Distribution and life history of windowpane, *Scophthalmus aquosus*, off the northeastern United States

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Abstract.—The windowpane, *Scophthalmus aquosus*, is a shallow water (<110 m), resident species of the Middle Atlantic Bight (and adjacent estuaries) and Georges Bank, although it may undergo short (both inshore-offshore and alongshore) migrations in response to seasonal temperature changes. Spawning occurred throughout the Middle Atlantic Bight during the period from 1977 to 1987 but was most pronounced on Georges Bank. The timing of spawning, determined from the collection of 2–4 mm larvae, varied with location; and a split spawning season (April–May and October–November) was evident in the Middle Atlantic Bight. Spawning on Georges Bank peaked in August. Although spawning occurred over a broad temperature range (5–23°C), the optimal temperature was 16–19°C in the Middle Atlantic Bight and 13–16°C on Georges Bank. Larval development occurred in areas of spawning and was most prolonged on Georges Bank, where the largest larvae (13–20 mm) were consistently found. Few larvae >8 mm were captured in the Middle Atlantic Bight. On the basis of samples from southern New Jersey, settlement probably occurs on the continental shelf and in adjacent estuaries of the Middle Atlantic Bight. The growth patterns of young of the year varied with the timing of spawning and subsequent settlement. In the first six months, fish of the spring-spawned cohort grew to 11–19 cm TL whereas those of the fall-spawned cohort grew to just 4–8 cm TL within that time. These data contribute to our understanding of the distribution and early life history of windowpane on the continental shelf, though the role of estuaries in the Middle Atlantic Bight is incompletely known.

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The windowpane, *Scophthalmus aquosus*, is an endemic bothid of the northwest Atlantic Ocean and is distributed from the Gulf of Saint Lawrence (47°N) to Florida (27°N) (Scott and Scott, 1988) but is most abundant from Georges Bank (42°N) to Chesapeake Bay (38°N) (Bigelow and Schroeder, 1953; Dery and Livingstone, 1982). Windowpane are distributed in shallow waters (<110 m, mostly <56 m) (Wenner and Sedberry, 1989; Thorpe, 1991). Their distribution extends shoreward to depths of 1–2 m (Warfel and Merriman, 1944) and they are often abundant in large estuaries such as Chesapeake Bay (Hildebrand and Schroeder, 1928), Delaware Bay (de Sylva et al., 1962), Sandy Hook Bay (Wilk and Silverman, 1976), Long Island Sound (Moore, 1947), and Narragansett Bay (Oviatt and Nixon, 1973; Jeffries and Johnson, 1973). Distribution patterns of juveniles and adults on the continental shelf between Nova Scotia and Cape Hatteras, North Carolina, are similar and indicate limited seasonal movement (Dery and Livingstone, 1982; Azarovitz and Grosslein, 1987; Thorpe, 1991). However, tagging experiments showed that some adults traveled about 150 km along the coast in three months (Moore, 1947). Juveniles (<24 cm total length [TL]) in the Georges Bank area were concentrated along the southern boundary of the bank and inshore along Long Island during spring (mean depth 26.6 m) and on the central portion of the bank in fall (mean depth 38.3 m) (Wigley and Gabriel, 1991). Recent estimates of length at sexual maturity show that 50% were mature between 21 and 23 cm TL (O'Brien et al., 1993).

Windowpane are currently exploited for human consumption, primarily in the Georges Bank area. Annual commercial landings from 1975 through 1988 averaged 2.03 million kg and peaked in 1985 at 4.21 million kg (ICNAF, 1977–85; NAFO, 1982–91). Relative abundance indices estimated from National Marine Fisheries Service (NMFS) research trawl surveys (Azarovitz, 1981) for 1964–89 show considerable year-to-year fluctuations in both numbers and biomass (Thorpe, 1991). Peaks in biomass appear to have occurred on Georges Bank during the mid-to-late-1970's and again in the mid-1980's.

Gonadal development (Wilk et al., 1990) and egg and larval distributions (Colton and St. Onge, 1974; Smith et al., 1975; Colton et al., 1979; Morse et al., 1987), show that spawning occurs from April through December. There is contradictory evidence for a split spawning season. Gonadal development (Wilk et al., 1990) indicated that spawning off New Jersey and New York peaks in May and again in September. Split spawning was reported to occur off Virginia and North Carolina (Smith et al., 1975) for Long Island Sound (Wheatland, 1956) and for Great South Bay, New York (Dugay et al., 1989; Monteleone, 1992). However, other studies found no evidence for a split spawning season in either Long Island Sound (Perlmutter, 1939) or in ocean waters north of Virginia (Smith et al., 1975). In addition, Colton and St. Onge (1974) collected larvae on Georges Bank from July to November and found no indication of a split spawning season. Spawning apparently occurs at bottom water temperatures of 6–20°C (Bigelow and Schroeder, 1953; Wheatland, 1956; Smith et al., 1975). Most spawning (70%) off Virginia and North Carolina was found over bottom temperatures between 8.5 and 13.5°C; spawning stopped when temperatures exceeded 15°C (Smith et al., 1975).

This study presents analyses of the reproductive seasonality of windowpane based on seasonal shifts in larval abundance and on their relationships to bottom water temperatures. Bottom trawl catches and published accounts of distribution and abundances are used to follow the fate of the young flatfish after they settle to the bottom. Together these data describe the seasonal distribution, abundance, and life history of windowpane in the Middle Atlantic Bight and on Georges Bank.

Materials and methods

Larvae

Data from a variety of sources have been analyzed (Table 1). Larval windowpane were collected from continental shelf waters from Cape Hatteras, North Carolina, to Nova Scotia during NMFS Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys from 1977 to 1987 (Sherman, 1980). Surveys were conducted six to eight times each year and occupied 150–180 stations (Fig. 1). At each station, a 61-cm bongo net array was lowered to within 5 m of the bottom or to a maximum depth of 200 m. Fish larvae from a 0.505-mm mesh net were identified to the lowest taxon possible, enumerated, measured (±0.1 mm) and rounded to the nearest whole millimeter as either notochord or standard length. Catches were standardized to the number of larvae under 100 m^2 of sea surface on the basis of the depth of the tow and the volume of water filtered (Sibunka and Silverman, 1984, 1989). An additional

Table 1

Sources of data on windowpane, *Scophthalmus aquosus*, that were analyzed for this study. See Figures 1 and 2 for location of sampling areas.

Source	Life stage	Location	Collecting gear	Sampling years	Sampling depths (m)	Number of samples	Number of fish collected
NMFS, MARMAP (Sherman, 1980)	Larvae	Nova Scotia–Cape Hatteras	Bongo nets	1977–1987	8–1,500	8,787	14,177
NMFS, Groundfish (Azarovitz, 1981)	Juveniles and adults	Nova Scotia–Cape Hatteras	Bottom trawl	1982–1990	5–366	7,099	26,433
Massachusetts Trawl Survey (Howe et al., 1979)	Juveniles and adults	Coastal Massachusetts	Bottom trawl	1982–1990	4–82	1,688	21,272
Milstein and Thomas, 1977	Eggs, larvae, juveniles, and adults	Great Bay, Mullica River, Beach Haven Ridge, NJ	Beach seines, Plankton nets, Bottom trawls	1972–1975	Seines: < 2 Plankton: 1.5–19.5 Trawls: 1–45	Seines: 1,524 Plankton: 166 Trawls: 717	127 801 5,309
New Jersey Trawl Survey[1]	Juveniles and adults	Coastal New Jersey	Bottom trawl	1988–1992	5–27	603	25,580

[1] See Footnotes 3 and 4 in the text.

