

**Abstract.**—Gonad-somatic index (GSI), the relation of ovarian to somatic weight, was calculated for 14 species of finfish that are yearlong residents of the New York Bight. Specimens were collected monthly from June 1974 through June 1975 in the ocean and associated estuarine waters of the Bight. Analysis indicated that alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, striped and northern searobin, and fourspot flounder are summer spawners; and summer and winter flounder are fall-winter spawners. Offshore hake exhibited a protracted spawning season with ripe females collected from spring through fall, while spotted hake and windowpane exhibited bimodal spawning patterns with two GSI peaks per year. The co-occurrence of spawning with appropriate food supply and environmental conditions is discussed on an individual-species as well as species-complex basis.

# Annual Cycles of Gonad-Somatic Indices as Indicators of Spawning Activity for Selected Species of Finfish Collected from the New York Bight

Stuart J. Wilk  
Wallace W. Morse  
Linda L. Stehlik

Sandy Hook Laboratory, Northeast Fisheries Science Center  
National Marine Fisheries Service, NOAA, Highlands, New Jersey 07732

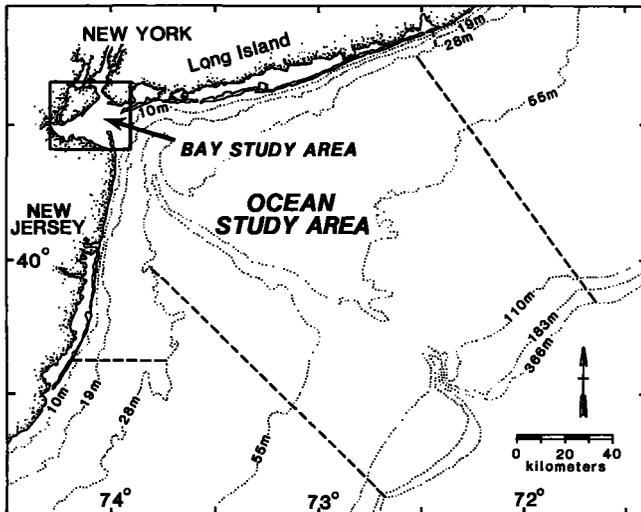
In temperate zones, reproduction of marine fish species is usually characterized by single annual peaks of spawning activity (Cushing 1969). Seasonal changes in the gonads of fishes, in preparation for reproduction, are known to be controlled by hormones, and triggered, sometimes well in advance of spawning, by photoperiod (Hoar 1969, Bye 1984). Minor variations in spawning time, during any given year, are believed to be related to temperature and to the overall condition of the fish (de Vlaming 1972, Bye 1984). Wootton (1984) defines reproductive "strategies" as the genetically determined pattern of spawning behavior, and reproductive "tactics" as the responses to exogenous cues during a single season.

The gonad-somatic index (GSI), the relation of ovarian weight to somatic weight, provides a measure of spawning readiness while removing variability attributable to fish size (Nikolskii 1963). The GSI has also been termed the gonosomatic index (de Vlaming et al. 1982) and maturity index (Morse 1981). Annual cycles in GSI can be thought of as an approximate measure of the energy expended for reproduction, which makes this information critical in formulating energy budgets relating to the balance between fish production and consumption.

Approximate spawning times for the most common species which occur in the New York Bight have been established based on the distribution of eggs and larvae (Colton et al. 1979) and published life-history information (Grosslein and Azarovitz 1982). However, detailed qualitative and quantitative information on annual cycles of spawning as determined by examination of maturity stages is lacking for many, if not most, of these same species. This study presents monthly variations in GSI as they relate to hydrographic observations for 14 species of fish which represent many of the dominant fishes found on the Middle Atlantic continental shelf and in associated estuarine waters (Wilk and Silverman 1976ab, Wilk et al. 1977; Colvocoresses and Musick 1984).

## Materials and methods

Fish were collected from June 1974 to June 1975 during monthly bottom surveys in the central portion of the New York Bight at the confluence of the Long Island, New York and New Jersey coastlines and the contiguous Sandy Hook-Lower-Raritan Bay estuary (Fig. 1). This area is characterized by seasonally intensive recreational and commercial fisheries and is influenced by a wide variety of anthropogenic activities (Gross 1976, Mayer 1982).



**Figure 1**

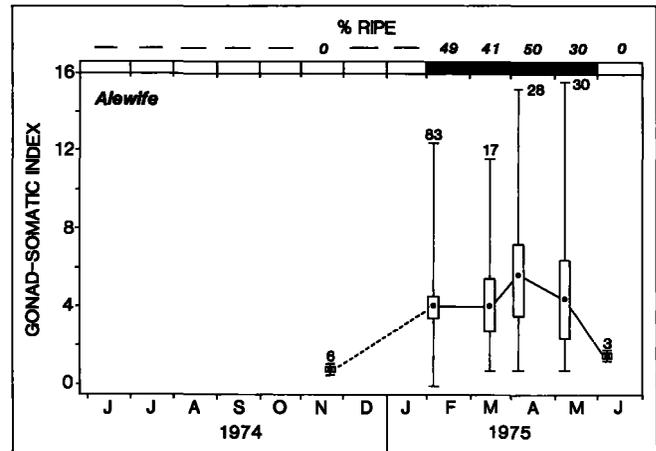
Middle Atlantic continental shelf with outlines of the ocean and estuarine (bay) study areas where finfish were sampled during a trawl survey of the New York Bight, June 1974–June 1975.

Two study areas, ocean and estuarine, were designated (Fig. 1). The ocean area was delineated by an imaginary set of lines extending seaward from points on Long Island, New York and New Jersey to the 28-m isobath and from the 28-m isobath to the edge of the continental shelf (366 m). This area corresponds to offshore strata 1–4 and inshore strata 6–17 of the Northeast Fisheries Center's resource trawl survey (Grosslein 1969). The estuarine study area included Sandy Hook, Lower, and Raritan bays.

Station locations in the ocean study area were selected by stratified random sampling design (Grosslein 1969). Strata boundaries were determined by depth as follows: 0–10, 11–19, 20–28, 29–55, 56–110, 111–183, and 184–366 m. A minimum of two stations per stratum was selected randomly to be sampled during each cruise. Inshore (0–28 m) and offshore (29–366 m) strata were sampled at rates of approximately one station per 515 and 1030 km<sup>2</sup>, respectively. An average of 49 ocean stations was sampled per cruise. Ocean stations were not sampled during December 1974 and January 1975.

The estuarine study area was divided into 103 potential sampling blocks. Except where interrupted by land, each block measured 1' of latitude by 1' of longitude, i.e., 1.8 km × 1.4 km (2.5 km<sup>2</sup>). A set of stations was selected randomly from these blocks and retained throughout the study. An average of 15 estuarine stations was sampled per cruise. Estuarine stations were not sampled during December 1974.

