A Brief Interpretation of Summer Flounder, *Paralichthys dentatus*, Movements and Stock Structure with New Tagging Data on Juveniles

RICHARD T. KRAUS and JOHN A. MUSICK

Introduction

Summer flounder, *Paralichthys dentatus*, is a valuable flatfish species that is highly sought by both commercial and recreational fishermen (National Marine Fisheries Service, 1999; NEFSC¹).

Richard T. Kraus is with the University of Maryland Center for Environmental Science, One Williams Street, P.O. Box 38, Solomons, MD 20688 [e-mail: kraus@cbl.umces.edu]. John A. Musick is with the College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, VA 23062. Views or opinions expressed or implied are those of the authors and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

ABSTRACT—Summer flounder, Paralichthys dentatus, are managed as a single stock along the Atlantic coast from the U.S.-Canada border to the southern border of North Carolina. Justification of the singlestock approach is based on lack of genetic evidence for multiple stocks and the difficulty presented by managing the species from Cape Hatteras to the U.S.-Canada border. In this review, we present an interpretation of various morphometric, meristic, biochemical, and tagging studies, published and unpublished, that indicate the presence of two, or possibly three, distinct stocks in the management area. In addition, we have included new data from a tagging study that was conducted on juveniles from *Virginia that aids in defining the stock(s)* north of Cape Hatteras. Summer flounder, overfished for the past two decades, is recovering, and reconsideration of proposed stock structure could have direct implications for management policy decisions.

Through the 1980's and 1990's, the stock exhibited classic symptoms of overfishing, including declines in landings, declines in abundance and recruitment indices, and an age-structure with predominately young fish, less than age-3 (NEFSC¹). Summer flounder are managed as a single stock along the U.S. Atlantic coast from the Canadian border to the southern border of North Carolina, and recent actions to rebuild the stock have sought to increase minimum size limits and reduce quotas (NEFSC¹). With recent quota reductions and an increase in minimum size limits, the age-structure has expanded, fishing mortality has decreased, and the stock is recovering (NEFSC¹). The stock structure of summer flounder is a crucial consideration for management, because the vital population rates, upon which regulations are based, should be homogeneous within a stock (Hilborn and Walters, 1992). In this paper, we present a review of information on the ecology and movements of summer flounder drawn largely from government documents and unpublished theses and dissertations. Collectively, these studies and new tagging data on juveniles suggest that there are multiple stocks within the management area.

Life Cycle

Several sources provide detailed life-cycle information; this brief background, with major points concerning spatial distribution of eggs, larvae, and juveniles, is based on Able and Kaiser.² Summer flounder migrate annually to inshore estuarine and coastal areas during the summer and to offshore areas on the continental slope during winter. Spawning takes place in the fall and winter and progresses from north to south along the continental shelf. In fall, winter, and spring, eggs and larvae can be found throughout shelf waters of the management area as far north as Georges Bank. Smith (1973) observed three concentrations of eggs that suggested separate spawning centers (and potential stocks): one off New Jersev. one along the Virginia North Carolina coast, and one south of Cape Hatteras, N.C. From November to April, pelagic larvae enter estuaries and coastal lagoons where they metamorphose, then remain inshore or near shore as benthic juveniles. With declining fall water temperatures, juveniles and adults depart from those inshore habitats.

Despite extensive sampling in the management area, juvenile summer flounder are only found from southern New Jersey to North Carolina (Smith and Daiber, 1977; Able et al., 1990; Burke et al., 1991; Malloy and Targett, 1991; Szedlmayer et al., 1992; Norcross and Wyanski, 1993). The absence of juveniles in northern New Jersev waters and estuaries farther north may be explained by low temperatures, which occur frequently during the settlement period and can cause acute juvenile mortality (Malloy and Targett, 1991; Malloy and Targett, 1994). An alternative explanation suggested by Able et al. (1990) is that northern juveniles might utilize a continental shelf nursery; however, sampling of the continental shelf for juvenile summer flounder has been unproductive, and fully metamorphosed larvae have never been reported from shelf waters.