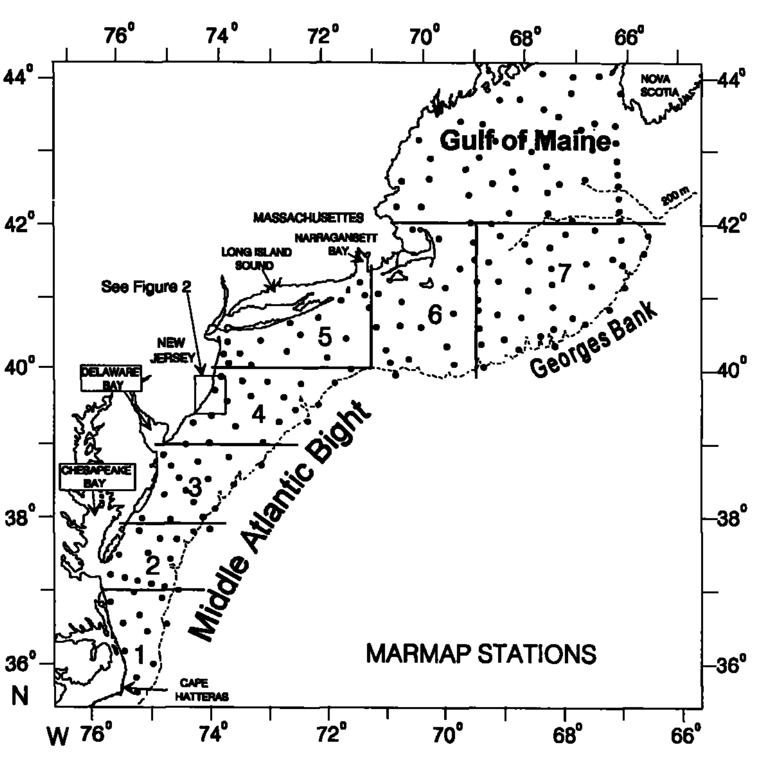

Figure 1

Sampling area for planktonic larvae in the northeastern United States, based on NMFS/MARMAP sampling stations, and important localities that are mentioned in the text. Typical sampling array of stations shown by dots. See Table 1 for further details. Middle Atlantic Bight = subareas 1–6, Georges Bank = subarea 7.

length-dependent correction was made to the catches to account for differences in day, night, and twilight catchability (Morse, 1989). Preliminary analysis of larval occurrence and bottom depth revealed that larvae are restricted to waters ≤100 m deep; therefore, only stations ≤100 m deep were used for calculating larval catch statistics. In addition, larvae were extremely rare north of 42°N (caught at only 24 of 2,470 stations); therefore, this area was not considered in the analysis. Mean catches of windowpane larvae were calculated by using the Delta method of Pennington (1983). Graphical plots of the distribution and abundance of larvae are presented as the average catch per 100 m^2 within 625 km^2 blocks of the survey area. Eggs and larvae were sampled at estuarine and inner continental shelf sites during 1972–75 (Table 1; Fig. 2). These sites included the Mullica River (water depth 1.8–10.6 m), Great Bay (1.5–10.7 m), Little Egg Inlet (4.6–8.8 m), in the vicinity of sand ridges outside Little Egg Inlet (3.0–16.5 m), and farther offshore of the sand ridge sites (16.2–23.5 m). At continental shelf sites, 15-minute tows were made at the surface (1.0-m plankton net, 0.5-mm mesh), at midwater and bottom depths (0.5-m plankton net, 0.5-mm mesh), and as oblique tows (bongo samplers, 0.2-m or 0.36-m diameter, 0.5-mm mesh). In the estuary tow times were reduced to 5–10 minutes but the same three nets were used at the same depths. Estimates of water volume filtered were determined with a flowmeter.

Juveniles and adults

Juvenile and adult windowpane (2–48 cm TL) were collected during the semiannual bottom trawl surveys of NMFS, Northeast Fisheries Science Center, from 1982 to 1991 (Azarovitz, 1981), during inshore surveys of the Commonwealth of Massachusetts Division of Marine Fisheries from 1988 to 1992 (Howe et al.[1]), and during the New Jersey Bureau of Marine Fisheries surveys from 1988 to 1992 (Byrne[2,3]). All three surveys used a stratified random-sampling design, and strata were based on depth and latitude. NMFS spring and fall surveys sampled about 350 stations during a 6–8 week period from Cape Fear, North Carolina, to Nova Scotia in depths from 3 to 366 m. Commonwealth of Massachusetts Division of Marine Fisheries sampled approximately 80–90 stations within 55-m depths in state coastal waters during May and September. New Jersey Bureau of Marine Fisheries sampled 25–39 stations in state coastal waters within 27 m of water every 6–10 weeks.

For the analysis of NMFS bottom trawl and plankton surveys, the sampling area was divided into seven subareas (Fig.1). Data from monthly collections of larval, juvenile, and adult windowpane near Little Egg Inlet, New Jersey, during 1973–74 (Fig. 2) were

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[1] Howe, A. B., D. MacIsaac, B. T. Estrella, and F. J. Germano Jr. 1979. Fishery resource assessment, coastal Massachusetts. Completion Rep., Massachusetts Div. Mar. Fish., Commercial Fish. Res. Div. Project No. 3-287-R-1, 34 p.

[2] Byrne, D. M. 1988. Inventory of New Jersey's coastal waters. New Jersey Dep. Environmental Protection, Div. Fish, Game, Wildl. Mar. Fish. Admin., Bur. Mar. Fish. Annual Rep. to U.S. Fish. Wildl. Serv.

[3] Byrne, D. M. 1990. Inventory of New Jersey's coastal waters. NJDEP, Div. Fish., Game, Wildl., Mar. Fish. Admin., Bur. Mar. Fish. Annual Rep. to U.S. Fish. Wildl. Serv.

summarized from Thomas et al.,[4] Thomas et al.,[5] and Milstein and Thomas (1977).

Results

Spawning season and location

We assumed that the temporal and spatial patterns of the distribution and abundance of the smallest larvae (2–4 mm) indicated the timing and the areas of spawning on the continental shelf (Fig. 3). Larvae were distributed from nearshore to mid-shelf in subareas 1–6 and over the shallower portion of subarea 7. The highest average concentrations of small larvae occurred in subarea 7, especially in the central portion. Larvae 2–4 mm long were first captured in April in subareas 1–3 and by May they were in all subareas (Table 2). Catches in subareas 1–4 clearly showed a split spawning season (Fig. 4), and similar, though less pronounced, patterns were evident in subareas 5 and 6. A peak in abundance of small larvae occurred in May and a larger peak occurred in November in subareas 1–4. Subareas 4–5 showed light spawning during spring and a significant peak in October. In subarea 6, split spawning was less discernible; only a slight peak in abundance of small larvae occurred in June, but major spawning was indicated in October. There was unimodal spawning, with the peak abundance in August, in subarea 7. Fall catches of small larvae in subareas 1–6 are often 5–20 times higher than peak catches earlier in the year.

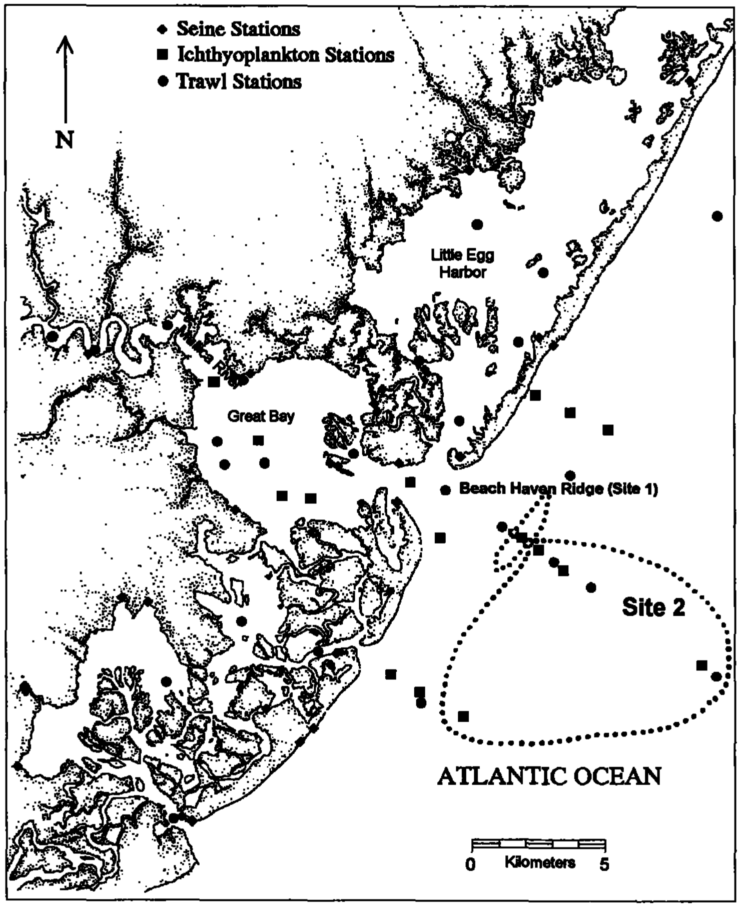

Figure 2

Sampling locations for seine, trawl, and ichthyoplankton samples in southern New Jersey habitats in the vicinity of Great Bay during 1970–74 based on Milstein and Thomas (1977). Site 2 includes all stations offshore of site 1. See Figure 1 for general location of sampling area.