Fish collections were made with otter trawls towed at approximately 6.5 km/hour for 15 and 30 minutes



**Figure 2**

Annual cycle of gonad-somatic indices for alewife *Alosa pseudoharengus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

at estuarine and ocean stations, respectively. Estuarine stations were sampled with a 9.1-m trawl and ocean stations with a Yankee #36 trawl. All specimens of each species, up to 35 individuals from each trawl station, were selected and frozen for later laboratory analysis. If the total catch of a species exceeded 35 individuals, a size-stratified sample of 25 to 35 specimens was frozen. At the laboratory each specimen was measured from the snout to the extent of the middle caudal fin ray ( $\pm 1.0$  mm), weighed ( $\pm 0.1$  g), sexed, and state of maturity determined by macroscopic evaluation when possible. Stage of ovarian development was determined visually, and designated immature, developing, ripe, or resting. Ovaries were weighed ( $\pm 0.01$  g) and GSI calculated (ovarian weight/fish weight  $\times 100$ ). It should be noted that only mature females were included in the calculation of GSI.

Temperature and depth observations were made at all stations. Vertical temperature profiles were obtained with expendable bathythermographs during ocean cruises and with portable temperature probes during estuarine cruises. Fathometers continually recorded depth during each trawl tow. Detailed information relative to survey design, methodology, species distribution and abundance, and associated hydrographic observations is given in Wilk et al. (1977).

## Results

The majority (93%) of all ripe females collected during the survey were caught in the ocean study area. Of the

**Table 1**

Observations relative to peak spawning activity for 14 finfish species, including mean and range of bottom temperature and depth for the month, or months, of highest gonad-somatic indices (GSI) at stations where ripe females occurred during a trawl survey of the New York Bight, June 1974–June 1975. Alewife and winter flounder data include only estuarine observations; bimodal spawners are indicated with an asterisk (\*) with observations given for both peaks; in some cases months were combined when sample sizes were small.

Species	Month	No. of fish	Occurrence/total no. of stations	Bottom temperature (°C)		Depth (m)	
				Mean	Range	Mean	Range
Alewife	Apr 75	18	7/14	5.4	4.5–6.0	6	5–11
Offshore hake	May/Jun 75	17	4/156	10.2	9.0–11.4	270	222–348
Silver hake	Aug 74	5	4/58	9.8	8.4–13.4	80	54–127
Red hake	Jun 75	68	23/72	8.0	5.7–12.5	60	12–264
Spotted hake*	Sep 74	42	7/56	14.8	11.0–17.3	30	12–86
Spotted hake*	Mar/Apr 75	10	4/109	10.5	7.4–12.3	113	75–139
Black sea bass	Jul 74	16	3/59	14.9	13.8–15.9	19	16–22
Butterfish	Jun 74 & 75	189	45/130	11.8	5.4–20.4	40	3–145
Northern searobin	Jul 74	21	8/59	15.1	13.8–16.5	20	15–27
Striped searobin	Jun 74 & 75	12	8/130	10.9	8.4–14.1	16	9–21
Summer flounder	Oct 74	51	22/60	13.7	10.5–14.7	35	11–97
Fourspot flounder	Jun 75	32	15/72	7.3	5.6–11.2	57	17–127
Windowpane*	Sep 74	150	23/56	15.7	10.3–19.4	26	10–65
Windowpane*	May 75	159	44/84	7.9	5.6–13.2	23	4–51
Yellowtail flounder	Mar 75	45	15/46	5.7	4.4–7.5	36	9–68
Winter flounder	Jan 75	5	3/9	5.7	4.8–6.5	5	3–7

total catch of ripe female alewife and winter flounder, 5 and 21%, respectively, were collected in the estuarine study area. This was expected since these species are known to inhabit the lower reaches of estuaries before moving upriver to spawn. Ripe female butterfish and windowpane were also collected in the estuarine study area, but made up <5% of the catch of all ripe females of those species. Eggs and larvae of these four species are known to occur in both Raritan Bay (Croker 1965) and the New York Bight (Clark et al. 1969; Smith et al. 1975, 1980). Silver hake, red hake, and summer flounder were also caught in the estuarine study area during some months; however, no ovarian development beyond the resting stage was observed. All data were pooled since there were no clear differences in time of spawning between bay and ocean samples of any species captured during the study. Detailed results and discussion for each species are given in the following sections.

### **Alewife *Alosa pseudoharengus***

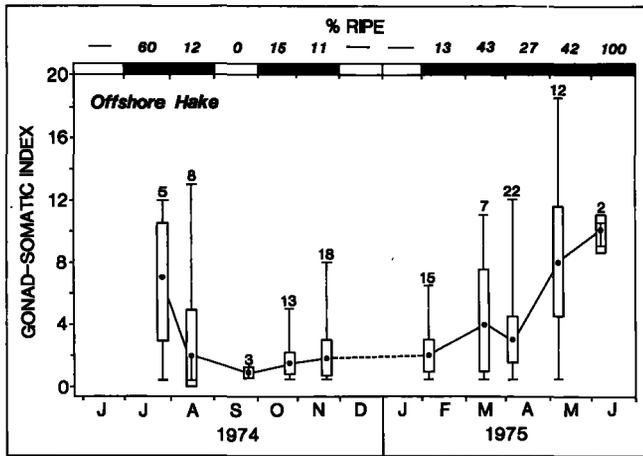
Mean GSI was highest in April, with ripe females, 145–345 mm, collected throughout the survey area from February through May (Fig. 2). These observations are similar to published spawning times for alewife in Connecticut inshore waters (Kissil 1969) and the Delaware River (Smith 1971). Farther north in

Canadian waters the species spawns primarily in May (Leim and Scott 1966).

Alewives are common in coastal waters from Newfoundland, Canada to North Carolina as they migrate to and from their riverine spawning grounds (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953, Leim and Scott 1966). The average temperature in the estuarine survey area during the April spawning peak was 5.4°C (Table 1).

### **Offshore hake *Merluccius albidus***

Mean GSI was highest during July 1974 and again in June 1975, with ripe females, 230–575 mm, collected in ocean waters during most months sampled (Fig. 3). The highest percentages of ripe ovaries were observed in spring and summer. In a review of historic ichthyoplankton surveys, Colton et al. (1979) stated that offshore hake larvae were present in the Middle Atlantic from June through September. Smith et al. (1980) collected eggs and larvae south of New England from April through June during 1977–79 ichthyoplankton surveys. They also collected eggs in late February–early March 1979 from stations south of Long Island, New York. Marak (1967) found eggs and larvae off Martha's Vineyard, Massachusetts, in April through July. Offshore hake, based on this as well as the aforementioned studies, has either a long or irregular spawn-



**Figure 3**

Annual cycle of gonad-somatic indices for offshore hake *Merluccius albidus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

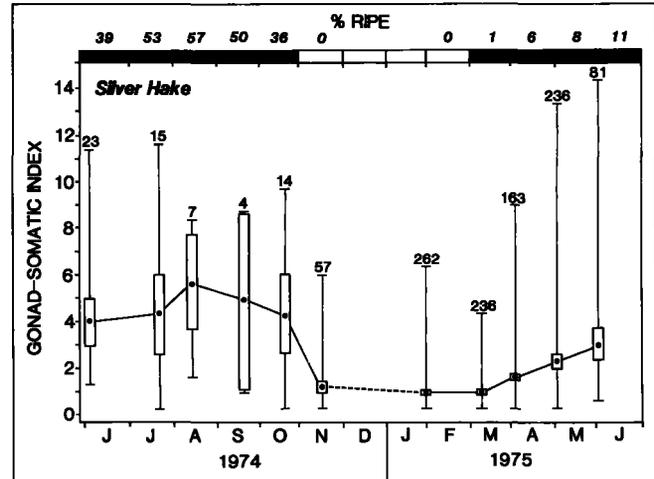
ing season or perhaps even spawns continually throughout the year.