The lack of information on fully metamorphosed larvae from the con-

¹NEFSC. 2000. Report of the 31st Northeast Regional Stock Assessment Workshop (31st SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 00-15, 400 p.

²Able, K. W., and S. C. Kaiser. 1994. Synthesis of summer flounder habitat parameters. U.S. Dep. Commer., NOAA Coastal Ocean Office, NOAA Coastal Ocean Program Decision Anal. Ser. 1, 68 p., Silver Spring, Md.

tinental shelf leaves the issue of an offshore nursery unresolved; however, the larval stage duration is variable and may be protracted over several months, with potential for large-scale dispersal of larvae. Rogers and Van Den Avyle³ related that eggs and larvae off New Jersey and Virginia might be carried passively by a dominant southwesterly flow toward estuaries of Virginia and North Carolina. If southwesterly transport of eggs and larvae was significant, then estuaries in the southern part of the range might contain both juveniles that were spawned off New Jersey and those that were spawned along the Virginia–North Carolina coastline (Rogers and Van Den Avyle³). Further, if there were no juvenile nursery on the shelf off New Jersey, then adult flounder in the northern part of the range would have to occur as a result of juveniles migrating from southern nurseries. Thus, there is a testable hypothesis that marked juveniles from estuaries in the southern part of the range will be recaptured to the north as adults. To test this hypothesis, we conducted a tagging study on juvenile summer flounder in Virginia and present the results in another section of this paper. In summary, spatial distribution of eggs suggests three spawning aggregations of summer flounder, and competing hypotheses to explain larval and juvenile distribution also suggest that larvae from the two northern most aggregations may intermingle as juveniles.

Phenotypic Variation

The potential existence of independent spawning aggregations of summer flounder in the management area has prompted many studies that compare phenotypic traits among groups determined a priori. While environmental factors affect expression of the traits and can confound interpretations, some have made efforts to control for environmental effects, and geographically distinct phenotypes have been described as evidence of multiple stocks. Latitudinal variation in growth rates has been observed through holding experiments, length frequency analysis, and through back-calculation of size-atage from hard parts (Dery, 1981; Powell, 1982; Szedlmayer et al., 1992; Malloy and Targett, 1994; Burke et al., 2000). Morphometric and meristic analyses were able to discriminate differences among individuals from north and south of Cape Hatteras (Ginsburg, 1952; Smith and Daiber, 1977; Wilk et al., 1980; Fogarty et al., 1983, Delaney, 1986). Gel-electrophoresis isozyme analysis further suggests that Cape Hatteras acts as a zoogeographic barrier to the mixing of populations from the north and south (Van Housen, 1984). The variation in growth rates provides a justification for managing multiple stocks (Burke et al., 2000), and the morphological, meristic, and biochemical results could be applied to identify landings from separate stocks. These phenotypic delineations of stock structure have not motivated managers to consider multiple stocks, and lack of a genetic basis for stock structure (Jones and Quattro, 1999) has been used to justify managing summer flounder as a single stock (NEFSC¹).

Mark-recapture Studies

Small amounts of mixing between populations can obscure genetic differences, even when there is sound justification for multiple stocks (Ryman and Utter, 1987). Further, stock integrity can be maintained behaviorally, without morphological differences. Patterns in the movements of summer flounder, inferred from mark-recapture studies, show distinct geographic groups that may overwinter together (refer to Figure 1 during the following discussion).

One group occurs as adults north of Cape Hatteras, N.C., during the summer, and these individuals move during the fall toward continental slope habitats off Virginia and North Carolina. Individuals tagged in the seaside estuaries of Long Island, N.Y., and inshore near Cape May and Sandy Hook, N.J., were recaptured to the south and east (yet north of Cape Hatteras), with the greatest number of recaptures from the shelf break during the winter months (Westman and Neville⁴, Murawski⁵). The pattern of recaptures suggested directed movement to shelf