The monthly progression of the peak catches of 2–4 mm larvae from the southern extreme of the study area in May to subarea 7 in July–September and the return of peak catches to subareas 1–3 in November indicate that water temperature may be controlling spawning times and areas (Fig. 4). Windowpane probably spawn on or near the bottom; therefore bottom water temperatures were used to indicate spawning temperatures. Only stations with bottom depths ≤100 m are presented. The maximum abundance of 2–4 mm larvae occurred at temperatures 15–19°C in subareas 1–6 and at 14–15°C in subarea 7 (Fig. 5). The range of bottom temperatures where larvae were caught was 5–23°C. The broadest range of temperatures for 2–4 mm larvae was in subarea 5. Maximum temperature of occurrence was highest in subarea 1 at 23°C and gradually decreased

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[4] Thomas, D. L., C. B. Milstein, T. R. Tatham, R. C. Bieder, F. J. Margraf, D. J. Danila, H. K. Hoff, E. A. Illjes, M. M. McCullough, and F. A. Swiecicki. 1974. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the site for the Atlantic generating station, New Jersey. Progress Rep. for the period January–December 1973. Vol. 1: Fishes. Ichthyological Associates, Inc., 709 p.

[5] Thomas, D. L., C. B. Milstein, T. R. Tatham, R. C. Bieder, D. J. Danila, H. K. Hoff, D. P. Swiecicki, R. P. Smith. G. J. Miller, J. J. Gift, and M. C. Wyllie. 1975. Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the site for the Atlantic generating station, New Jersey. Progress Rep. for the period January–December 1974. Vol. I: Fishes. Ichthyological Associates, Inc., 490 p.

northward to 16°C in subarea 7. Minimum temperatures ranged from 5 to 9°C, but no clear latitudinal trend was evident. Over 80% of all larvae 2–4 mm long throughout the study area were collected over bottom temperatures 16–19°C, which indicate preferred spawning temperatures. Only in subareas 5 and 7 were larvae captured in significant numbers at temperatures below 15°C. Over 85% of larvae in subarea 7 occurred at temperatures 13–16°C, and 16°C was also the maximum bottom temperature recorded in subarea 7.

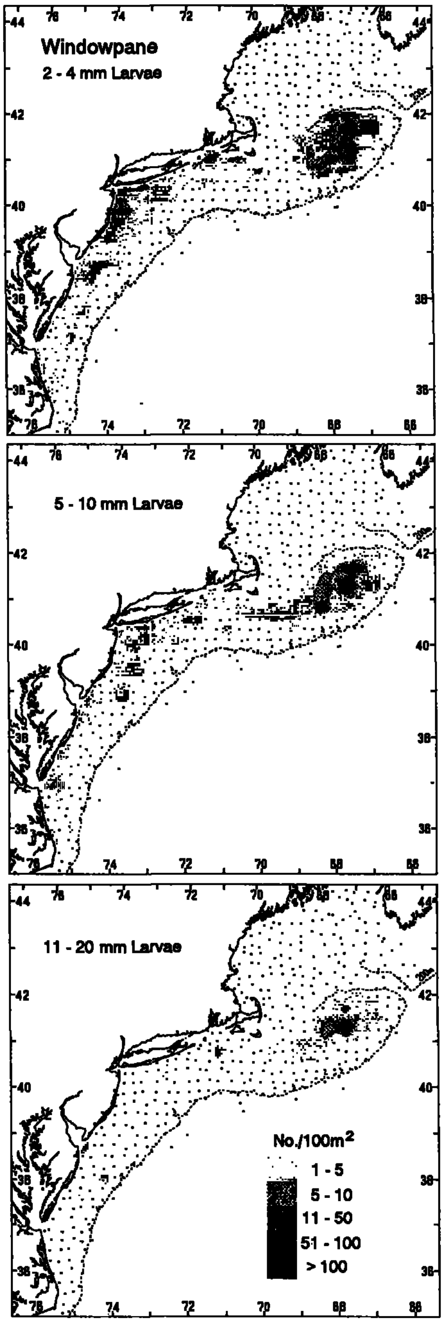

Figure 3

Distribution and abundance of windowpane, *Scophthalmus aquosus*, larvae for three size classes, based on NMFS/MARMAP sample collections. See Table 1 for additional details.

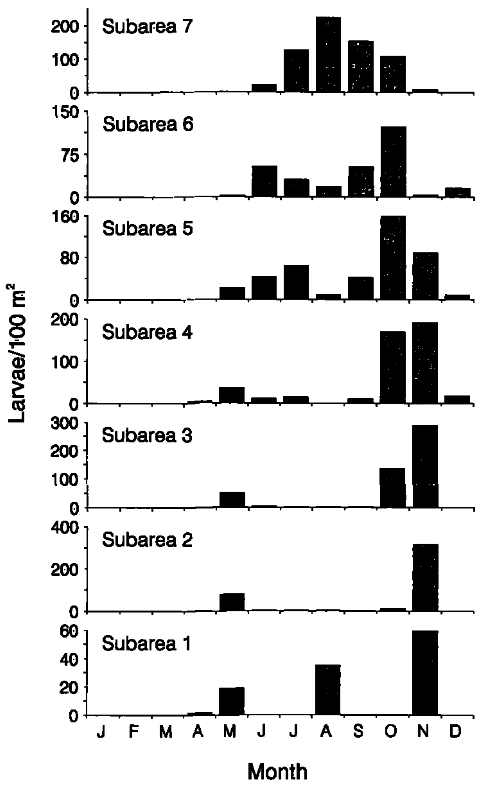

Figure 4

Monthly abundance 2–4 mm windowpane, *Scophthalmus aquosus*, larvae by subarea, based on NMFS/MARMAP sampling.

Although the preferred spawning temperature range (16–19°C) spans just 4°C, the total range of temperatures (5–23°C) indicates that spawning may not be tied exclusively to water temperatures. In subareas 1–3, bottom waters in the preferred range of temperature (16–19°C) are available most months (Fig. 6). However, even though spawning in these subareas is bimodal (see Fig. 4), the peak in spawning clearly occurs at 17°C (see Fig. 5). In subarea 7, spawning occurs at the highest bottom temperatures recorded (13–16°C) in this subarea (Fig. 6). These temperatures are available from July through November (Fig. 6), a range that nearly corresponds to the months of maximum spawning (Table 2; Fig. 4). Thus, in subarea 7 the occurrence of the highest tempera-

Table 2

Abundance (mean number/100 m^2) of windowpane, *Scophthalmus aquosus*, larvae by subarea and length (mm) from MARMAP surveys off northeastern United States during 1977–87. N_t = total number of stations sampled; N_0 = number of stations with windowpane; Mn = mean number/100 m^2 for 2–20 mm larvae; and SE = standard error of Mn.

Length (mm)	January							February						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2														
3														
4														
5														
6	1.22		1.65		2.42									
7			1.53											
8														
9	0.90	4.82												
10														
11														
12														
13												0.84		
14														
15														
16														
17														
18														
19														
20														
N_t	30	18	24	25	60	52	65	60	41	52	45	39	41	87
N_0	2	1	2	0	1	0	0	0	0	0	0	1	0	0
Mn	1.20	2.68	1.99		1.61							1.03		
SE	0.85	2.68	1.38		1.61							1.03		

Length (mm)	March							April						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2										1.05				
3								0.66	0.51	1.56				
4														
5														
6														
7														
8														
9														
10														
11														
12	0.30													
13														
14														
15					0.56									
16														
17														
18														
19														
20														
N_t	121	99	111	102	145	115	89	77	50	80	107	169	112	187
N_0	1	0	0	0	1	0	0	2	1	2	0	0	0	0
Mn	0.28				0.72			0.53	0.59	2.81				
SE	0.28				0.72			0.37	0.59	2.21				

Table 2 (continued)

Length (mm)	May							June						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2	1.92	9.08	3.14	7.86	10.98		0.22				4.17	6.11	12.55	5.72
3	11.86	28.37	21.29	14.67	5.28	3.21		0.71		0.46	5.16	19.89	6.81	6.42
4	11.24	11.75	7.14	2.75	1.70			0.74	3.12	1.19	5.75	9.61		4.23
5	4.97	6.03	2.60	1.00	0.63				3.49		3.12	3.14		1.68
6	2.03	1.73	0.78							1.12	1.07	2.36		0.75
7	0.77	1.06	1.07				0.37		1.14	0.86	0.29	0.36		
8		0.92	0.47								0.25			
9										1.63				
10			0.45											
11														
12		0.21												
13														
14														
15							0.21							
16														
17														
18	0.35													
19														
20														
N_t	130	86	112	111	167	121	171	65	48	66	73	93	75	81
N_0	38	28	38	18	22	1	2	1	3	6	16	34	3	8
Mn	48.44	120.31	61.70	22.68	14.44	1.43	0.9	2.54	11.77	7.56	26.32	73.41	25.35	23.87
SE	11.75	35.83	13.19	7.84	4.17	1.43	0.6	2.54	7.65	3.33	9.30	15.62	18.47	12.26

