

# Biology and Population Changes of Northern Sand Lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight

Gary A. Nelson and Michael R. Ross  
Department of Forestry and Wildlife Management, University of Massachusetts  
Amherst, MA 01003, USA

## Abstract

Trends in temporal and spatial abundance, and population size structure of the sand lance, *Ammodytes dubius*, were examined based on trawl survey data from 1963 to 1988. Reproduction, age structure and growth were evaluated in 1986-88 from the Gulf of Maine to Middle Atlantic Bight region off eastern USA. Relative abundance indices which were near zero prior to 1976, increased dramatically (5-10 fold) from 1976 to 1981 in all regions studied. Subsequently, abundance dropped from 1982 to 1987.

Gonadal recrudescence of *A. dubius* begins in late July and males appeared to mature earlier in a reproductive season than females. Estimates of fecundity ranged from 1,169 to 22,904 ova per female for sand lance 137 to 213 mm total length. Maximum age estimated from otoliths and vertebrae was 5 years. Age at 50% maturity was age II for all regions in spring. Comparison of Von Bertalanffy growth curves derived for *A. dubius* from the study regions to published values from Newfoundland and Nova Scotia suggests a decline in length and age with declining latitude.

## Introduction

Sand lances (genus *Ammodytes*) are zooplanktivorous, semi-demersal, schooling perciforms that range in the Northwest Atlantic from Greenland to Cape Hatteras, North Carolina, USA (Leim and Scott, 1966). Winters and Dalley (1988) concluded that two species of sand lance, *A. americanus* and *A. dubius*, co-occur within this range. The former species inhabits very shallow bays and estuaries, while the latter is found in deeper, offshore waters (Nizinski *et al.*, 1990).

Sand lances serve as an important link between zooplankton and marine piscivores throughout the Northwest Atlantic. Adults are forage for Atlantic cod (*Gadus morhua*), silver hake (*Merluccius bilinearis*), spiny dogfish (*Squalus acanthias*), bluefish (*Pomatomus saltatrix*), little skates (*Raja erinacea*) and winter skates (*R. ocellata*), pollock (*Pollachius virens*) and other economically-important species (Bigelow and Schroeder, 1953; McEachran *et al.*, 1976; Langton and Bowman, 1980; Bowman and Michaels, 1981; Boreman, 1983; Winters, 1983; Bowman *et al.*, 1984a). Larvae and juveniles are consumed by Atlantic herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and post-smolt Atlantic salmon (*Salmo salar*) (Bowman *et al.*, 1984b; Dutil and Contu, 1988). Humpback (*Megaptera novaeangliae*) and finback (*Balaenoptera physalus*) whales also feed extensively on sand lance (Overholtz and Nicolas, 1979), as do coastal birds such as com-

mon terns (*Sterna hirundo*) (Powers and Brown, 1987).

Humpback whale distribution appears to be correlated with sand lance abundance in the Gulf of Maine (Payne *et al.*, 1986). In 1986, humpback whales and spiny dogfishes changed distribution from their traditional summer feeding grounds on Stellwagen Bank to shelf slopes east of Provincetown, Massachusetts (Mayo *et al.*, 1987; G. Waring, National Marine Fisheries Service, Woods Hole Laboratory, Woods Hole, Massachusetts, pers. comm). This distributional shift was presumably related to declining sand lance abundance on Stellwagen Bank (G. Waring, pers. comm.).

Despite their importance as forage, very little is known about the biology and population dynamics of post-larval sand lance in the Northwest Atlantic. Only localized populations of *A. dubius* on the Scotian Shelf (Scott, 1968; 1973), Grand Bank (Winters, 1981; 1983) and coastal Newfoundland (Winters, 1989), and *A. americanus* along coastal New England (Westin *et al.*, 1979; Richards, 1982) have been studied. No investigation has been directed specifically toward *A. dubius* from the center to southern extent of its range. This study was undertaken to document trends in spatial and temporal abundance and size structure of sand lance populations based on historical trawl survey data, and to evaluate reproduction, age and growth of *A. dubius* in the Gulf of Maine to the Middle Atlantic Bight.

## Materials and Methods

### Historical data

Data used were collected from 1963 to 1988 by the National Marine Fisheries Service (NMFS), Woods Hole, Massachusetts, in a synoptic bottom trawl survey to analyze trends in historical abundance and size composition of *A. dubius* populations. The survey was based on a stratified-random sampling design for continental shelf water >27 m in depth, partitioned into strata of unequal area based on depth and geographic location (Fig. 1A; Grosslein, 1969; Azarovitz, 1981). From 1963 to 1967, sampling was conducted in autumn, and intermittently in winter and summer. A spring survey was added to the annual schedule in 1968. Sam-

pling effort was expanded in 1972 to include the nearshore waters between 5 m and 27 m depth. Sampling generally occurred in the following months: winter — January to February, spring — March to May, summer — June to August, and autumn — September to November.