waters off New Jersey, followed by gradual southerly movement along the shelf break. More recent tagging efforts off Jones Beach, N.Y., further supported the tendency for the northern stock to remain north of Cape Hatteras (with one exceptional recapture far to the south in Georgia (Monaghan⁶)). In coastal areas near Oregon Inlet, N.C., adult summer flounder moved offshore during fall and winter, but tagging data did not indicate any significant tendency to move to the south or north (Burke et al., 2000). Individuals tagged in estuaries and coastal areas of Virginia over-wintered at the shelf break off of Virginia and North Carolina, and a pattern of egress in which many individuals moved south along the Virginia–North Carolina coastline before moving offshore was also evident (Desfosse, 1995). The two apparent fall movement behaviors that occur north of Cape Hatteras (moving immediately offshore vs. following the coastline) provide a mechanism to explain the spawning aggregations indicated by Smith (1973). Van Housen (1984) termed these contingents the offshore and trans-Hatteras stocks; however, the integrity of these behaviors is still uncertain. The spring migration of adults to inshore areas appears to balance the fall migration. Individuals tagged off Cape Cod, at Hudson Canyon, and off the Virginia-North Carolina coast on their presumed wintering grounds were later recaptured inshore to the north and east (Burke et al., 2000) (Monaghan⁶, Hamer and Lux⁷, Lux and Nichy⁸, Gillikin⁹).

³Rogers, 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. U.S. Dep. Inter., Fish Wildl. Serv. FWS/OBS-82/11.15 and U.S. Army Corps Engr. TR EL-82-4, 14 p.

⁴Westman, J. R., and W. C. Neville. 1946. Some studies on the life history and economics of the fluke, *Paralichthys dentatus*, of Long Island waters. A report printed under sponsorship of the Islip Town Board. Islip, N.Y., 15 p.

⁵Murawski, W. S. 1970. Results of tagging experiments of summer flounder, *Paralichthys dentatus*, conducted in New Jersey waters from 1960–1967. N.J. Div. Fish, Game Shellfish., Nacote Creek Res. Sta., Misc. Rep. 5M, 25 p.

⁶Monaghan, J. P. 1996. Migration of paralichthid flounders tagged in North Carolina. N.C. Div. Mar. Fish., Completion Rep. Grant F-43, 44 p.

⁷Hamer, P. E., and F. E. Lux. 1962. Marking experiments on fluke (*Paralichthys dentatus*) in 1961. Minutes of the 21st meeting of the North Atlantic Section, Atlantic States Marine Fisheries Committee, Dinkler-Plaza Hotel, Atlanta, Georgia, September 27, 1962. App. MA-6.



Figure 1.—A conceptual model of major seasonal movements of adult summer flounder. For geographic reference, the shoreline from North Carolina to Rhode Island and the 200, 500, and 1,000 m depth contours are shown to demarcate the limits of the continental shelf. Important locations that are discussed in the text are labeled in frame "A". Fall and spring migration routes are depicted in frames "B" and "C", respectively. The solid arrows indicate the patterns exhibited by the northern stock, and the dashed arrow indicates that seasonal egress or ingress of the southern stock may not always occur. Also shown are the wintering areas of hypothesized "offshore" and "trans-Hatteras" stocks (vertically and horizontally hatched areas, respectively) in which the southern extent is uncertain. Note that the indicated movements of the southern stock are not intended to identify specific inlets through which flounder move, but rather that primary movement patterns are to-and-from offshore and more southern areas. The text provides further explanation of proposed stock identities.

Movements and integrity of the group of summer flounder that occurs north of Cape Hatteras are also supported by data from the American Littoral Society (ALS). The ALS conducts a recreationalangler-based tagging program, and data were obtained from Gary Shepherd at the NMFS Northeast Fisheries Science Center, Woods Hole, Mass. (personal commun.). Excluding erroneous release locations (n=23), 2,350 recaptures were reported from 32,997 releases during the years 1983 to 1999 (5 tagged flounder were re-released and captured again and multiple recaptures of the same fish were treated as independent recaptures). Of these recaptures, 2,301 contained

given according to release area and the season of recapture. When latitudinal movements were observed in both directions, a Chi-square analysis was performed to test the null hypothesis of equal recapture frequency between north and south directions of movement.

