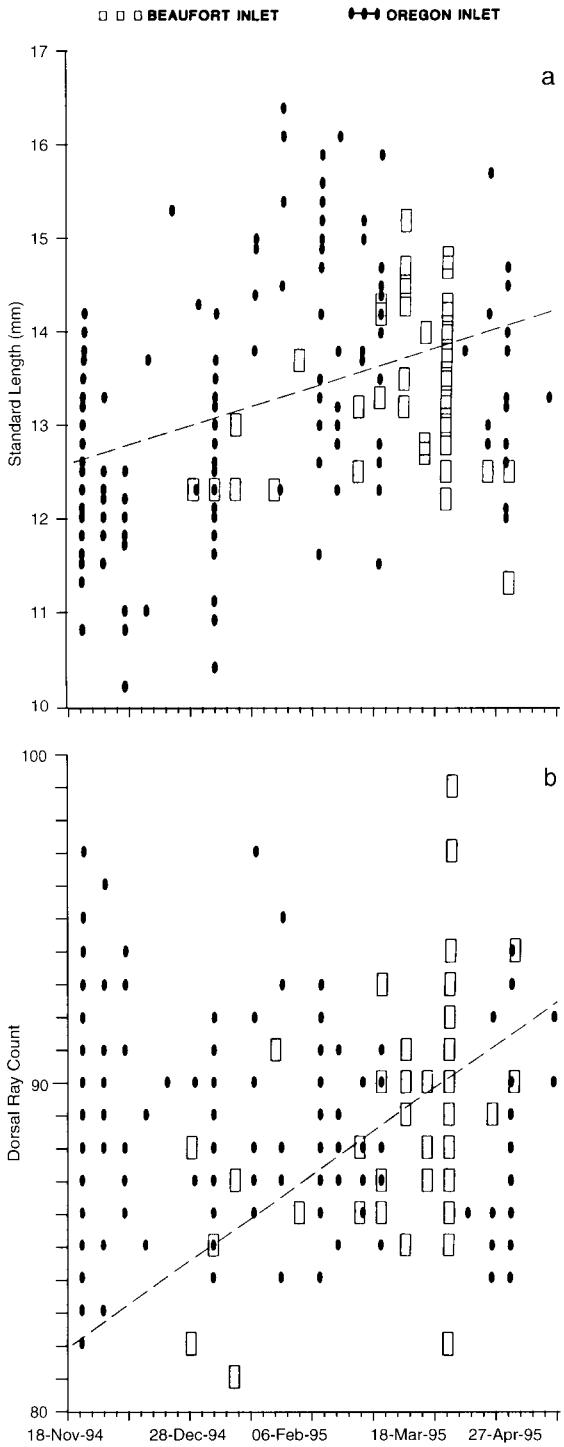


Fig. 3. Trends in: (a) length (mm); and (b) dorsal ray count (n) of summer flounder sampled weekly during the immigration season of 1994–1995 at Oregon and Beaufort Inlets.

exceeding 50% at 5‰ and 80% at 2.5‰ and differed between the two salinity treatments ($p < 0.05$). Mortality of southern fish was less than 40% at both 2.5 and 5‰ during settlement and did not differ between treatments ($p > 0.60$).

4. Discussion

Our understanding of the complexity of genetic structure of marine flatfish populations shows that structure can vary from geographically aggregated local populations that can be shown to be genetically distinct, to populations for which no evidence of genetic structure can be found despite wide geographic ranges (Bailey, 1997). The later situation can be explained by gene flow due to larval dispersal and the ability of adults to make extensive migrations. Summer flounder are migratory batch spawners, with high fecundity and pelagic eggs so that during spawning migrations eggs are dispersed in time and space. Given this life history the recent conclusion of Jones and Quattro (1999) that there was no evidence for genetic subdivision of the summer flounder at Cape Hatteras seems reasonable. However, a number of observations suggest that we should not accept the lack of genetic evidence as proof that the stock is homogeneous north and south of this zoogeographic boundary. The same study did find evidence of genetic structure in the northern portion of the species range where no obvious zoogeographic boundary exists. This evidence is difficult to reconcile with the apparent lack of structure relative to Cape Hatteras. Sampling problems could be responsible for the apparent lack of structure as fish samples from the South Atlantic Bight consisted exclusively of juvenile fish. This could bias results if initially mixed groups sort themselves out due to differential mortality or migration. Another alternative explanation is that genetic structure does exist relative to Cape Hatteras but was not detected due to the resolving power of the molecular techniques used. Given these alternatives it would seem prudent to consider Jones and Quattro's conclusion of little genetic structure in the summer flounder population as preliminary until studies with adults and higher resolution methods have been tested.