Offshore hake range from Georges Bank to the coast of South America along the continental shelf break in depths >100 m (Bigelow and Schroeder 1955, Leim and Scott 1966). They are the deepest ranging species described in this study, being found between 162 and 366 m, the survey extreme. They were collected within a relatively restricted temperature range throughout the year, with little or no seasonal changes.

### Silver hake *Merluccius bilinearis*

Ripe females, 202–590 mm, were collected in ocean waters during a long spawning season, March through October, with mean GSI highest from July to October (Fig. 4). A protracted spawning season for this species in the Middle Atlantic is supported by two ichthyoplankton surveys: (1) Fahay (1974) collected eggs during 1966 from May through November with a peak in June–July; and (2) Sherman et al. (1984) reported larvae were collected during 1977–79 from April through November, with a peak in August.

Silver hake are found over all bottom types from the intertidal zone to the 200-m isobath from Nova Scotia, Canada to Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Leim and Scott 1966). During August, the month of highest mean GSI, silver hake were found well offshore where temperatures were moderate (Table 1). During the remainder of the year females were captured throughout the entire survey area at a



**Figure 4**

Annual cycle of gonad-somatic indices for silver hake *Merluccius bilinearis* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

wide variety of depths (4–335 m) and temperatures (4.3–19.2°C).

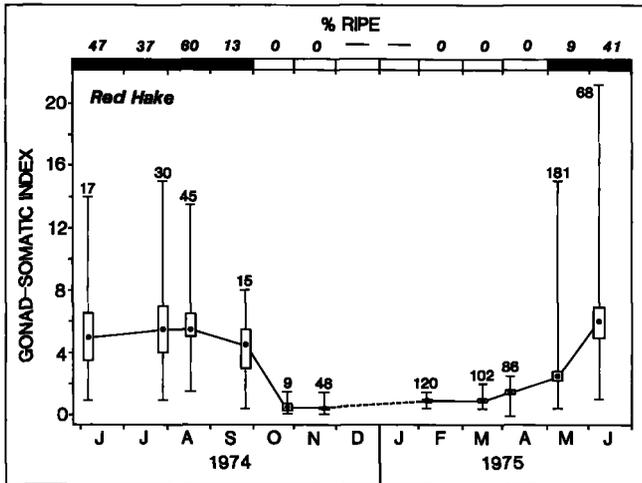
### Red hake *Urophycis chuss*

Mean GSI was highest during the summer; however, ripe females, 225–621 mm, were present from May through September (Fig. 5). Colton et al. (1979) reported the occurrence of larvae in the Middle Atlantic from May through October with a peak in June or July. Off the southern New England coast, adults migrate offshore to the continental slope and spawn during May through September at temperatures of 5–11°C (Musick 1969, 1974).

Red hake were among the deepest spawners observed during the study with a mean capture depth of 60 m in June 1975 during the height of the spawning cycle (Table 1). The mean temperature of 8.0°C at time of spawning agrees with previously reported observations. It is noteworthy that five specimens in spawning condition were caught at two nearshore ocean stations at which the depth and temperature were 25 and 27 m and 15.3 and 17.1°C, respectively. These observations, to some degree, broaden the spawning depth and temperature ranges reported by Musick (1969, 1974).

### Spotted hake *Urophycis regia*

Spotted hake exhibited a bimodal or split spawning pattern which was characterized by two mean GSI peaks,

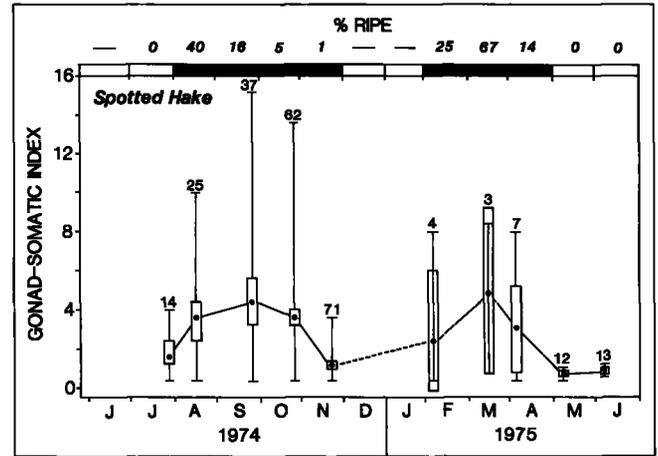


**Figure 5**

Annual cycle of gonad-somatic indices for red hake *Urophycis chuss* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

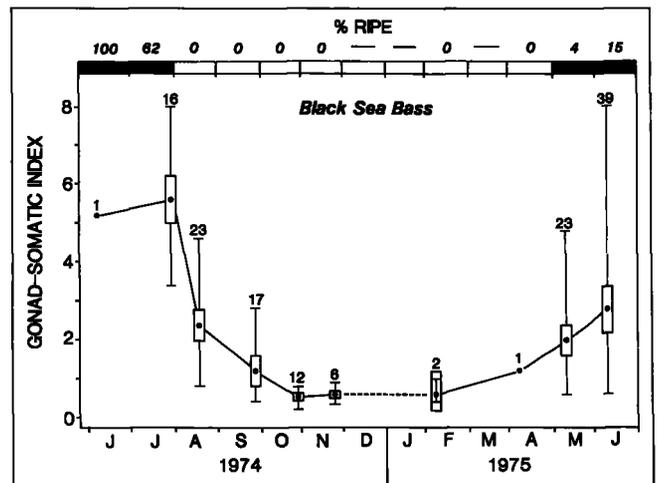
one during March followed by another in September (Fig. 6). Ripe females, 283–396 mm, were collected from February through April. In addition, ripe females, 191–360 mm, were present again from August through November. Colton et al. (1979) suggested a spawning time of August through April with an October peak, but did not allude to a bimodal spawning pattern. Barans (1969) observed ripe females, with a minimum length of 225 mm, in the Chesapeake Bight from August through November. In collections made off the Carolinas, ripe spotted hake were found during December (Bigelow and Schroeder 1953).

In the September sample, ripe females were caught at depths between 12 and 86 m and temperatures of between 11.0 and 17.3°C. In contrast, during March and April ripe females were caught at much deeper and cooler locations (Table 1). Spotted hake range from southern New England to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953); however, they are most abundant south of Chesapeake Bay (Barans 1969). In the Chesapeake Bight, Barans (1969) reported their temperature range as 6–20°C, with a preferred range of 10–12°C. In addition, he gave 190 mm as the minimum length for 1-year-old females, and >280 mm for 2-year-olds. If the spotted hake captured during this study follow the size at ages given by Barans (1969), the population present in spring is composed primarily of older fish, with young-of-the-year and yearlings migrating into the area during summer and fall. The apparent split spawning season observed during this study may be attributable to dissimilar



**Figure 6**

Annual cycle of gonad-somatic indices for spotted hake *Urophycis regia* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.