Release
Releas

Release	Season					
area	recaptured	North	South	None	Total	
Hudson River to Long Island	Spring	18	12	32	62	
and areas north and east	Summer**	110	56	704	870	
	Fall	32	23	178	233	
	Winter	22	28	1	51	
Sandy Hook, N. J.,	Spring*	33	15	19	67	
to Cape Henry, Va.	Summer**	167	27	498	692	
	Fall*	45	23	154	222	
	Winter**	18	58	12	88	
Coastal areas from Cape Henry, Va.,	Spring			2	2	
to Hatteras Inlet, N.C.	Summer			4	4	
	Fall		1	8	9	
	Winter		1		1	

Table 1.—Summer flounder mark-recapture data from the American Littoral Society's (Sandy Hook, N.J.) recreational-angler-based tagging program, provided by Gary Shepherd (personal commun.). Recapture frequencies are

*Chi-square test *p*-value<0.01

**Chi-square test *p*-value<0.001

enough information to determine latitudinal movement, north or south. In the majority of recaptures (n=1,612, 70%), no latitudinal movement from the release area was observed (Table 1). Of the flounder that were released north of Cape Henry, Va., and exhibited latitudinal movement, there were more recaptured north of the release locations in all seasons except winter (Table 1). None of the flounder released north of Cape Henry, Va., were recaptured south of Cape Hatteras, N.C. South of Cape Henry, Va., few recaptures were observed (n=16) and only two of these indicated movement, which was to the south (Table 1). In general, the ALS data support expected seasonal movements of summer flounder

⁸Lux, F. E., and F. E. Nichy. 1981. Movements of tagged summer flounder, *Paralichthys dentatus*, off southern New England. *In* NEFC Lab Ref. Doc. 80-34. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Woods Hole Lab., Mass.

⁹Gillikin, J. W., Jr. Unpubl. manuscr. cited in, K. W Able. and S. C. Kaiser. 1994. Synthesis of summer flounder habitat parameters. NOAA Coastal Ocean Office, Silver Spring, Md., NOAA Coastal Ocean Program Decision Anal. Ser. 1, 68 p.

north of Cape Hatteras and segregation of this group from populations south of Cape Hatteras.

A second group of summer flounder in the management area occurs in the sounds and estuaries of North Carolina during the summer and offshore to the shelf break during the winter. Monaghan⁸ tagged adult and juvenile summer flounder in the sounds of North Carolina and observed no recaptures from outside of the sounds that were north of Cape Hatteras (excluding those within 20 km of the release areas). Additional tagging effort in North Carolina supported hypothesized seasonal migrations of northern and southern stocks of summer flounder, and significant non-random movement to the south was observed during summer, fall, and winter in those fish tagged south of Cape Hatteras, N.C. (Burke et al., 2000). Therefore, spawning aggregations south of Cape Hatteras may be comprised of summer flounder from inshore areas of North Carolina, and individuals from groups north and south of Cape Hatteras likely intermingle during winter. The potential integrity and mixing of these groups has important implications for management, especially in light of the fact that the majority of coastwide landings come from the North Carolina winter trawl fishery (NEFSC¹).

New Tagging Data

In the studies reviewed thus far, there appears to be segregation of summer flounder that occur in North Carolina during the summer from those that occur north of Cape Hatteras, and there is a restricted spatial distribution of inshore juveniles from southern New Jersey to Virginia in the northern group. Further, Desfosse (1995) observed that adults recaptured to the north and east of Virginia were smaller (in TL) and younger at the time of tagging than those recaptured near the release areas. Thus, it was apparent that information on the recruitment of juveniles to adult landings was needed to understand the spatial dynamics of summer flounder, and a tagging study was conducted on iuveniles from estuaries in Virginia. The initial results were part of a thesis (Kraus, 1998); however, since it was written, the number of reported recaptures has more Table 2.—Recapture data from fishery landed summer flounder (Kraus, 1998). A total of 10,607 juvenile summer flounder were released: 7,228 in Chesapeake Bay at Middlegrounds (M), Kiptopeake (K), and the York River (Y), and 3,379 at Wachapreague (W) on the seaside of Virginia's Eastern Shore. Growth rate is calculated as the change in size from release to capture, or growth in millimeters of total length (TL), divided by the days at large (DAL).