Length (mm)	July							August						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2	1.25	0.24	0.57	6.01	0.98	1.99		6.57	0.51			2.29	4.95	10.73
3	1.34		1.77	4.78	12.08	4.23	15.78	5.06	1.57			2.29	3.54	43.10
4		0.47		2.82	8.82	1.95	17.74	1.15	0.66		0.27	0.78	3.44	27.05
5			0.51	2.78	6.44	1.03	21.00	0.18			0.85		0.65	15.49
6				1.83	2.29	3.15	13.79					0.52	3.36	10.08
7				0.95	1.70	0.41	13.58	0.30				0.44	0.45	9.28
8					0.92	1.25	9.62					0.34	1.74	8.05
9					0.64	0.41	4.03						1.50	5.66
10					0.07		9.25							3.49
11							3.89						1.27	2.71
12							2.22						0.31	2.23
13					0.20		0.88							0.43
14				0.21			0.88					0.12		0.48
15							0.67							0.46
16							0.47							0.12
17						0.41								0.33
18														0.21
19														
20														0.24
N_t	70	53	93	112	172	106	130	113	90	104	100	148	114	184
N_0	2	2	5	25	58	14	49	4	4	0	2	19	15	88
Mn	2.67	2.15	4.73	31.08	105.97	25.38	370.70	15.37	4.46		1.96	12.62	33.67	402.90
SE	2.07	1.52	2.23	7.49	18.68	7.61	85. 96	12.42	2.47		1.56	3.25	12.61	69.39

Table 2 (continued)

Length (mm)	September							October						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2		0.92	2.62	0.37	5.02	4.79	14.36		2.78	7.42	23.15	16.83	7.26	3.05
3	0.39		3.16	0.86	12.67	34.27	22.09		3.22	27.73	40.14	36.13	21.79	15.46
4			1.89	0.53	12.97	5.50	13.86	1.55	3.50	13.93	17.11	10.47	11.05	13.79
5					4.83	2.69	15.01			8.92	2.60	2.89	5.15	12.85
6		0.48			0.70		11.81			2.74	2.49	2.02	3.57	8.02
7					2.53		9.32			1.17	1.04	0.48	1.48	7.02
8							6.89				1.30	0.26	0.36	3.79
9							5.17					0.86	0.80	2.24
10						1.14	7.94						0.20	1.73
11							3.69							2.78
12							11.18							1.20
13		0.50					0.79							0.41
14	0.56						0.20							0.28
15							0.98							
16							0.23							
17							0.41							
18							0.44							0.08
19							0.84							0.18
20														
N_t	89	70	85	55	78	58	66	38	23	39	86	144	144	207
N_0	3	3	10	3	15	12	39	1	5	9	27	70	43	93
Mn	0.89	2.11	13.14	2.58	64.64	46.80	396.08	1.14	19.13	147.66	211.80	198.13	129.16	258.85
SE	0.56	1.26	4.83	1.79	28.72	18.85	93.03	1.14	10.28	94.39	85.34	39.61	29.41	39.61

Length (mm)	November							December						
	Subareas							Subareas						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
2	14.79	27.50	35.64	4.83	4.25									
3	43.69	68.11	70.02	36.63	24.93		1.20				3.74	2.68		
4	26.22	29.84	41.32	11.90	13.18	1.32	6.11				7.83	9.47	1.95	
5	10.01	9.87	17.29	5.07	6.77	1.57	2.50					4.89	1.83	
6	7.11	2.48	12.07	4.65	2.03		4.89					4.37		
7	1.74	0.20	7.87	0.68	0.62	2.36	6.89			2.20		3.79		
8	0.63	0.88	0.88	0.77			3.45			2.52	2.96	1.95		
9			0.48				1.58					3.48		
10			0.21	0.45						4.75			1.60	
11						1.59						1.24		
12														
13														
14														
15			0.49											
16														
17										1.61				
18												0.52		
19												0.64		
20														
N_t	87	55	76	68	89	86	118	0	6	12	17	67	66	86
N_0	31	14	24	29	39	5	22		0	2	1	18	3	0
Mn	210.47	364.35	247.31	116.86	80.4	3.63	28.05			27.7	27.35	58.6	3.92	
SE	90.79	196.19	109.43	37.2	18.16	1.64	7.13			20.54	27.35	17.36	2.23	

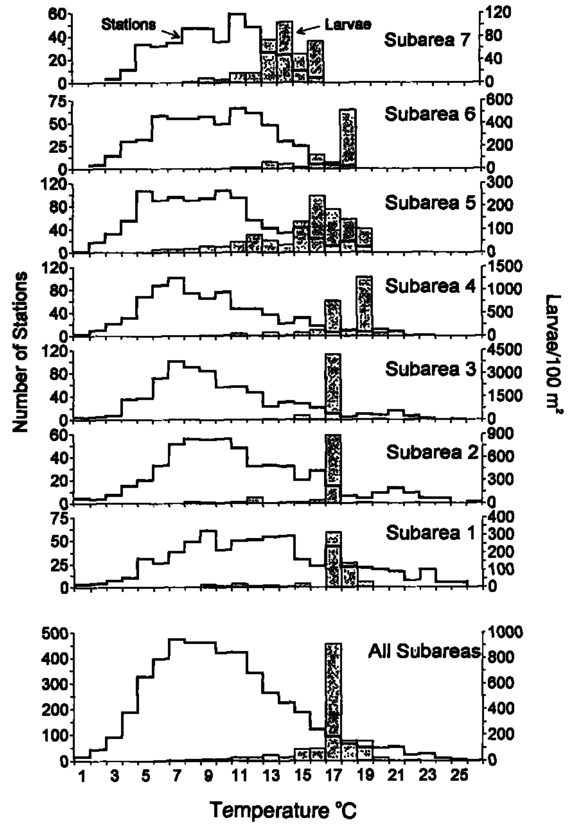

Figure 5

Abundance of 2–4 mm windowpane, *Scophthalmus aquosus*, larvae by subarea relative to bottom water temperature during 1977–87.

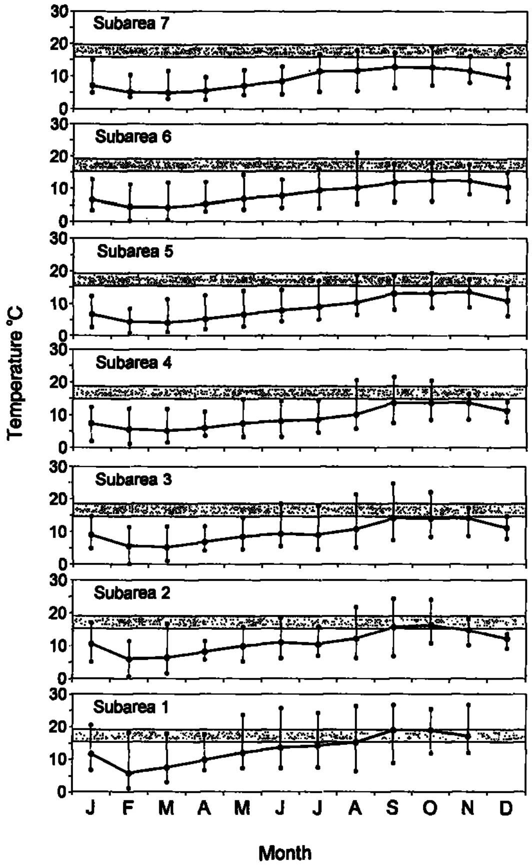

Figure 6

Monthly temperature means and ranges by subarea of the continental shelf of the northeastern U.S. during 1977–87. Shaded bar is the preferred spawning temperatures (16–19°C) for windowpane, *Scophthalmus aquosus*.

tures, which approaches the preferred temperatures, suggests that spawning here may be triggered by the highest temperatures available. Subareas 4 and 5 are intermediate, with preferred temperatures available from July to November (Fig. 6); yet spawning occurs from May to December (Table 2; Fig. 4). Peak spawning occurs in October, a full three months later than the first record of preferred spawning temperatures.

Larval distribution and abundance

Larvae were captured every month on the continental shelf (Table 2). January–April catches were very low in subareas 1–3 and 5 and were totally absent elsewhere. Larvae were caught in all subareas in May and were most abundant in subarea 2. By June, larval abundances were highest in subarea 4, and from July to October subarea 7 had the highest larval catches. Throughout August and September, abundances in subareas 5 and 6 were intermediate, and catches in subareas 1–4 remained very low. By October, catches of larvae decreased somewhat in subarea 7 and increased in all other subareas. November catches showed a continued decline in subarea 7 and began to decrease in subareas 4–6. Catches increased to their highest levels in subareas 1 and 2, whereas subarea 3 catches remained at October levels. In December, no larvae were captured in subarea 7, a few large larvae occurred in subarea 3, and only moderate catches were made in subareas 4–6. The nearly total absence of larvae in subareas 1–4 during December is attributed to the low number of stations sampled and not necessarily to the disappearance of larvae within this area.