Sampling stations were randomly selected within each stratum and allocated among strata in rough proportion to stratum area. At each station, a standard #36 or #41 Yankee otter trawl with a 1.25 cm stretched mesh codend liner was towed at approximately 3.5 knots for 30 min; depth and bottom temperature measurements data were also taken (Azarovitz, 1981). Fish captured in the otter trawl were brought onboard, sorted to species, counted, weighed collectively to the nearest 0.1 kg and measured individually to the nearest cm.

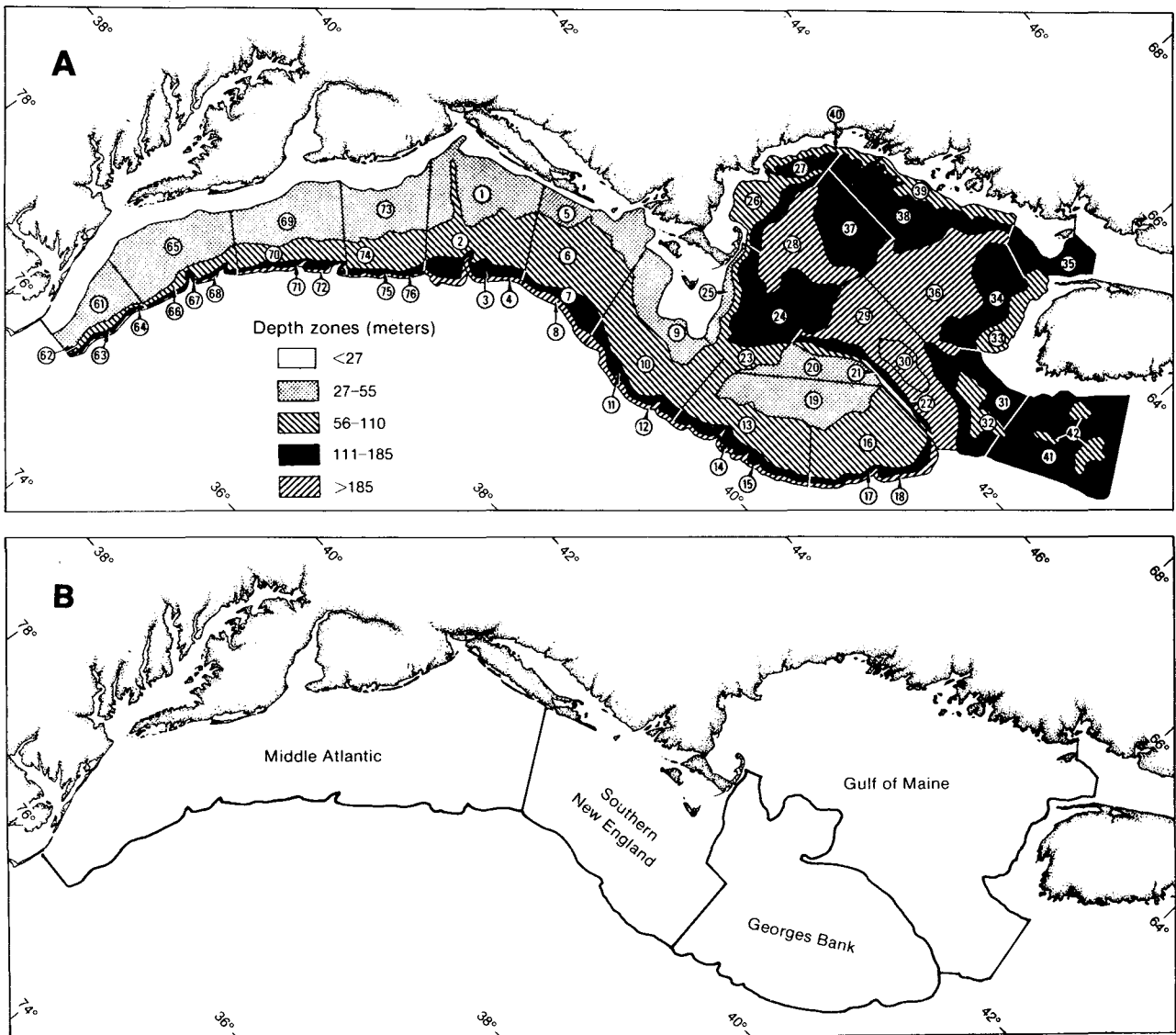


Fig. 1. (A) Northwest Atlantic area from Nova Scotia to Cape Hatteras, North Carolina delineated into strata by depth and (B) subdivided into regions for analytical purposes. The inshore strata (<27 m) are not individually labeled.