Release data		ta	Capture data				
Date	Location	Size (TL)	Date	Location	DAL	Growth	Growth rate (mm/day)
9/11/95	M ¹	247	9/1/97	Cape Henlopen, NJ	721	343	0.48
9/14/95	M ¹	235	5/24/97	Mattituck, NY	618		
8/8/96	W ¹	182	6/14/97	Jamaica Bay, NY	310	290	0.94
8/19/96	K1	273	6/26/97	Shark River, NJ	311	268	0.86
8/19/96	K1	275	8/22/96	Kiptopeake, VA	3		
8/21/96	K1	232	9/4/98	Niantic Bay, CT	744	536	0.72
8/26/96	K1	228	8/8/97	Jamaica Bay, NY	347	313	0.90
9/10/96	W ¹	156	6/7/99	Moriches Bay, NY	1,000	474	0.47
8/5/97	W^2	171	6/4/99	Moriches Bay, NY	668	360	0.54
8/5/97	W^2	174	8/15/98	Holgate Bay, NJ	375	220	0.59
8/7/97	W^2	167	8/23/98	Wantagh Park, NY	381	443	1.16
8/14/97	K ²	217	6/28/99	Great Bay, NJ	683	314	0.46
8/14/97	K ²	226	7/9/99	Great Bay, NJ	694	404	0.58
8/19/97	K ²	223	9/25/99	Ocean City, MD	767	486	0.63
9/7/97	W^2	130	5/31/99	Chesapeake Bay, VA	631	303	0.48
9/7/97	W^2	237	7/14/99	Staten Is., NY	675	398	0.59
9/7/97	W^2	216	10/24/98	N. Wildwood Beach, NJ	412	335	0.81
9/9/97	W^2		8/2/99	Beach Haven Inlet, NJ	692		
9/10/97	W ¹	245	9/26/98	11 mi. offshore, NJ	381		
9/10/97	W ¹	185	9/30/98	Atlantic City, NJ	385		
9/23/97	K ²	228	7/25/99	Lavallette, NJ	670	382	0.57
9/25/97	Y ²	214	5/30/98	Tangier Sound, VA	247		
9/26/97	Y ²	246	9/1/98	Nassau Co. Park, NY	340		
8/7/97	W ²	183	7/23/00	New London, CT	1,081	262	0.24

¹T-bar tag FF-99 was used during 1995-97.

²T-bar tag FD-94 was used during 1997.

than doubled, and a trend has become apparent. A detailed description of the study is given by Kraus (1998), but, briefly, 10,607 juvenile summer flounder were marked and released in Chesapeake Bay and the seaside tidal creeks and lagoons of Virginia's Eastern Shore during the years 1995–97. The tagging and reward system was designed to rely on reporting of marked fish by commercial and recreational fishermen. Fishery dependent recapture information (including individual growth rates) is tabulated here to make it available to people working on summer flounder (Table 2).

There were 261 recaptures (238 by our own research gear), but only 23 of these were at large for more than 40 days (and none of these were recaptured by research gear), which gives a long-term recapture rate of 0.2%. Except for one fish recovered in a commercial pound net in Tangier Sound, Va., all long-term recaptures were taken in the recreational fishery, and 21 were recaptured north of the release areas (Maryland to Connecticut). Of the mark-recapture studies that have been conducted on summer flounder, these results represent the lowest overall recapture rate to date (see Figure 2).

Significant tag shedding and growth and mortality effects were not indicated by holding studies. In addition, the absence of returns from the commercial fishery was expected during the first winter after tagging because the juveniles were either inaccessible (trawling is not allowed in state waters) or too small to be retained by the gear (lower mesh size limits are set to allow escapement of young flounder) or by the fishermen (most were sub-legal size). Catches have historically been split 60% and 40% between the commercial and recreational fisheries, respectively (NEFSC¹). In light of recreational recaptures from fish that were at large from 310 to 1,081 days, there is no satisfactory explanation for the absence of commercially reported recaptures of fish at large for more than 1 year (save speculation about nonparticipation by commercial fishermen). Regardless, these results demonstrate that juvenile summer flounder from Virginia can recruit to New England estuaries as adults, which lends support to the hypothesis of Rogers and Van Den Avyle³ that larvae on the New Jersey shelf occur as juveniles in more southern estuaries. In addition, there is no evidence to suggest that juveniles from Virginia are part of the group of summer flounder that occurs in the inshore areas of North Carolina.