The size of larvae captured on the continental shelf varies between subareas (Table 2). Few larvae >8 mm were captured in subareas 1–4; only 18 of 3,282 stations contained these larvae. In subareas 5 and 6, 27 of 2,461 stations had larvae >8 mm long. Larvae >13 mm were captured in only 10 of 5,743 stations in subareas 1–6. In contrast, in subarea 7, 89 of 1,473 stations had >8 mm larvae and 31 stations had >13 mm larvae. In an attempt to interpret the trend of increasing maximum lengths from south to north, the abundances at length and mortality estimates for larvae ≤20 mm, grouped by subarea, were calculated (Table 3). The maximum larval length of catches >0.1/100m^2 and mortality for each subarea is shown in Figure 7. If avoidance of the sampling gear occurs because of settlement within a narrow size interval (e.g. 1–3 mm), then the catches should show a precipitous decrease in abundance at settlement. No such abrupt decrease can be seen in the data (see Tables 2 and 3); thus the declines in abundance with size are due to other causes. Alternatively, if we assume that decreases in larval abundance are due to mortality, then the percentage of mortality per mm of growth is highest in subarea 1 (63%), intermediate in subareas 2–5 (range 48–56%), declines to 38% in subarea 6, and is lowest in subarea 7 (30%). Estimated mortalities are inversely related to the maximum lengths of captured fish and decrease from south to north along the coast (Fig. 7). The relatively high mortality indicated for larvae in subareas 1–5 could explain the truncated larval length frequencies seen there, particularly during the months of July–October (Table 2).

Larger larvae in the Middle Atlantic Bight subareas may move into or are more abundant in shallow nearshore areas of the continental shelf and estuaries and thus may not be available to the collecting gear. Typically, NMFS/MARMAP sampling is not undertaken in estuaries and is limited to depths >10 m on the continental shelf. During the MARMAP study, approximately 13% of all tows were taken in depths ≤20 m, whereas only 0.3% were taken in water depths <10 m. In the vicinity of Little Egg Inlet, New Jersey, larvae were abundant on the inner continental shelf and in the estuary (Fig. 8). Eggs and larvae were least abundant in the Mullica River, more abundant farther down the estuary in Great Bay and at Little Egg Inlet, and most abundant on the adjacent portion of the inner continental shelf (Fig. 8). Eggs and larvae were abundant in the estuary during spring, but both were most abundant on the continental shelf during the fall.

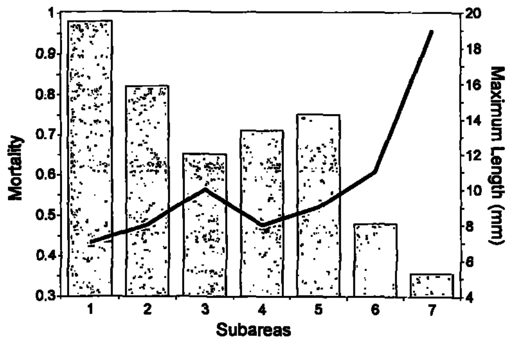

Figure 7

Length-dependent mortality rates and the maximum larval lengths of catches >0.1/100 m^2 by subarea from NMFS MARMAP sampling of windowpane, *Scophthalmus aquosus*, off the northeast United States.

Juvenile and adult distribution and abundance

Windowpane are distributed over much of the continental shelf, as well as in estuaries in the Middle Atlantic Bight. Large juvenile and adult windowpane (>10 cm TL) were collected from the western portion of the Gulf of Maine to Cape Hatteras, North Carolina (Figs. 9, 10), in depths from 5 to 207 m. In the Gulf of Maine, there were few fish of this size collected from coastal Maine, but they were more abundant off the coast of Massachusetts, subarea 6 (Fig.

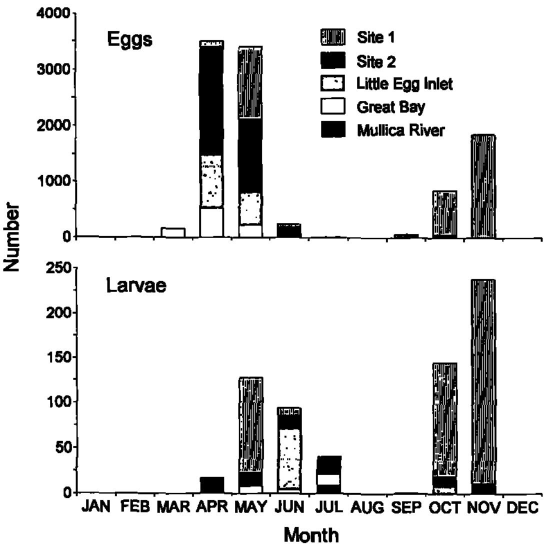

Figure 8

Monthly patterns of distribution and abundance of windowpane, *Scophthalmus aquosus*, eggs and larvae from the vicinity of Little Egg Inlet, New Jersey, during 1972–75, as modified from Milstein and Thomas (1977). See Figure 2 for sampling locations.

Table 3

Mean number (Mn) of windowpane, *Scophthalmus aquosus*, larvae (number/100 m^2) by length (in mm) for seven subareas off northeastern United States, 1977–87. N = Total number of stations sampled in each subarea. An exponential equation, $Mn = a \times \exp(-bL)$, was fit to the data. N_0 = number of stations with windowpane larvae; SE = standard error of the mean; $M(\%)$ = estimated mortality as $\%^{-\mathrm{mm}}$ (i.e. $100(1-\exp(-b))$; SEE = standard error of the estimate; and I_L = length interval fit to the equation.

Length (mm)	Subarea 1			Subarea 2			Subarea 3			Subarea 4		
	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE
2	23	2.71	0.87	28	4.81	1.44	34	4.49	1.31	40	4.83	1.17
3	48	7.39	1.84	34	12.18	3.67	69	11.94	2.55	77	11.30	2.10
4	37	4.82	1.15	35	5.70	1.33	44	6.15	1.49	46	4.43	0.96
5	26	1.92	0.51	20	2.44	0.73	22	3.03	0.91	36	1.83	0.34
6	14	1.17	0.38	13	0.65	0.20	20	1.75	0.55	17	1.22	0.35
7	7	0.37	0.15	5	0.29	0.16	14	1.24	0.43	8	0.39	0.16
8	1	0.08	0.08	3	0.27	0.16	5	0.23	0.11	7	0.36	0.15
9	1	0.02	0.02	1	0.09	0.09	2	0.17	0.13			
10	—	—	—	—	—	—	4	0.19	0.10	2	0.04	0.03
11	—	—	—	—	—	—	—	—	—	—	—	—
12	1	0.05	0.05	1	0.04	0.04	—	—	—	—	—	—
13	—	—	—	1	0.06	0.06	—	—	—	—	—	—
14	1	0.07	0.07	—	—	—	—	—	—	1	0.03	0.03
15	—	—	—	—	—	—	1	0.06	0.06	—	—	—
16	—	—	—	—	—	—	—	—	—	—	—	—
17	—	—	—	—	—	—	1	0.03	0.03	—	—	—
18	1	0.06	0.06	—	—	—	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—	—
N		716			543			744			768	
a		233.28			133.26			82.22			79.70	
b		0.981			0.822			0.653			0.713	
M (%)		62.5			56.0			48.0			51.0	
r^2		0.96			0.98			0.95			0.97	
SEE		0.457			0.301			0.376			0.263	
I_L		3–9			3–9			3–10			3–8	

Length (mm)	Subarea 5			Subarea 6			Subarea 7		
	N_0	Mn	SE	N_0	Mn	SE	N_0	Mn	SE
2	104	5.77	0.78	37	3.28	0.65	78	4.84	0.74
3	169	12.59	1.33	55	8.18	1.45	174	16.68	1.88
4	110	6.41	0.76	38	3.54	0.65	165	12.98	1.37
5	67	2.93	0.41	19	1.60	0.40	136	10.75	1.28
6	38	1.42	0.25	16	1.59	0.48	122	7.29	0.86
7	22	0.86	0.21	8	0.53	0.20	95	6.55	0.93
8	11	0.35	0.12	4	0.33	0.19	70	4.65	0.77
9	8	0.44	0.22	5	0.56	0.30	33	2.74	0.67
10	1	0.01	0.01	4	0.20	0.10	34	3.18	0.79
11	1	0.06	0.06	2	0.25	0.20	29	2.15	0.55
12	—	—	—	1	0.04	0.041	19	1.86	0.64
13	2	0.05	0.04	1	—	—	14	0.39	0.12
14	1	0.01	0.01	—	—	—	10	0.31	0.11
15	1	0.04	0.04	—	—	—	13	0.31	0.09
16	—	—	—	—	—	—	3	0.12	0.07
17	—	—	—	1	0.05	0.05	4	0.11	0.06
18	1	0.02	0.02	—	—	—	4	0.11	0.06
19	1	0.03	0.03	—	—	—	4	0.12	0.07
20	—	—	—	—	—	—	2	0.05	0.04
N		1286			841			1852	
a		134.70			24.43			67.64	
b		0.754			0.481			0.358	
M (%)		53.0			38.2			30.1	
r^2		0.89			0.92			0.96	
SEE		0.788			0.467			0.387	
I_L		3–11			3–12			3–20	

9). Small juveniles (≤10 cm TL) show a similar distributional pattern, although they tend to be more abundant in shallower depths. Few have been collected in the Gulf of Maine, but they were distributed over most of Georges Bank, especially in the central portion. They were found closer to shore in the Middle Atlantic Bight than on Georges Bank. Small juveniles (≤10 cm TL) were found in 4–82 m in Massachusetts nearshore waters, but their average capture depth was 23 m. In New Jersey nearshore waters (5–27 m), larger juveniles and adults were abundant during all months, but small juveniles (≤10 cm TL) were rare (Fig. 11).