In this study, the continental shelf extending from Nova Scotia to Cape Hatteras was subdivided into the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions based on topographic and bathymetric characteristics (Fig. 1B).

**Abundance.** Relative abundance indices, computed as the stratified mean number per standardized tow (Fogarty, 1985), were calculated separately for the inshore (5–27 m depth) and offshore (>27 m depth) areas of each region by year and by season. Sand lance catch data (numbers) were transformed using  $\ln(X+1)$  prior to calculation, to stabilize the variance and reduce the influence of sampling variability between tows (Sokal and Rohlf, 1981; Fogarty 1985). To examine abundance of *A. dubius* in relation to depth, offshore strata of each region were grouped into depth zones of 27–55 m (D1), 56–110 (D2), 111–183 (D3), and 186–366 m (D4) (Fig. 1A). Abundance indices were then calculated for the inshore (IN) and four offshore depth zones of each region. Differences in the seasonal distribution of stratified means between depth zones from spring 1972 to spring 1988 were tested by Kruskal-Wallis ANOVA procedures applied to the stratified means using BMDP3S (BMDP, 1981). When catches between depth zones were found significantly different at  $P \leq 0.05$ , a Z test for Multiple Comparisons of Mean Ranks (Gibbons, 1976) was used to indicate the direction of significance between successive depth zones. Data for D1 (27–55 m) were not available for the Gulf of Maine. Likewise, there was no inshore depth strata set for Georges Bank.

**Size structure.** Initial analyses indicated changes in the size structure of sand lance had occurred over time. Least squares regression and Spearman's coefficient of rank correlation test (Sokal and Rohlf, 1981) were used to analyze the time series of sand lance length data of each region for spring and autumn.

## Biology

Sand lance for ageing and maturity analyses ( $n = 4,868$ ) were frozen whole at sea during NMFS survey cruises from spring 1986 to spring 1988. Spring samples in 1986 were collected from the Georges Bank and Middle Atlantic regions only. Specimens were obtained from all regions in spring of 1987 and 1988. Summer collections of sand lance were made during a 1987 NMFS juvenile groundfish cruise on Georges Bank only. Autumn samples were taken in 1986 and 1987 from Georges Bank and in 1987 from the Middle Atlantic. Supplemental inshore collections ( $n = 311$ ) from inshore strata of the Gulf of Maine and Southern New England regions in spring of 1987 and 1988 were supplied by the Massachusetts Division of Marine Fisheries. In subsequent analyses, all data from 1986 to 1988 were combined by season to investigate overall trends rather than year-to-year variability.

**Length-weight relations.** Total length ( $TL \pm 1$  mm), except when caudal fin lobes were damaged, was measured on all individuals in 1986 to 1988. Fork length ( $FL \pm 1$  mm) and total weight ( $TW \pm 0.001$  g, measured after each individual was blotted dry) measurements were collected from all specimens in 1986 and 1987, and from random subsamples of individuals in 1988. Fork length was related to total length by  $FL = -1.227 + 0.982 \cdot TL$  ( $r^2 = 0.999$ ,  $n = 3,344$ ). Total length was used in analyses of length-weight relations, reproduction and growth.

Seasonal regression equations of  $\log_{10}$ -transformed length and weight data were generated by the least squares method. One-way analysis of covariance (Sokal and Rohlf, 1981) using BMDP1V (BMDP, 1981) was used to test for differences between regression slopes and adjusted means by sex, season and region. If ANCOVA results were significant, Tukey's test for Multiple Comparisons (Zar, 1984) was used to detect differences between pairs of regression parameters.

**Age determination.** Sagittal otoliths for ageing studies were collected in 1986 and 1987 from subsampled individuals. Sand lance from each survey stratum were sorted into 5 mm length categories and a number of individuals, proportional to the number within each length interval, were randomly selected from each length interval (Kimura, 1977). Approximately 33–75% of the individuals were subsampled from each survey stratum. In 1988, otoliths were excised only from those individuals randomly selected for fork length and total weight measurements. Sagittae were removed, cleaned of soft tissue material, and stored dry in coin envelopes. Additionally, a 10–15 mm section of vertebrae was extracted from the region between the pectoral fin base and tip from subsampled individuals ( $n = 289$ ) for use in age validation.