Despite the ability of summer flounder to make

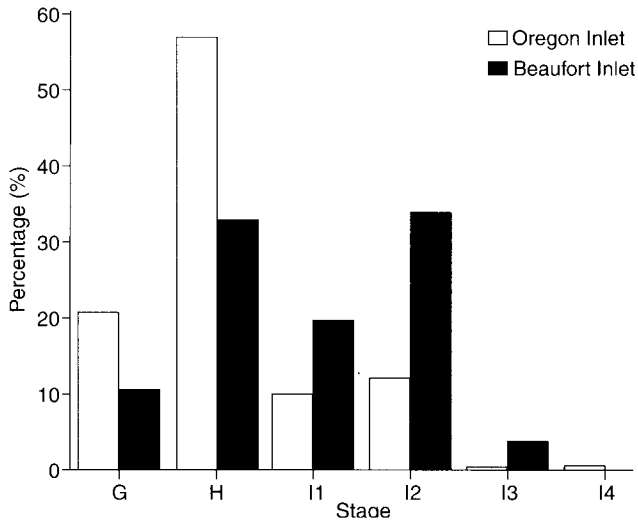
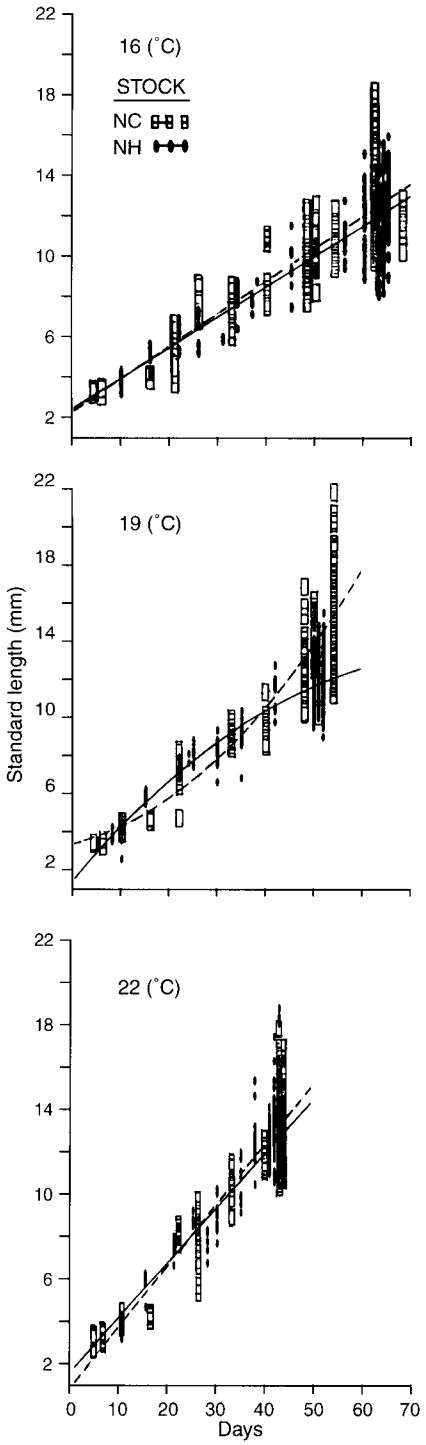


Fig. 4. Developmental stage distribution of summer flounder larvae captured at Oregon and Beaufort Inlets during 1994–1995.

extensive migrations, tagging studies have generally supported the concept of division of the species into relatively discrete spawning groups. In the Mid Atlantic Bight spawning starts in September in inshore waters and spreads offshore and south. Egg collections indicate that peak spawning occurs in October and November and is greatly reduced or absent in winter. A second small peak of spawning in the southern portion of the Mid Atlantic Bight has been observed in April and May (Berrien and Sibunka, 1999). Spawning migrations of summer flounder from southern New England, New York and New Jersey are generally offshore to the shelf edge and a strong tendency to return to the same summering grounds is evident (Poole, 1962; Murawski, 1970; Lux and Nichy, 1981). Movement southward along the coast was also observed in some studies (Weber, 1984; Desfosse et al., 1990) and may be due to variations in bottom water temperature (Lux and Nichy, 1981). Smith (1973) concluded that "one segment of the species" spawns principally north of Delaware Bay, a second from Virginia to Cape Hatteras and a third south of Cape Hatteras. Desfosse et al. (1990) hypothesised that two stocks may be present in Virginia waters; a "northern" stock that migrates offshore to spawn and a "southern" stock that migrates south to coastal waters off North Carolina.