Summary

Currently, summer flounder are managed as a single stock, and a single study (Jones and Quattro, 1999) that failed to observe a genetic basis for multiple stocks is cited to justify the approach. However, there is morphological, meristic, biochemical, and migratory information that indicates at least two, and possibly three. distinct stocks are present in the management area. One stock can be defined as the group of individuals that occupies the sounds and estuaries of North Carolina during summer and spawns south of Cape Hatteras. A second stock can be defined as those individuals that occupy inshore and coastal areas north of Cape Hatteras during the summer and spawn off New Jersey and along the Virginia-North Carolina coast. These two stocks potentially over-winter together in the offshore waters of Virginia and North Carolina, and evidence suggests they can be identified by various phenotypic traits. In addition, there is evidence of two spawning aggregations in the northern stock from which offspring intermingle as juveniles in Virginia estuaries. The spawning aggregation that occurs in shelf waters off New Jersey is comprised of individuals that move offshore towards the continental slope on their seasonal migration cycle. Individuals from the second spawning aggregation that occurs north of Cape Hatteras appear to stay near shore as they migrate, following the Virginia-North Carolina coastline, and are primarily comprised of adults from Virginia waters. The identity of these groups is less certain than the identity of stocks north and south of Cape Hatteras. For management applications, studies are warranted that test for heterogeneity in the productivity and vital rates of northern and southern stocks of summer flounder. In addition, among several studies the trend in recapture rate over time (Figure 2), which is also correlated with latitude, indicates a decline in recent decades. This suggests that future markrecapture studies of summer flounder will have to tag extremely large numbers to expect recapture numbers that are comparable to earlier studies (before 1980).



Figure 2.—Overall recapture rates from studies on summer flounder plotted by publication year (dots). These data points are labeled by text footnote number or literature citation. Note that the declining trend is also associated with the latitude of the areas in which fish were tagged. Also plotted are recapture rates calculated from American Littoral Society (ALS) tagging data. For a given release year, ALS recapture rates were calculated both based on the total number of recaptures that have been observed through 1999 (solid line), and excluding recaptures from the same year that release occurred (dashed line).

Alternative methods to conventional tagging, such as using otolith chemistry as a natural tag (Thresher, 1999), may be warranted to gain a more complete understanding of spatial distribution, ontogenetic migrations, and stock identity in summer flounder. Consideration of stock structure in the management of summer flounder could have far reaching implications to stock rebuilding efforts and future policy decisions.

Acknowledgments

We dedicate this paper to the memory of our dear friend and vessel captain, Julian Anthony Penello, for generously providing his knowledge, assistance, and his own vessel the F/V Anthony Anne, to our disposal to conduct this research. We acknowledge Joseph C. Desfosse for the substantial contribution he made to earlier flounder tagging studies, which prompted the present study, and we would like to thank James P. Monaghan, Jr. for providing North Carolina Division of Marine Fisheries tagging data. This project was funded by the Virginia Marine Resources Commission Recreational Saltwater License Fund, and the first author was supported by a National Science Foundation grant (OCE-9812069) during manuscript preparation. This is contribution #2515 of the Virginia Institute of Marine Science, Gloucester Point, Va.