Otolith edges were classified as either opaque or hyaline to determine time of opaque zone formation. Otolith length was measured under a binocular microscope at 45x using a calibrated ocular micrometer, and otolith length to fish length relationships were derived using least squares regression. Prior to age determination, otoliths were split transversely across the collum of the sulcus acousticus with a scalpel blade to expose hidden growth rings. One otolith half was then rested upon black velvet to enhance hyaline zones, submerged in a 50% ethanol solution and viewed under a binocular dissecting microscope at 45x using reflected light. Cleaned vertebrae were viewed in the same manner.

Annuli were identified using criteria defined by Reay (1972), Scott (1973) and Jearld (1983). Otolith and vertebral annuli were identified as the widest, most

well-defined hyaline ring, preceded by an opaque zone that passed through the sulcus groove in the otolith section or entirely around the vertebral centrum, respectively. Age determination was repeated three times on all otoliths and vertebrae. If two of the three age readings were in agreement, the value was accepted. If age varied between all readings, the structure was not included in the analysis (13% of the otoliths examined). *A. dubius* larvae hatch between December and February (Potter and Lough, 1987), thus a 1 January birthdate was assumed for all sand lance.

**Sex ratios, maturity and fecundity.** Gonads were excised from individuals selected for age-structure subsampling, identified microscopically as ovaries or testes, blotted dry on a paper towel, weighted to the nearest 0.001 g and further classified macroscopically into the following maturity stages: Stage 0 — immature, Stage I — resting, Stage II — developing, Stage III — ripe, Stage IV — spent and Stage V — recovering. Stages II through V follow Macer (1966), where 0 and I were identified by the following criteria:

#### Female

**Stage 0.** Gonad is small in relation to body cavity. The *tunica albuginea* is transparent and colorless. Under microscopic examination, oogonia are visible but they do not fill the lumen of the gonad.

**Stage I.** *Tunica* is thick, almost opaque; color is pink to pale. Occasionally the lumen is filled with visible oocytes; mostly filled with jelly-like material.

#### Male

**Stage 0.** Gonad is small in relation to body cavity, almost threadlike. *Tunica* is transparent and colorless. The separation between testicular lobes on the ventral side is prominent; the inner edges of the lobes are rounded, not angled. Outer edges of the lobes are tapered slightly.

**Stage I.** *Tunica* is thick, almost opaque; color is gray to off-white. Separation between lobes not prominent. Inner edges of testicular lobes viewed from the ventral side are angled. Outer lobe edges are tapered sharply.

Chi-square analyses were used to test for regional deviations from a hypothetical 50:50 sex ratio in all seasons. Length and age at 50% maturity were estimated using probit analysis (Finney, 1971). Seasonality of reproduction was determined from monthly gonadosomatic indices (GSI), calculated as:

$$\text{GSI} = \text{Gonad weight} / (\text{Total weight} - \text{Gonad weight}) * 100$$

To estimate fecundity, ovaries classified as Stage II were excised from females collected on Georges Bank in October of 1986 and 1987. Each ovary was placed in a 15 ml vial. Boiling water was added until the entire gonad was covered and, after the vials cooled, they were agitated vigorously. This method disintegrated the thin *tunica albuginea* and left oocytes floating freely in the solution. Vial contents were preserved in modified form-alcohol (Nelson, 1990). The solutions were examined before and after agitation and no evidence of ova degradation was found. However, shrinkage of the chorion of some ova was evident in some samples, but this occurred in only a small fraction (<5%) of ova. Boiling water, therefore, appeared to have minimal effect on ova dimensions.

The diameter of 50–150 randomly chosen ova were measured from each female, and an oocyte diameter of 0.15 mm was selected as the lower limit of the mature ova size distribution. Each sample was washed gently through an appropriately-sized sieve (0.13 mm) to discard oogonia. Fecundity estimates were made by subsampling with a Folsom splitter (Van Guelphen *et al.*, 1982). Fractions were selected randomly and diluted to 200 ml prior to each splitting. Air was passed into the solution with an aquarium air tube to continuously circulate the eggs and minimize the potential biases associated with clumping and size dependent stratification. The entire sample was split three times (a proportion of 1/8 of the whole), and after the last split, ova from one randomly selected fraction were counted under a binocular dissecting microscope at 7X. Total fecundity was estimated by multiplying this subsample value by 8. Coefficients of variation (CV = standard deviation/mean) were calculated for replicates of each individual sample to obtain an estimate of the subsampling error between trials. The relationships between mean fecundity and total length, total weight and age were estimated using least squares regression.