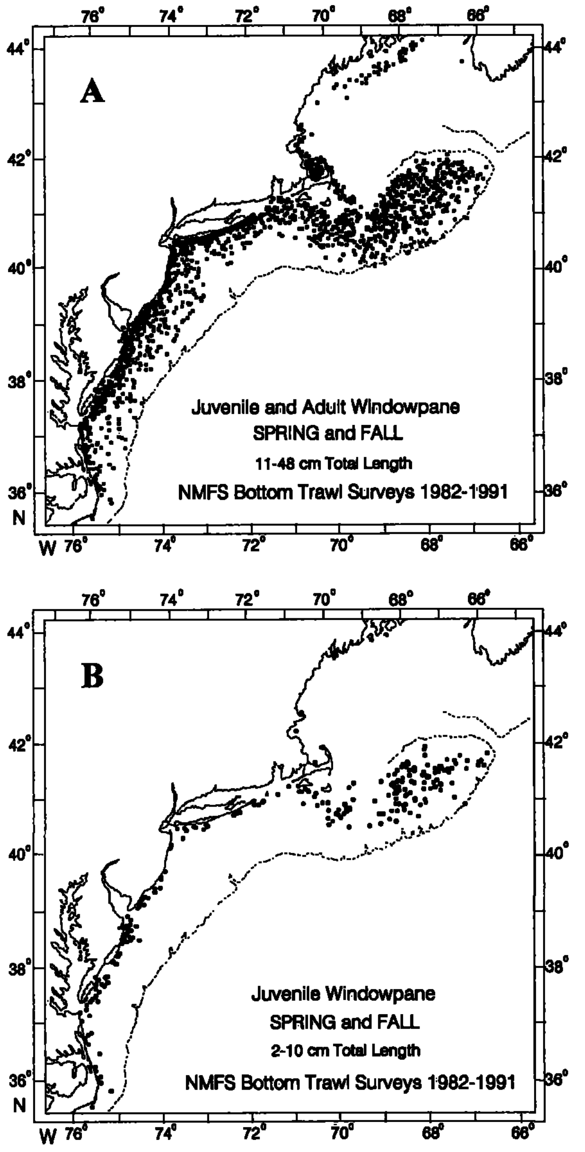

Figure 9

Occurrence of two size classes of windowpane, *Scophthalmus aquosus*, from spring and fall NMFS groundfish surveys during 1982–91.

The seasonal patterns of abundance of windowpane, based on NMFS bottom trawl survey catches, varied markedly on the continental shelf (Table 4). Fall catches of fish ≤10 cm TL in subareas 1–5 averaged ≤0.01 individuals per tow, 0.22 per tow in subarea 6, and 6.24 per tow in subarea 7. Spring catches of these fish ranged from 0.07 to 0.46 fish per tow across all subareas, with the highest catches in subareas 2 and 3, which were 30 to 50 times higher than those in the fall. In contrast to catches of fish ≤10 cm TL, catches of fish 11–20 cm TL showed little variation across subareas in the fall (0.72–1.82 fish/tow), whereas spring catches were low in subareas 1 and 2 (0.09 fish/tow) and high in subareas 5 and 6 (1.15–1.25 fish/tow). In general, adult fish (>20 cm TL) catches were consistently low in subarea 1, increased along the coast in subareas 2–6, and peaked in subarea 7. This pattern of adult catches differed for fish 21–30 cm TL in the spring, when the peak catches occurred in subarea 3.

The NMFS and Massachusetts fall and spring bottom trawl surveys were analyzed to determine whether the abundance of small juvenile windowpane reflects the areal patterns in larval distribution and abundance mentioned above. NMFS stations, for spring and fall combined, at which windowpane (11–48 cm TL) were captured are shown in Figure 9A, and stations that contained juveniles (≤10 cm TL) are shown in Figure 9B. Although adults occur in the northern Gulf of Maine, no juveniles were collected there. The spatial patterns of abundance for juveniles on the continental shelf coincide with the patterns of abundance for larvae (see Figs. 3 and 9B). The inverse relationship of catches of juveniles in the fall with larval mortality (r=–0.99, P<0.05) seems to support the conclusion that mortality is controlling recruitment; however, spring catches show no such relationship (r=0.12, P<0.93). To test the possibility that juveniles migrate to an area nearshore (<10 m depths) or to estuarine habitats in the southern part of the survey area in the fall and were not sampled by the trawl gear, we calculated the weighted mean capture depths in each subarea for five size classes (Table 4). Small juveniles (≤10 cm TL) were captured at only 4 of 779 stations in subareas 1–4 in the fall at depths of 10–24 m. Larger juveniles (11–20 cm TL) were more abundant and were captured at weighted mean depths 17–19 m. Adults (21–30 cm TL) were found in slightly deeper water (means= 22–27 m) and adults >30 cm TL were captured at only 12 stations in mean depths from 14 to 38 m. Weighted mean depths of capture within each subarea differed little between fall (10–38 m) and spring (15–47 m) surveys or between size classes, although a weak trend of increasing depth with size was

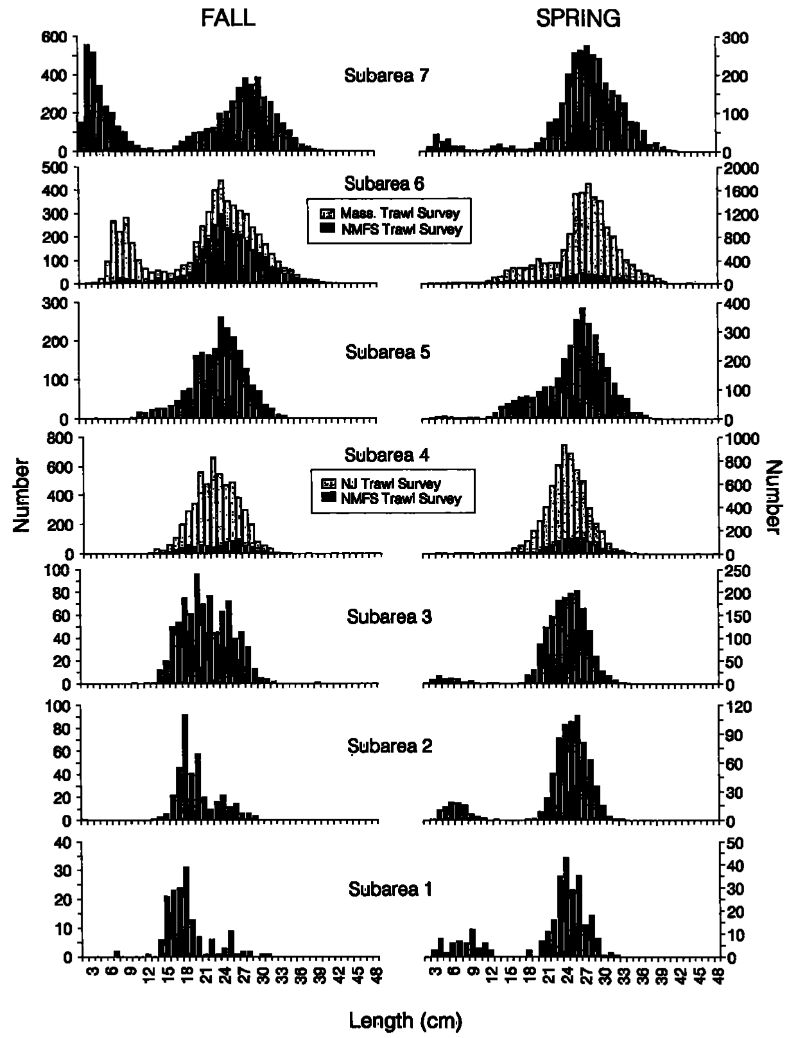

Figure 10

Length-frequency distribution of windowpane, *Scophthalmus aquosus*, from subareas indicated in Figure 1 during NMFS fall and spring groundfish surveys. See Table 1 for additional details.

evident. However, these results do not clearly indicate an inshore movement of juvenile fish during fall on the continental shelf, although eggs, larvae, and juveniles can be found in some estuaries.