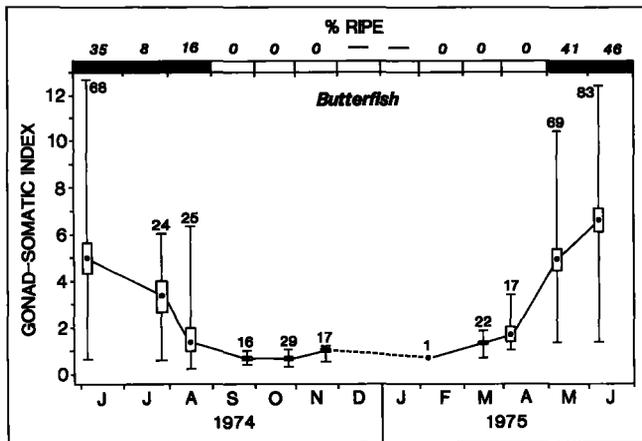
**Figure 7**

Annual cycle of gonad-somatic indices for black sea bass *Centropomus striata* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

distributional patterns of specific age groups at the northernmost extreme of the species range.

**Black sea bass *Centropomus striata***

Mean GSI was highest during July, with ripe females, 184–452 mm, collected from May through July (Fig. 7). Black sea bass are protogynous hermaphrodites with the size at which females become males extremely



**Figure 8**

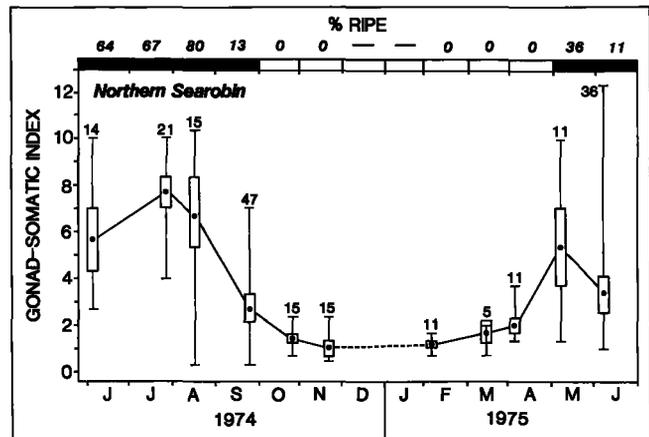
Annual cycle of gonad-somatic indices for butterfish *Peprilus triacanthus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

variable (Kendall and Mercer 1982). In this study female and male black sea bass were in the range 173–452 and 178–556 mm, respectively. Bigelow and Schroeder (1953) reported spawning from mid-May through June off southern New England and New Jersey. To date, black sea bass eggs have not been reported from plankton collections. However, larvae have been collected from Long Island, New York waters from mid-May to June (Perlmutter 1939) and from offshore New York Bight waters from June through November (Kendall 1977).

Black sea bass are common from Cape Cod, Massachusetts to Florida (Hildebrand and Schroeder 1928, Bigelow and Schroeder 1953). In the Middle Atlantic, they migrate northward and inshore in spring and offshore and southward in fall (Kendall and Mercer 1982). Mean temperature and depth of occurrence in July, the month of highest mean GSI, were among the warmest and shallowest of the survey (Table 1).

### Butterfish *Peprilus triacanthus*

Highest mean GSI occurred in June 1974 and again in May and June 1975, with ripe females, 124–242 mm, being present throughout the survey area from May through August (Fig. 8). The butterfish is a migratory semi-pelagic species which ranges from Newfoundland, Canada to Florida (Bigelow and Schroeder 1953, Leim and Scott 1966). Colton et al. (1979) reported butterfish spawning in the Middle Atlantic from May through October with a peak in July or August. Smith et al. (1980) collected eggs off North Carolina during spring and larvae off New Jersey during early summer.



**Figure 9**

Annual cycle of gonad-somatic indices for northern searobin *Prionotus carolinus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Kawahara (1978) reported the spawning time of butterfish in the Middle Atlantic as April or May through August. Butterfish were collected at a wide range of temperatures and depths during the months of peak GSI (Table 1).

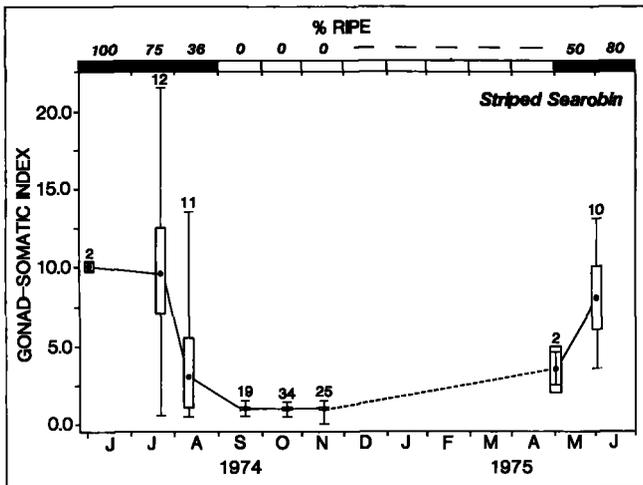
### Northern searobin *Prionotus carolinus*

Highest mean GSI was in July; however, ripe females, 143–341 mm, occurred from May through September (Fig. 9). According to Richards et al. (1979), based on data from the north shore of Long Island, New York, GSI rose early in May, peaked in late May, and declined gradually through June and July. Colton et al. (1979) reported spawning from Block Island, Rhode Island to Cape Hatteras, North Carolina from May through November.

Eggs and larvae of *Prionotus* spp. are among the dominant ichthyoplankton occurring in the Middle Atlantic from New Jersey to Cape Hatteras, North Carolina during June through October (Smith et al. 1980, Sherman et al. 1984). This survey demonstrated that northern searobin favored warm shallow inshore waters during peak spawning (Table 1); however, from November through April they favored depths >50 m.

### Striped searobin *Prionotus evolans*

Highest mean GSI occurred during June and July 1974 and again in June 1975, with ripe females, 204–414 mm, present from May through August (Fig. 10). Richards et al. (1979) determined spawning time for striped searobin to be almost the same as northern



**Figure 10**

Annual cycle of gonad-somatic indices for striped searobin *Prionotus evolans* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

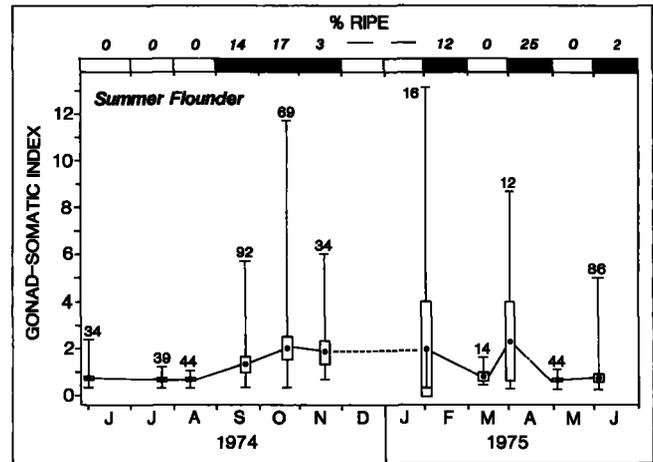
searobin. Perlmutter (1939) collected larvae off Long Island, New York between May and June; and Herman (1963) reported spawning from June through August off Narragansett Bay, Rhode Island.