Larval immigration and movement data from North Carolina indicate that spawning of summer flounder from south of Hatteras may be distinct from spawning of resident and southward migrating fish north of Cape Hatteras. Mark recapture data indicated that significant movement of northern fish was only evident in summer, when the expected movement north was apparent. In contrast fish tagged south of Hatteras showed movement south during this period, a trend that apparently continues through the fall and winter. These differences in movement patterns of adults may explain the difference in the timing of spawning and peak recruitment of larvae in the two regions. The pattern of larval immigration observed at Oregon Inlet in 1994–1995 is consistent with larval data from the shelf of North Carolina north of Cape Hatteras (Able et al., 1990) and supports the finding that peak spawning north of Hatteras occurs in the fall (Berrien and Sibunka, 1999). Examination of seasonal variability of summer flounder ingress at Beaufort Inlet (Fig. 8) shows that peak immigration generally occurs in the spring and may result from spawning of southern fish during late winter and spring.

Phenotypic variation between summer flounder from regions north and south of Cape Hatteras might be expected based on environmental (temperature and salinity) habitat (distribution of estuaries, live bottom, submarine canyons, and extent of the continental shelf) and faunal differences and may be responsible for observed differences in life history parameters and movement patterns of adults. Differences in



larvae entering the sounds of North Carolina through Oregon and Beaufort Inlets may result from differences in environmental conditions under which larvae develop and differences in the parent stock. Differences in temperature and currents north and south of Hatteras would be expected to influence growth, development and transport of larvae. The increasing trend in size at Oregon and in dorsal ray count at Beaufort Inlet over the season might be expected given the different temperature regimes during the spawning season in the two regions. Size at a given developmental stage increases as growth rate decreases and consequently generally increases as temperature decreases (Seikai et al., 1986). At Oregon Inlet, where immigration started during the fall when coastal waters were warm and continued as water temperature fell, larval size would be expected to increase as the season progressed since the range of development at immigration of summer flounder is limited to metamorphosing larvae (Fig. 4, Burke et al., 1998). The number of fin rays increases with increasing environmental temperature during larval development (Fig. 6, Kinoshita et al., 2000). At Beaufort Inlet immigration commenced in the winter though the major portion of recruitment occurred in spring and the number of fin rays would be expected to increase over the season as the coastal waters warmed during spring.

Laboratory experiments with northern and southern groups were performed under the assumption that adaptation to regional environmental and habitat differences have occurred so that one group would be expected to perform better on a given trial. For example it was expected that growth of the northern group would be better than the southern group in the low temperature treatment, the opposite at high temperature. Clearly our expectations were not met. The pattern of growth observed at 19°C suggests a difference in growth rate may develop after settlement and transformation to the juvenile stage, a possibility supported by the work of Malloy and Targett (1994) with juvenile summer flounder. Results of salinity trials indicated that the southern group was more

Fig. 5. Growth of two groups of summer flounder at three temperatures in the laboratory. Group originating from northern (NH) and a southern (NC) broodstocks were reared at constant temperatures of 16, 19 and 22°C.

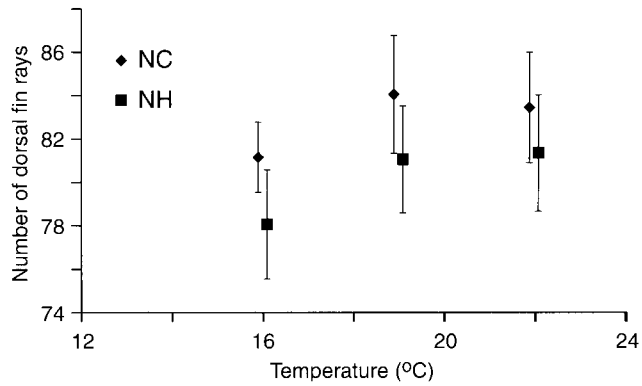


Fig. 6. Numbers of dorsal fin rays of two groups of summer flounder reared at three temperatures. Groups originating from northern (NH) and a southern (NC) broodstocks were reared at constant temperatures of 16, 19 and 22°C.