Literature Cited

- Able, K. W., R. E. Matheson, W. W. Morse, M. P. Fahay, and G. Shepherd. 1990. Patterns of summer flounder, *Paralichtys dentatus*, early life history in the mid-Atlantic Bight and New Jersey estuaries. Fish. Bull. 88:1–12.
- Burke, J. S., J. M. Miller, and D. E. Hoss. 1991. Immigration and settlement pattern of *Para-lichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Neth. J. Sea Res. 27:393–405.
- _____, J. P. Monaghan, and S. Yokoyama. 2000. Efforts to understand stock structure of summer flounder (*Paralichthys dentatus*) in North Carolina, USA. Neth. J. Sea Res. 44:111–122.
- Delaney, G. R. 1986. Morphometric and meristic stock identification of summer flounder, *Paralichthys dentatus*. Coll. William and Mary, Williamsburg, Va, M.A. thesis, 47 p.

¹⁰Ross, S. W., J. H. Hawkins, D. A. Devries, C. H. Harvell, and R. C. Harris, Jr. 1982. North Carolina estuarine finfish management program. N.C. Dep. Nat. Resour. Community Develop., Div. Mar. Fish., Completion Rep. Proj. 2-372-R, 171 p. This footnote is only referenced on Figure 2.

- Dery, L. M. 1981. Post workshop age and growth study of young summer flounder. *In* R. W. Smith, L. M. Dery, P. G. Scarlett, and A. Jearld, Jr. (Editors), Proceedings of the summer flounder (*Paralichthys dentatus*) age and growth workshop, 20 21 May 1980, Woods Hole, MA, p. 7–11. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-I 1, 30 p.
- Desfosse, J. C. 1995. Movements and ecology of summer flounder, *Paralichthys dentatus*, tagged in the southern Mid-Atlantic Bight. Coll. William and Mary, Gloucester Point, Va., Ph.D. dissert., 187 p.
- Fogarty, M. J., G. DeLaney, J. J. W. Gillikin, J. C. Poole, D. E. Ralph, P. G. Scarlett, R. W. Smith, and S. J. Wilk. 1983. Stock discrimination of summer flounder (*Paralichthys dentatus*) in the Middle and South Atlantic Bights: results of a workshop. Woods Hole, Massachusetts. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/NEC-18, 8 p.
- Ginsburg, I. 1952. Flounder of the genus Paralichthys and related genera in American waters. U.S. Fish Wildl. Serv., Fish. Bull. 52: 267–351.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, N.Y., 570 p.
- 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(1):129–135.

- Kraus, R. T. 1998. Tagging and habitat utilization of juvenile summer flounder, *Paralichthys dentatus*. M.S. thesis. Coll. William and Mary, Williamsburg, Va., 148 p. Malloy, K. D., and T. E. Targett. 1991. Feed-
- 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.
- and ______. 1994. Effects of ration limitation and low temperature on growth, biochemical condition, and survival of juvenile summer flounder from two Atlantic coast nurseries. Trans. Am. Fish. Soc. 123: 182–193.
- NMFS. 1999. Our living oceans. Report on the status of U.S. living marine resources, 1999. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/SPO-41. 301 p.
- NMFS-F/SPO-41, 301 p. Norcross, B. L., and D. M. Wyanski. 1993. Interannual variation in the recruitment pattern and abundance of age-0 summer flounder, *Paralichthys dentatus*, in Virginia estuaries. Fish. Bull. 92:591–598.
- Poole, J. C. 1962. The fluke population of Great South Bay in relation to the sport fishery. N.Y. Fish Game J. 9(2):93–117.
- Powell, A. B. 1982. Annulus formation on otoliths and growth of young summer flounder,

Paralichthys dentatus, from Pamlico Sound, N.C. Trans. Am. Fish. Soc. 111:688–693.

- Ryman, N., and R. Utter. 1987. Population genetics and fishery management. Univ. Wash. Press, Seattle, 420 p.
 Smith, S. M., and F. C. Daiber. 1977. Biology of
- Smith, S. M., and F. C. Daiber. 1977. Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull. 71:527–548.
- 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.
- 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 1:120–128.
- Thresher, R. È. 1999. Elemental compositions of otoliths as a stock delineator in fishes. Fish. Res. (Amst.) 43:165–204.
- Res. (Amst.) 43:165–204. 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.
- Van Housen, G. 1984. Electrophoretic stock identification of summer flounder, *Paralichthys dentatus*. Coll. William and Mary, Williamsburg, Va., M.A. thesis, 66 p.