This study indicated temperature preferences during spawning were somewhat cooler than those of the northern searobin, while depths were similar (Table 1). However, throughout the remainder of the year, striped searobin were collected in comparatively warmer and shallower waters than northern searobin.

### Summer flounder *Paralichthys dentatus*

Ripe females, 309–716 mm, were collected from September through November, and sporadically from February to June (Fig. 11). Although there were several slight peaks in GSI during the spawning season, these probably resulted more from individual sample variability than actual peaks in spawning activity (Fig. 11). Morse (1981), using additional maturity data from the New York Bight, reported spawning from September through March with a peak in October. Smith (1973) reported that eggs and larvae began to appear in September off Long Island, New York and southern New England, and occurred farther southward as fall progressed. After December, recently hatched larvae were common only south of Chesapeake Bay (Smith 1973).

Summer flounder range between Nova Scotia, Canada and Florida with their center of abundance lying in the Middle Atlantic region (Leim and Scott



**Figure 11**

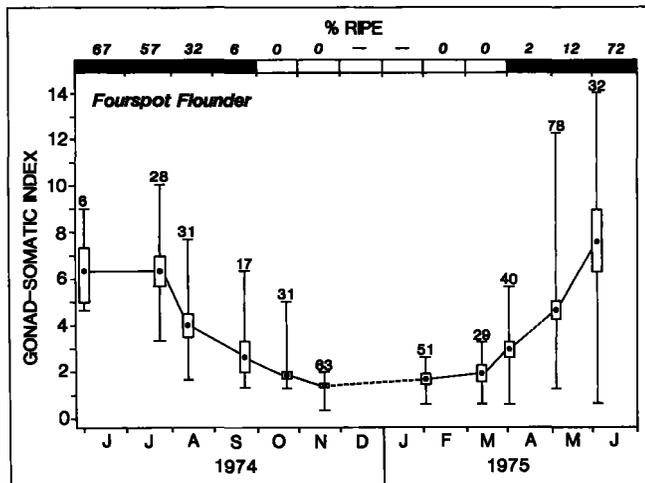
Annual cycle of gonad-somatic indices for summer flounder *Paralichthys dentatus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

1966, Guthertz 1967, Wilk et al. 1980). They migrate to shallow coastal waters and bays in summer, then offshore in fall (Bigelow and Schroeder 1953). At the GSI peak in October, developing females were collected in relatively warm shelf waters (Table 1). Depths of collection for summer flounder varied during the year, from a mean of 11 m in July to 92 m in April, reflecting their seasonal migration pattern.

### Fourspot flounder *Paralichthys oblongus*

Mean GSI were highest in June and July 1974 and again in June 1975, with ripe females, 153–419 mm, present from April through September (Fig. 12). Smith et al. (1975) found small larvae off North Carolina and Chesapeake Bay in May and June, and off New Jersey and New York in July and August.

Fourspot flounder are widely distributed on the continental shelf between Georges Bank and Cape Hatteras, North Carolina (Bigelow and Schroeder 1953, Guthertz 1967). In the New York Bight, they inhabit the entire shelf, with deepest occurrences during winter (Ralph 1982). Collections from this survey indicate they were deepest during February and March, averaging 90 and 92 m, respectively, moving somewhat inshore during the rest of the year, but always at depths averaging >40 m. They were collected over a wide range of depths and temperatures during the June spawning peak (Table 1). Smith et al. (1975) collected larvae between 6 and 9°C at depths of 35–80 m.



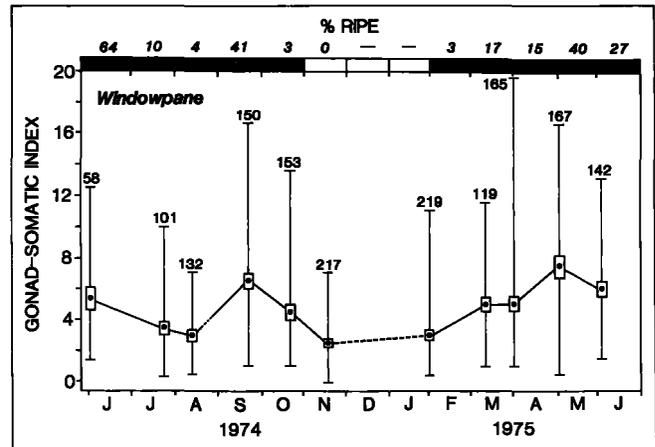
**Figure 12**

Annual cycle of gonad-somatic indices for fourspot flounder *Paralichthys oblongus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

### Windowpane *Scophthalmus aquosus*

The GSI plot for windowpane was bimodal, with peaks in May and again in September (Fig. 13). Ripe females, 201–387 mm, were collected from February through October, indicating that windowpane may spawn to some degree in the New York Bight during most of the year. Unfortunately, data for winter are lacking. There was no conclusive evidence that the two peaks represented spawning of either different populations or age classes. In September the mean lengths were 261 and 230 mm for females and males, respectively; in May, windowpane were somewhat more abundant and larger with mean lengths of 285 and 247 mm for females and males, respectively.

Split spawning of windowpane has been reported previously in the Middle Atlantic region. In 1952 and 1953, Wheatland (1956) found eggs from May through early July and again from late September through November in Long Island Sound, New York. Temperatures in the Sound were  $>20^{\circ}\text{C}$  from late July through September when eggs were not present. Smith et al. (1975) proposed two patterns of spawning for windowpane depending on latitude. First, off New Jersey and New York one prolonged spawning season was hypothesized based on the occurrence of 2–6 mm larvae on the inner shelf from June through December 1966. Bottom temperatures on the inner shelf that year ranged between 6 and  $17^{\circ}\text{C}$  during August (Clark et al. 1969). Second, off Virginia and North Carolina spawning was interrupted as indicated by the occur-



**Figure 13**

Annual cycle of gonad-somatic indices for windowpane *Scophthalmus aquosus*, collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

rence of larvae in April through June and again in November and December 1966. During summer 1966 bottom temperatures ranged between 15 and  $25^{\circ}\text{C}$  (Clark et al. 1969). Smith et al. (1975) therefore concluded that in waters  $>20^{\circ}\text{C}$  windowpane stop spawning.