Juvenile length frequencies and growth

Understanding patterns of age composition and growth in our study area is confounded by location and timing of spawning. For our purposes we will follow the patterns for Georges Bank (subarea 7) and the Middle Atlantic Bight off New Jersey (subarea 4), because they appear quite different. In subarea 7, where there is a specific peak in spawning, larvae first appear in relatively large numbers in June at sizes ranging from 2 to 6 mm (Table 2). They reach peak abundance in August when they range from 2 to 20 mm (Table 2; Fig. 4). By the fall they are well represented in bottom trawl collections at sizes of 2–14 cm TL (Fig. 10). By spring they are probably represented by the two smaller modes over the range from 3 to 16 cm TL (Fig. 10). The similar size ranges from fall to spring suggest that little or no growth occurs over the winter. By the following fall, this group has probably attained sizes of ≥17 cm TL and cannot be separated from older fish by length alone

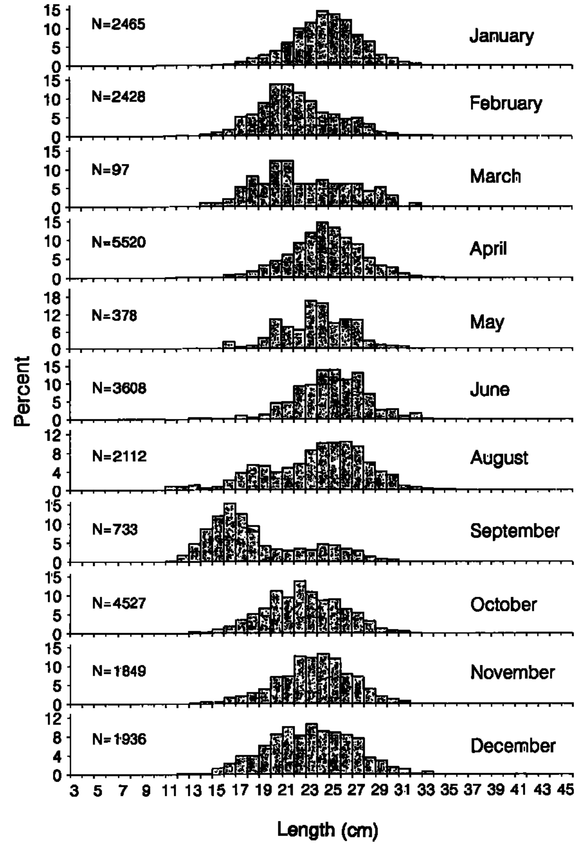

Figure 11

Monthly length-frequency distribution for windowpane, *Scophthalmus aquosus*, collected during an inshore trawl survey off the coast of New Jersey, 1988–92. See Table 1 for additional details.

(Fig. 10). In subarea 4 off New Jersey, where spawning was shown to be bimodal, the earliest peak was in May and the second was in October–November (Fig. 4; Table 2). However, there is no evidence of large numbers of small juveniles in the spring or fall in the NMFS survey (Fig. 10) or in the monthly catches of the New Jersey trawl surveys (Fig. 11). Conversely, in the vicinity of Little Egg Inlet, New Jersey, the appearance of eggs and larvae in both the estuary and in nearshore ocean waters corresponds well with two spawning periods (Fig. 7). Evidence of spring-spawned fish is first indicated by small numbers at 4 cm TL in June (Fig. 12). By July, these fish are 3–8 cm TL and in August they are 4–11 cm TL. In September, catches of small fish decreased, and fish lengths ranged from 8 to 17 cm TL. Catches of these spring-spawned fish further decreased by October, when very few juveniles were captured. This same cohort first appeared in nearshore surveys off New Jersey in August and by September the fish were 11–19 cm TL (Fig. 11). By October they cannot be easily differentiated from older fish on the basis of length, but some of these fish were probably captured in the fall collections by NMFS surveys on the continental shelf (Fig. 10). They do not appear to be abundant in estuary or ocean collections until the following April–May when most are >16 cm TL (Fig. 12).

Fall-spawned larvae were first collected in September in subarea 4 at lengths of 2–4 mm (Fig. 4; Table 2). The peak abundance was in October and November when they were 2–10 mm. These fish first appeared as settled juveniles in the vicinity of Little Egg Inlet in November at 3–4 cm TL, and by December they were 4–7 cm TL (Fig. 12). Fall-spawned juveniles were not evident in the nearshore (Fig. 10) or in deep-water surveys (Fig. 12). During January–March, fish 4–8 cm TL were abundant in the ocean catches and may not have grown much during these cold-water months (Fig. 12). From March to May, small juveniles moved gradually into the bay and began to grow again. A clear separation between the fall-spawned fish (5–12 cm TL) and the spring-spawned fish (>16 cm TL) can be seen in May (Fig. 12). The fall-spawned fish continued to grow and were 18–26 cm TL by October when they were about 1 year old. They may not have grown during the late fall and winter, given the similarities in length frequencies from October to December. These fish left the bay beginning in June, and by October few fall-spawned fish were present in the bay. The evidence for the existence of spring- and fall-spawned cohorts is most evident in July and August in New Jersey where both are represented by the two dominant length-frequency modes in both the bay and the adjacent ocean (Fig. 12).

Discussion

Distribution and abundance

Windowpane is a resident of the Middle Atlantic Bight and Georges Bank, although it does show some small-scale seasonal inshore-offshore movement. Evidence from ocean trawl surveys throughout the study area showed little difference in the preference of juveniles for relatively shallow waters from spring and fall depth distributions (Table 4). Evidence from tagging experiments in Long Island Sound (Moore, 1947) indicates that windowpane do not undertake extensive migrations in response to either seasonal temperature changes or for purposes of spawning. However, research trawl surveys show some evidence of an offshore movement during winter in response to low

Table 4

Summary of fall and spring catches (depths <100 m) of windowpane, *Scophthalmus aquosus,* from NMFS groundfish trawl surveys off the northeast United States, 1982–91. N_t = total stations sampled; D_m = mean depth of N_t; N_0 = number of stations with windowpane; M_t = mean catch per tow for N_t; and D_0 = weighted mean depth of N_0. See Figure 1 for location of subareas.

				Length (cm)															
				≤10			11–20			21–30			31–40			>40			
Subarea	Season	N_t	D_m	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0	N_0	M_t	D_0	
1	Fall	178	31	1	0.01	17	34	0.72	18	9	0.15	27	1	0.01	30	0	—	—	
2	Fall	185	31	1	<0.01	24	53	1.42	19	40	0.57	27	0	—	—	0	—	—	
3	Fall	209	35	1	<0.01	22	66	1.82	19	77	2.27	27	6	0.03	38	0	—	—	
4	Fall	211	38	1	<0.01	10	52	1.18	17	91	2.61	22	5	0.04	14	0	—	—	
5	Fall	384	36	4	0.01	15	89	1.28	41	176	4.33	43	59	0.22	47	0	—	—	
6	Fall	306	49	18	0.22	31	57	1.05	33	105	6.67	35	64	1.35	39	5	0.02	42	
7	Fall	435	65	70	6.24	47	76	0.78	48	166	5.61	51	155	2.60	49	2	<0.01	47	
1	Spring	199	33	15	0.21	17	10	0.09	22	47	1.04	23	3	0.02	23	0	—	—	
2	Spring	179	33	21	0.46	15	11	0.09	19	94	3.34	22	8	0.04	26	0	—	—	
3	Spring	209	33	25	0.34	18	28	0.68	17	118	6.95	19	22	0.14	20	0	—	—	
4	Spring	226	40	12	0.16	16	31	0.39	17	99	4.36	20	23	0.16	26	2	0.01	47	
5	Spring	436	39	18	0.09	24	142	1.15	57	258	5.23	63	146	1.07	47	2	0.01	41	
6	Spring	305	49	16	0.07	33	79	1.25	53	147	4.17	53	105	1.94	40	5	0.02	43	
7	Spring	368	65	23	0.23	52	43	0.27	73	143	3.40	73	167	2.14	52	4	0.01	57	

water temperatures (Wigley and Gabriel, 1991; Lange and Lux[6]).