tolerant of low salinity conditions during metamorphosis than the northern group (Fig. 8). This supported the assumption that the southern group was more likely to use estuarine nurseries where exposure to low salinity during settlement was probable. Water temperatures in Mid Atlantic Bight estuaries may fall below 0°C, which can be lethal to summer flounder. It has been speculated that larvae may settle on the shelf and immigrate to estuaries as juveniles in the spring (Able et al., 1990). Temperature had a similar effect on fin formation of both groups (Fig. 7). The significance of consistently higher numbers of rays in the Southern group is not clear since this may relate to variability among individuals rather than stocks. In contrast to these results, Ginsburg (1952) compared meristics of summer flounder from Chesapeake Bay and from North Carolina waters and found lower numbers in North Carolina flounders. Rearing conditions had a strong effect on fin ray development in both groups as they exhibited much lower ray numbers than wild summer flounder. It is unlikely that this is an effect of temperature since spawning appears to occur between 12–19°C (Smith, 1973). A more likely cause of low fin ray numbers is nutrition, which has been shown to affect other developmental

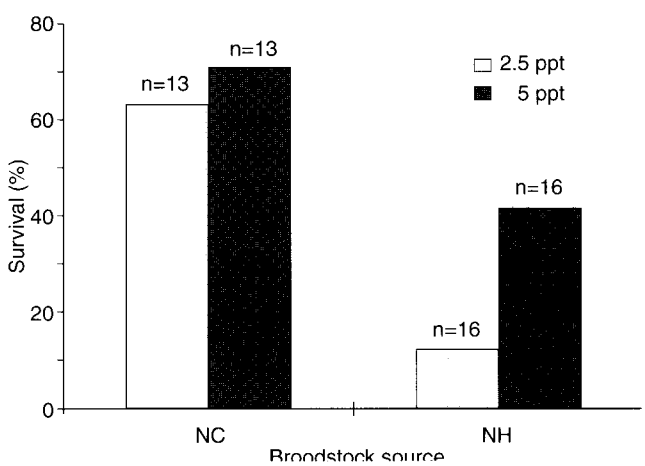


Fig. 7. Survival of summer flounder through settlement in low salinity challenge experiments. Single larvae originating from northern (NH) and a southern (NC) broodstocks were introduced into rearing containers containing 2.5 and 5‰ water and their survival monitored at constant temperature.

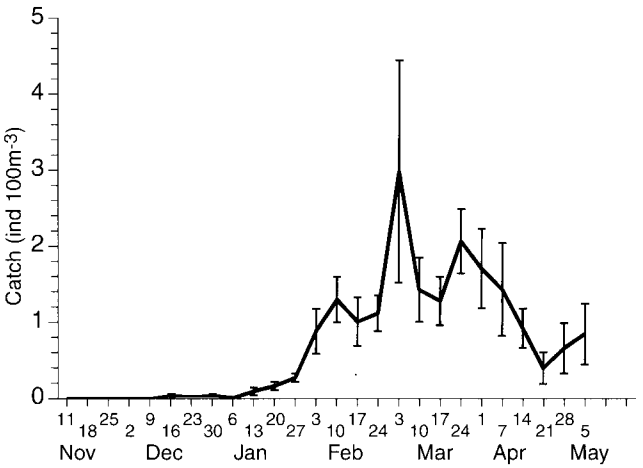


Fig. 8. Mean weekly catch (± standard error) of summer flounder sampled at Beaufort Inlet from 1986 to 1996.

processes such as pigmentation development in flatfish (Seikai et al., 1987). The clear morphological difference in fin ray number between the hatchery-reared flounder and wild summer flounder probably reflects a variety of physical and behavioural differences between wild and hatchery-reared fish. Any efforts to enhance summer flounder stocks with hatchery-reared fish must consider the phenotypic as well as the genotypic variability of flounder released to the sea.

These results support earlier studies, which concluded that different stocks exist relative to the zoogeographic boundary at Cape Hatteras. At present, the northern and southern groups should be considered functional stocks since currently there is no evidence that they are genetically distinct (Jones and Quattro, 1999). The importance of summer flounder warrants further work on dynamics and stock structure. Techniques such as DNA microsatellite analysis, tagging combined with molecular genetics and the utilisation of naturally occurring tags (Bailey, 1997) should prove useful in clarifying the structure of this important coastal species.

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