Windowpane were collected during the May GSI peak at  $5.6\text{--}13.2^{\circ}\text{C}$  and 4–51 m; while during the September peak they were collected at higher temperatures but at similar depths (Table 1). In July and August, when GSI decreased noticeably, maximum bottom temperatures were  $20\text{--}22^{\circ}\text{C}$  at nearshore stations. Based on the results of this survey, coupled with the previously cited historical observations, a split spawning season is probably typical for windowpane in the New York Bight with continuous spawning occurring only during unusually cold summers.

### Yellowtail flounder *Limanda ferruginea*

Highest mean GSI occurred from February to April, with ripe females, 212–422 mm, collected in October and November and February through May (Fig. 14). Howell (1983) observed female yellowtail off Rhode Island beginning to mature in September, with the peak GSI in April. Colton et al. (1979) reported spawning in the Middle Atlantic from April through August with peaks in May and June. Smith et al. (1975) found the largest concentrations of larvae off New Jersey in April and May. They also reported larvae in abundance off southern New England in May and June.

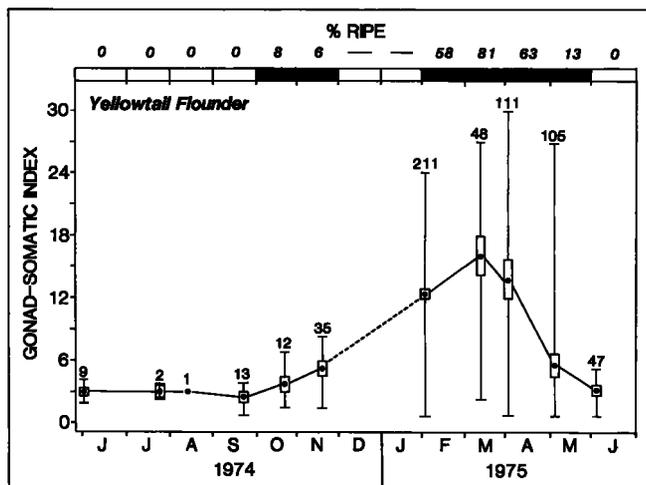


Figure 14

Annual cycle of gonad-somatic indices for yellowtail flounder *Limanda ferruginea* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

Yellowtail flounder commonly occur from Nova Scotia, Canada to Delaware Bay (Bigelow and Schroeder 1953, Leim and Scott 1966). Smith et al. (1975) considered the population center to be on Georges Bank, with migration along the southern New England shelf eastward in spring and westward in fall (Lux 1963). In the New York Bight, few were caught in summer. In March of this survey, the period of greatest gonad development, they were collected on the inner shelf at 9–68 m and 4.4–7.5°C (Table 1).

### Winter flounder

#### *Pseudopleuronectes americanus*

Highest mean GSI occurred during January in the estuarine survey area and during February in the ocean survey area (Fig. 15). Ripe females, 169–432 mm, were collected from September through April with 21% occurring in Raritan Bay. GSI declined rapidly after February; however, spawners were likely upriver beyond the range of this survey. Smith et al. (1975) captured larvae at inshore stations between the offing of Delaware Bay and Block Island Sound, Rhode Island from April through June, with spawning beginning in the south and progressing northward. Perlmutter (1947) reported spawning from December through May and concluded that the peak time varied with temperature. Percy (1962) found evidence of spawning from mid-February through April in the Mystic River estuary, Connecticut. Croker (1965) found winter flounder

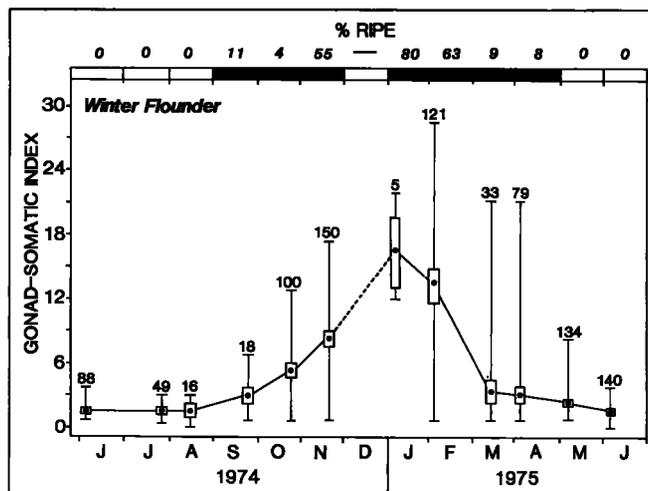


Figure 15

Annual cycle of gonad-somatic indices for winter flounder *Pseudopleuronectes americanus* collected in the New York Bight, June 1974–June 1975, including monthly means, ranges, 95% confidence intervals, and number examined. In addition, percent ripe females per month is given on the upper axis.

larvae in plankton collections in Sandy Hook Bay, New Jersey from April to June.

Although the water temperature at actual spawning sites is unknown, the average bottom temperature in Raritan Bay during January, the month of highest mean GSI, was 5.7°C. Of all the species encountered during this survey, winter flounder were collected in the coldest water.

## Discussion

According to Braum (1978), most temperate zone fishes spawn in one of three generic seasonal patterns: spring, summer, or fall-winter. Based on the current study, alewife and yellowtail flounder are spring spawners; silver and red hake, black sea bass, butterfish, northern and striped searobin, and fourspot flounder are summer to fall spawners, while spotted hake and summer and winter flounder are fall-winter through early spring spawners. Offshore hake and windowpane belong to none of these groups, but appear to have protracted spawning seasons, i.e., these species' GSI were elevated, ovaries were ripe, and eggs and larvae were collected from spring through fall. Offshore hake inhabit the deeper waters of the Bight which are less influenced by changes in light and temperature. In contrast, windowpane inhabit the shallow, more seasonally influenced, inshore environs.

In temperate seas, there are distinct annual cycles of light intensity, temperature, nutrients, and winds

which drive cycles of productivity. An abundant source of food must be available for adult fish to produce stored fat for subsequent gamete production (de Vlaming 1972). Plankton of the right size, density, and quality must be available to pelagic larvae at the critical time of first feeding. As an example, the spawning of yellowtail flounder corresponds to the spring increase in zooplankton off southern New England (Sherman et al. 1984). The maximum concentration of zooplankton in the Middle Atlantic occurs from mid- to late-summer which coincides with the peak concentrations of larval searobins and butterfish as well as numerous other species (Sherman et al. 1984). The fishes that reproduce in the New York Bight during winter have already accumulated fat reserves during the summer and fall. Releasing eggs during winter may give a survival advantage to the larvae since many other fishes, potential competitors and predators, have migrated from the area and there is, therefore, little competition at a crucial time of development.

A short spawning season, represented by a steep GSI curve with a single peak, is a common strategy in temperate marine zones. Black sea bass, butterfish, and the searobins had the shortest spawning seasons, with ripe fish present for only 3–5 months. These four species are abundant during summer in the Middle Atlantic (Wilk and Silverman 1976ab, Wilk et al. 1977, Colvocoresses and Musick 1984), but not on the more boreal Georges Bank (Overholtz and Tyler 1985). They were collected at the highest average temperatures during their reproductive peaks (Table 1). Most of the other species described are abundant in both regions and were collected in colder waters.