There appears to be evidence of latitudinal variation in depth preference from south to north (Table 4). The actual depth preference in subareas 1–4 may be shallower than indicated because NMFS seldom samples in depths <10 m. For example, in subarea 4, juveniles migrated or settled into an estuary during spring and tended to move into the ocean during summer (Fig. 12). Few juvenile windowpane were caught inside the estuary by the fall when they had reached lengths between 18 and 26 cm TL. These seasonal movements in and out of estuaries and bays may account for the larger numbers of juveniles taken on the continental shelf in the Middle Atlantic Bight in the spring (Table 4; Fig. 10), although the lack of small juveniles in nearshore waters off New Jersey (Fig. 10) is difficult to explain. In contrast, the Massachusetts trawl survey, which sampled similar depths to those in the New Jersey trawl survey, captured large numbers of juvenile windowpane in the fall. Clearly juvenile windowpane are also a component of fish assemblages in other estuaries on the basis of reports from Narragansett Bay (Herman, 1963), Long Island Sound (Moore, 1947), Sandy Hook Bay (Wilk and Silverman, 1976), Delaware Bay (de Sylva et al., 1962), Chesapeake Bay (Hildebrand and Schroeder, 1928), North Carolina (Weinstein, 1979), South Carolina (Wenner et al., 1982), and Georgia (Dahlberg, 1972). Thus, further sampling in the shallow nearshore ocean waters and in adjacent estuaries will be necessary to understand completely the nature of seasonal movements and the patterns of habitat use of juveniles, at least in subareas 1–5.

Timing and location of spawning

The extensive latitudinal sampling program has helped to discern the seeming inconsistency in the literature regarding the presence of a bimodal spawning season. Split spawning (i.e. peaks in spring and fall) has been previously reported in Long Island Sound, New York (Wheatland, 1956), Great South Bay, New York (Monteleone, 1992), and on the continental shelf off Virginia and North Carolina (Smith et al., 1975). However, Colton et al. (1979), Perlmutter (1939), and Smith et al. (1975) reported no evidence for split spawning north of Virginia. We found evidence for a split spawning season in all areas except Georges Bank (Fig. 4). Taken together, the available information shows that windowpane begin spawn-

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[6] Lange, A. M. T., and F. E. Lux. 1978. Review of the other flounder stocks (winter flounder, American plaice, witch flounder and windowpane flounder) off the Northeast United States. U.S. Dep. Commer., NMFS, Northeast Fish. Sci. Center, Woods Hole Lab. Ref. No. 78-44, Woods Hole, MA 02543.

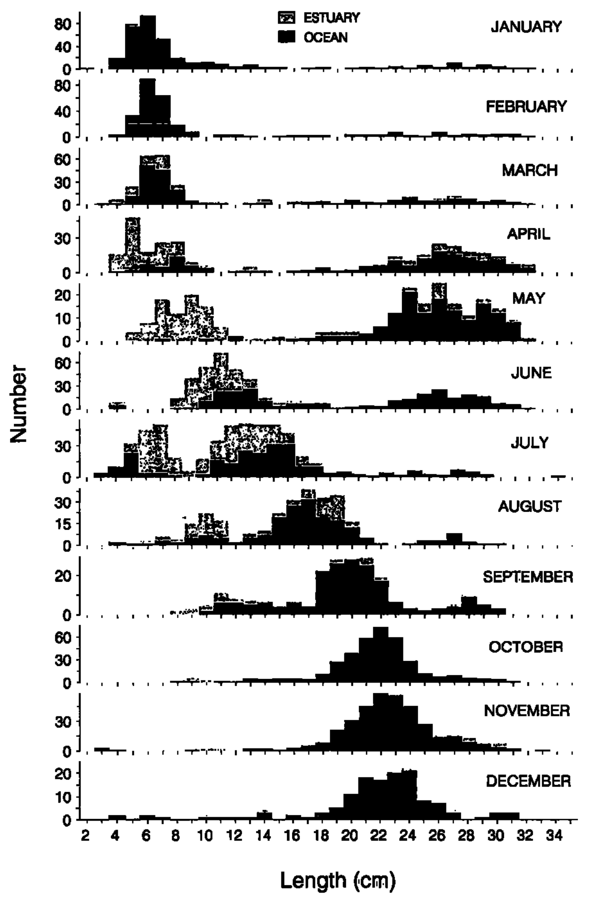

Figure 12

Length-frequency distribution of windowpane, *Scophthalmus aquosus*, by month, based on collections in the estuarine and ocean in the vicinity of Little Egg Inlet, New Jersey, as modified from Milstein and Thomas (1977). Estuarine samples represent all samples not taken in the ocean. Station locations are indicated in Figure 2.

ing at the southern portion of the Middle Atlantic Bight (south of Chesapeake Bay) in April or May. Peak spawning progresses northward as waters warm, and spawning reaches Georges Bank by July and August. As waters cool during fall, spawning moves south to off New York and New Jersey, and by November spawning is again centered in the southern part of the Middle Atlantic Bight. The split spawning season pattern has also been verified for New Jersey in the vicinity of Little Egg Inlet (Fig. 8) and farther south at Hereford's Inlet, New Jersey (Keirans, 1977).

Seasonally varying temperatures clearly influenced the timing of spawning. We found maximum numbers of small larvae at temperatures between 16 and 19°C in subareas 1–5 (Fig. 5), except on Georges Bank where the maximum larval abundance occurred at temperatures (13–16°C), approximately those reported by Smith et al. (1975). They found 70% of small larvae over bottom water temperatures between 8.5 and 13.5°C between Cape Hatteras and Block Island (subareas 1–5). It appears that spawning during the single year (1965–66) of their study occurred at temperatures around 6°C, colder than our findings from a data set that was more extensive both temporally and latitudinally.

Reports of eggs from Great Bay (Fig. 8) and Hereford's Inlet (Keirans, 1977), New Jersey, Chesapeake Bay, Virginia (Olney, 1983; Olney and Boehlert, 1988), Long Island Sound (Wheatland, 1956; Richards, 1959; Perlmutter, 1939), Great South Bay on Long Island (Monteleone, 1992), and Narragansett Bay, Rhode Island (Herman, 1963; Bourne and Govoni, 1988), strongly suggest that spawning occurs in the lower portions of estuaries in the Middle Atlantic Bight. These sources imply that the influence of estuaries on the early life history of windowpane may be important in the Middle Atlantic Bight.

Age and growth

Growth after settlement was markedly different between the spring- and fall-spawned cohorts in New Jersey waters. The spring-spawned cohort grew quickly during the summer and reached sizes of 11–19 cm TL in September, approximately 4 months later (Fig. 12). The fall-spawned cohort, exposed to winter temperatures soon after settlement, apparently did not grow during the winter and grew to only 4–8 cm TL six months later in March (Fig. 12). Thus, the timing of spawning (spring vs. fall) influences growth rates and the age and size composition of young of the year.

Reported estimates of growth from scale annuli, regardless of spawning season, were quite different. In studies for Long Island Sound and North Carolina age-2+ fish averaged only 11.7 cm TL (Moore, 1947) and 10–13 cm TL (Shelton, 1979), respectively. Sizes at age 1 reported for our study area were 18 cm TL (Grosslein and Azarovitz, 1982) and 14.5 cm TL (Thorpe, 1991) and were more consistent with our results, although the season of spawning could easily affect size at age. Clearly, more detailed studies of spawning times and their effects on age composition and growth of juveniles are needed before we can completely understand the population dynamics of this species.

Nursery areas

In general, the distribution of larvae and juveniles on the continental shelf coincided and showed that at least some juveniles settled in areas of larval concentration, although this pattern was not as strong for the Middle Atlantic Bight as it was for Georges Bank. Larval abundance on Georges Bank was high and recently settled juveniles were clearly abundant there in the fall but less so in the spring (Fig. 10). Slightly larger individuals were also evident off Massachusetts in the fall (Fig. 10), but they were not caught in the deeper waters of the continental shelf further south (subareas 1–5, Fig. 10). Size at settlement appears to differ between Georges Bank and the Middle Atlantic Bight. Larvae >10 mm were collected only rarely in the Middle Atlantic Bight but were relatively abundant on Georges Bank. This pattern of catches could arise from 1) the large larvae avoiding capture by transforming and settling earlier in the south, 2) the differences in mortality between regions, or 3) the unavailability of larger larvae to the sampling gear because they entered the unsampled surf-zone or the numerous estuaries in the southern part of the study area. This last possibility is clearly not an option for Georges Bank larvae that do not make extensive migrations (50–75 km) to the nearshore areas of Massachusetts. We have shown that mortality estimates are higher in the Middle Atlantic Bight than on Georges Bank. Settlement in estuaries in the Middle Atlantic Bight is also possible because larger planktonic larvae (K. W. Able, D. A. Witting, and M. P. Fahay, unpubl. data) and small juveniles were collected from these areas in New Jersey (this study, Figs. 8 and 12; Allen et al., 1978), Delaware (Pacheco and Grant, 1973), and Long Island (Warfel and Merriman, 1944). Yet to be resolved are the reasons for the differences in the size of larvae and the apparent mortalities in the different geographic regions, as well as for the subsequent effect of size on settlement and the location of nursery areas throughout the range of windowpane.

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