Sherman et al. (1984) describe a ubiquitous or protracted spawning strategy for certain species including silver hake and *Urophycis* spp., in which eggs are produced for several months and, although mortality is high, some larvae survive when environmental conditions and food supply are properly matched. In this study, ripe female offshore silver and spotted hake, as well as windowpane, summer, and winter flounder, were collected for 5 or more months. Eggs and small larvae of these species were observed for many more months in other surveys (Clark et al. 1969; Smith et al. 1975, 1980; Colton et al. 1979).

Eggs are typically released from the ovaries of fishes in batches (Bagenal 1978). In species with short reproductive periods, these batches are released in the span of a few days with all individual fish spawning at about the same time. In multiple or serial spawners, batches of eggs mature and are shed several times during a long spawning season (Bagenal 1978, Burt et al. 1988). Examples of protracted spawners are silver hake which produce as many as three batches of eggs per spawning season (Fahay 1974) and summer flounder which

produce up to six batches (Morse 1981). Summer flounder had the lowest mean GSI of any species collected during this survey, apparently because their eggs develop in batches and are released over an extended period. In contrast, the highest mean GSI noted were for yellowtail and winter flounder which produce only one batch of eggs per season (Howell 1983, Burton and Idler 1984). In both species, GSI increased gradually in fall through winter as eggs matured, with highest GSI levels being reached just prior to spring spawning. Similarly, Burton and Idler (1984) reported that GSI of winter flounder in Canadian waters gradually rose during the 8 months before spawning takes place in June.

A high GSI does not always parallel a high level of fecundity (Bagenal 1978). As an example, larger summer, yellowtail, and winter flounder have exhibited fecundities of over 1 million (Bigelow and Schroeder 1953, Morse 1981, Lux and Livingstone 1982); egg production in each of these species is accomplished, however, on different timetables.

Spotted hake and windowpane, both protracted spawners, had bimodal GSI curves. Various sizes of developing and ripe female spotted hake were collected in fall, while a few large ripe females were collected in spring. These findings may reflect behavioral differences among size or age classes, or perhaps the migratory habits of discrete unit stocks. Windowpane exhibited two GSI peaks in the New York Bight during 1974–75; however, continuous larval production throughout the summer was noted in an earlier survey of the area (Smith et al. 1975). Windowpane are permanent residents in the Bight; that is, no evidence of seasonal migration was found during this survey based on observed changes in abundance, size structure, or distribution of collections. Rather than a result of emigration, the bimodal GSI curve exhibited by windowpane may very well be a result of a reproductive tactic in which spawning is curtailed during the year if temperature rises above a preferred level.

Some of the most important and prolific commercial fisheries taking place in temperate seas around the world are based on families of fishes, such as gadids (codfishes and hakes) and pleuronectids (flounders), that are typically very fecund and produce relatively small pelagic eggs (Garrod and Horwood 1984). Of the species described in this study, the pleuronectids, yellowtail and winter flounder, and the bothid, summer flounder, have been reported to have extremely high fecundities. Such species are well-suited for commercial exploitation since they can recover rapidly from natural or man-induced depletion. The gadids described in this study are all small-bodied, mature early at a relatively small size, and produce many tiny pelagic eggs over a protracted spawning period; however, they

are not as fecund as larger and more robust gadid species such as Atlantic cod *Gadus morhua* (Hislop 1984).

A variety of reproductive strategies and tactics are used by the species to adapt to seasonal shifts in environmental parameters in the Middle Atlantic in general and the New York Bight specifically. In this way the entire region is continually used for reproduction by a wide range of economically and ecologically important species of resident and migratory finfish. These spawning adaptations contribute to the high diversity and abundance of finfish found in the Middle Atlantic region.

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## Citations

- Bagenal, T.B.**  
1978 Aspects of fish fecundity. In Gerking, S.D. (ed.), Ecology of freshwater fish production, p. 75-101. John Wiley and Sons, NY.
- Barans, C.A.**  
1969 Distribution, growth and behavior of the spotted hake in the Chesapeake Bight. M.S. thesis, College of William and Mary, Williamsburg, 53 p.
- Bigelow, H.B., and W.C. Schroeder**  
1953 Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.  
1955 Occurrence off the Middle and North Atlantic United States of the offshore hake, *Merluccius albidus* (Mitchell) 1818, and of the blue whiting *Gadus (Micromesistius) poutassou* (Risso) 1826. Bull. Mus. Comp. Zool., Harv. Univ. 113: 205-226.
- Braum, E.**  
1978 Ecological aspects of the survival of fish eggs, embryos and larvae. In Gerking, S.D. (ed.), Ecology of freshwater fish production, p. 102-131. John Wiley and Sons, NY.
- Burt, A., D.L. Kramer, K. Nakatsuru, and C. Spry**  
1988 The tempo of reproduction in *Hyphessobrycon pulchripinnis* (Characidae), with a discussion on the biology of 'multiple spawning' in fishes. Environ. Biol. Fish. 22:15-27.
- Burton, M.P., and D.R. Idler**  
1984 The reproductive cycle in winter flounder, *Pseudopleuronectes americanus* (Walbaum). Can. J. Zool. 62:2563-2567.
- Bye, V.J.**  
1984 The role of environmental factors in the timing of reproductive cycles. In Potts, G.W., and R.J. Wootton (eds.), Fish reproduction: Strategies and tactics, p. 187-205. Academic Press, London.
- Clark, J.W., W.G. Smith, A.W. Kendall Jr., and M.P. Fahay**  
1969 Studies of estuarine dependence on Atlantic coastal fishes. Data report I: Northern section, Cape Cod to Cape Lookout. R/V *Dolphin* cruises 1965-66: zooplankton volumes, mid-winter trawl collections, temperatures and salinities. U.S. Dep. Int., Bur. Sport Fish. Wildl. Tech. Pap. 28, 132 p.
- Colton, J.B. Jr., W.G. Smith, A.W. Kendall Jr., P.L. Berrien, and M.P. Fahay**  
1979 Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull., U.S. 76:911-915.
- Colvocoresses, J.A., and J.A. Musick**  
1984 Species associations and community composition of Middle Atlantic Bight continental shelf demersal fishes. Fish. Bull., U.S. 82:295-313.
- Croker, R.A.**  
1965 Planktonic fish eggs and larvae of Sandy Hook estuary. Chesapeake Sci. 6:92-95.
- Cushing, D.H.**  
1969 The regularity of the spawning season of some fishes. J. Cons. Int. Explor. Mer 33:81-92.
- de Vlaming, V.L.**  
1972 Environmental control of teleost reproductive cycles: A brief review. J. Fish. Biol. 4:131-140.
- de Vlaming, V.L., G. Grossman, and F. Chapman**  
1982 On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31-39.
- Fahay, M.P.**  
1974 Occurrence of silver hake, *Merluccius bilinearis*, eggs and larvae along the Middle Atlantic continental shelf during 1966. Fish. Bull., U.S. 72:813-834.
- Garrod, D.J., and J.W. Horwood**  
1984 Reproductive strategies and the response to exploitation. In Potts, G.W., and R.J. Wootton (eds.), Fish reproduction: Strategies and tactics, p. 367-384. Academic Press, London.
- Gross, M.G. (editor)**  
1976 Middle Atlantic continental shelf and the New York Bight, special symposia, vol. 2. Am. Soc. Limnol. Oceanogr., Lawrence, KS, 441 p.
- Grosslein, M.D.**  
1969 Groundfish survey program of BCF, Woods Hole. Commer. Fish. Rev. 31:22-30.
- Grosslein, M.D., and T.R. Azarovitz (editors)**  
1982 Fish distribution. MESA Atlas Monogr. 15, NY Sea Grant Inst., Albany, 182 p.
- Gutherz, E.J.**  
1967 Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Dep. Int., Fish Wildl. Serv., Circ. 263, 47 p.
- Herman, S.S.**  
1963 Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103-109.
- Hildebrand, S.F., and W.C. Schroeder**  
1928 Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, 388 p.
- Hislop, J.R.G.**  
1984 A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the North Sea. In Potts, G.W., and R.J. Wootton (eds.), Fish reproduction: Strategies and tactics, p. 311-329. Academic Press, London.

- Hoar, W.S.**  
1969 Reproduction. In Hoar, W.S., and D.J. Randall (eds.), Fish physiology, vol. 3, p. 1-72. Academic Press, NY.
- Howell, W.H.**  
1983 Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferruginea*. Fish. Bull., U.S. 81:341-355.
- Kawahara, S.**  
1978 Age and growth of butterfish, *Peprilus triacanthus* (Peck), in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Sel. Pap. 3:73-78.
- Kendall, A.W. Jr.**  
1977 Biological and fisheries data on black sea bass, *Centropristis striata* (Linnaeus). Tech. Ser. Rep. 7, Sandy Hook Lab., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., Highlands, NJ 07732, 29 p.
- Kendall, A.W., and L.P. Mercer**  
1982 Black sea bass, *Centropristis striata*. In Grosslein, M.D., and T.R. Azarovitz (eds.), Fish distribution. MESA Atlas Monogr. 15, p. 82-83. NY Sea Grant Inst., Albany.
- Kissil, G.W.**  
1969 Contributions to the life history of the alewife, *Alosa pseudoharengus* (Wilson), in Connecticut. Ph.D. thesis, Univ. Connecticut, Storrs, 111 p.
- Leim, A.H., and W.B. Scott**  
1966 Fishes of the Atlantic coast of Canada. Fish. Res. Board Can., Bull. 155, 485 p.
- Lux F.E.**  
1963 Identification of New England yellowtail flounder groups. Fish. Bull., U.S. 63:1-10.
- Lux, F.E., and R. Livingstone Jr.**  
1982 Yellowtail flounder, *Limanda ferruginea*. In Grosslein, M.D., and T.R. Azarovitz (eds.), Fish distribution. MESA Atlas Monogr. 15, p. 117-119. NY Sea Grant Inst., Albany.
- Marak, R.R.**  
1967 Eggs and early larval stages of the offshore hake, *Merluccius albidus*. Trans. Am. Fish. Soc. 96:227-228.
- Mayer, G.F.**  
1982 Ecological stress and the New York Bight: Science and management. Estuarine Res. Fed., Columbia, SC, 715 p.
- Morse, W.W.**  
1981 Reproduction of the summer flounder, *Paralichthys dentatus* (L.). J. Fish Biol. 19:189-203.
- Musick, J.A.**  
1969 The comparative biology of two American Atlantic hakes, *Urophycis chuss* and *U. tenuis* (Pisces: Gadidae). Ph.D. thesis, Harvard Univ., Cambridge, 150 p.  
1974 Seasonal distribution of sibling hakes, *Urophycis chuss* and *U. tenuis* (Pisces, Gadidae) in New England. Fish. Bull., U.S. 72:481-495.
- Nikolskii, G.V.**  
1963 The ecology of fishes. Academic Press, NY, 352 p.
- Overholtz, W.J., and A.V. Tyler**  
1985 Long-term responses of the demersal fish assemblages of Georges Bank. Fish. Bull., U.S. 83:507-520.
- Pearcy, W.G.**  
1962 Ecology of an estuarine population of winter flounder *Pseudopleuronectes americanus* (Walbaum). Bull. Bingham Oceanogr. Coll. 13:5-78.
- Perlmutter, A.**  
1939 An ecological survey of young fish and eggs identified from tow-net collections. In A biological survey of the salt waters of Long Island, 1938, part 2, p. 11-71. NY State Conserv. Dep., Suppl. 28th Annu. Rep, Albany.  
1947 The blackback flounder and its fishery in New England and New York. Bull. Bingham Oceanogr. Coll. 11:1-92.
- Ralph, D.**  
1982 Fourspot flounder, *Paralichthys oblongus*. In Grosslein, M.D., and T.R. Azarovitz (eds.), Fish distribution. MESA Atlas Monogr. 15, p. 113-114. NY Sea Grant Inst., Albany, NY.
- Richards, S.W., J.M. Mann, and J.A. Walker**  
1979 Comparison of spawning seasons, age, growth rates, and food of two sympatric species of searobins, *Prionotus carolinus* and *Prionotus evolans*, from Long Island Sound. Estuaries 2:255-268.
- Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont**  
1984 Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18:1-19.
- Smith, R.A.**  
1971 The fishes of four low salinity tidal tributaries of the Delaware River estuary. M.S. thesis, Cornell Univ., Ithaca, 304 p.  
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., U.S. 71:527-548.
- Smith, W.G., J.D. Sibunka, and A. Wells**  
1975 Seasonal distributions of larval flatfishes (Pleuronectiformes) on the continental shelf between Cape Cod, Massachusetts and Cape Lookout, North Carolina, 1965-66. NOAA Tech. Rep. NMFS SSRF-691, 68 p.
- Smith, W.G., D.G. McMillan, C. Obenchain, P. Rosenberg, A. Wells, and M. Silverman**  
1980 Spawning cycles of marine fishes of northeastern United States based on broadscale surveys of eggs and larvae, 1977-79. Int. Counc. Explor. Sea ICES CM 1980/L:66, 22 p.
- Wheatland, S.B.**  
1956 Oceanography of Long Island Sound, 1952-1954. VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanogr. Coll. 15:234-314.
- Wilk, S.J., and M.J. Silverman**  
1976a Fish and hydrographic collections made by the research vessels *Dolphin* and *Delaware II* during 1968-72 from New York to Florida. NOAA Tech. Rep. NMFS SSRF-697, 159 p.  
1976b Summer benthic fish fauna of Sandy Hook Bay, New Jersey. NOAA Tech. Rep. NMFS SSRF-698, 16 p.
- Wilk, S.J., W.W. Morse, D.E. Ralph, and T.R. Azarovitz**  
1977 Fishes and associated environmental data collected in the New York Bight, June 1974-June 1975. NOAA Tech. Rep. NMFS SSRF-716, 53 p.
- 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.
- Wootton, R.J.**  
1984 Strategies and tactics in fish reproduction. In Potts, G.W., and R.J. Wootton (eds.), Fish reproduction: Strategies and tactics, p. 1-12. Academic Press, London.