**Growth analyses.** A von Bertalanffy growth function,

$$L_t = L_\infty * (1 - \exp^{-k * (t - t_0)})$$

was fitted to individual lengths-at-age data using SAS nonlinear regression (NLIN) with the optional derivative-free (DUD) method (SAS Institute, 1988) for all seasons, regions and years combined. Age in years was designated with a decimal extension that represented the month of capture standardized to ten (e.g. 2 years 6 months is equal to 2.5 years).

## Results

### Historical data

**Abundance.** Number-per-tow indices for *A. dubius* fluctuated markedly from autumn 1963 to spring 1988 in all regions (Table 1). In the Gulf of Maine region, both

TABLE 1. Transformed stratified mean number-per-tow (relative abundance indices) and coefficients of variation (CV = sd/mean\*100) for *A. dubius* in the inshore and offshore areas of each region during spring and autumn.

Year	Gulf of Maine				Georges Bank		Southern New England				Middle Atlantic			
	Inshore		Offshore		Offshore		Inshore		Offshore		Inshore		Offshore	
	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
<b>Spring</b>														
1968			0.01	99.6	0.47	26.8			0.05	99.9			0.23	53.4
1969			0.06	70.5	0.18	52.2			0.06	66.6			0.00	0.0
1970			0.00	0.0	0.12	63.1			0.00	0.0			0.39	39.8
1971			0.03	59.5	0.06	66.4			0.00	0.0			0.17	84.2
1972			0.02	50.2	0.04	57.0			0.03	99.8			0.04	99.9
1973			0.02	74.2	0.22	33.3	0.11	97.6	0.16	53.8	0.03	62.9	1.05	19.1
1974			0.00	0.0	0.23	31.8	0.13	28.8	0.14	49.3	0.00	98.0	0.32	41.7
1975			0.00	0.0	0.11	28.7	0.00	0.0	0.06	63.7	0.27	47.4	0.11	42.5
1976			0.03	41.1	1.51	12.0	5.39	16.3	0.57	38.6	1.61	12.8	1.37	18.6
1977			0.05	57.0	0.87	17.7	1.68	30.4	0.50	31.9	0.73	18.3	0.27	37.5
1978			0.00	0.0	0.74	15.4	1.29	24.4	1.29	20.1	2.03	15.3	2.23	14.4
1979	0.73	43.0	0.08	38.9	0.71	18.4	2.57	26.6	0.72	21.3	1.78	13.1	1.60	18.0
1980	1.52	14.7	0.16	52.4	0.94	17.1	3.08	11.6	1.07	16.5	2.19	8.9	1.60	18.0
1981	1.06	70.8	0.18	50.9	1.18	19.4	4.03	5.1	0.67	47.8	2.91	9.2	3.19	14.0
1982	0.10	98.9	0.02	99.7	0.86	20.6	1.97	27.2	0.72	33.5	0.92	12.0	1.33	16.7
1983	1.18	23.4	0.01	99.8	1.12	15.7	1.86	6.5	0.76	33.0	0.79	14.2	0.71	35.9
1984	0.73	49.6	0.03	46.0	0.39	26.4	2.41	16.4	0.41	48.8	0.85	12.2	0.74	31.6
1985	0.93	11.8	0.01	99.8	0.18	39.0	1.36	13.2	0.63	30.1	1.78	15.3	0.57	30.3
1986	0.16	42.7	0.00	0.0	0.51	27.2	0.83	54.0	0.16	61.1	0.81	8.8	0.10	40.5
1987	0.24	42.5	0.03	46.7	0.65	25.0	1.23	14.5	0.52	31.0	0.86	11.0	0.63	21.6
1988	1.52	21.7	0.21	40.4	0.80	17.7	3.62	12.8	0.48	33.2	2.95	9.9	1.45	20.2
<b>Autumn</b>														
1963					0.02	99.8			0.00	0.0			0.00	0.0
1964			0.02	81.0	0.03	74.0			0.00	0.0			0.00	0.0
1965			0.04	83.8	0.04	85.2			0.00	0.0			0.00	0.0
1966			0.00	0.0	0.12	33.9			0.00	0.0			0.00	0.0
1967			0.01	99.9	0.04	60.7			0.00	0.0			0.08	99.8
1968			0.02	71.3	0.16	29.6			0.00	0.0			0.08	54.0
1969			0.02	82.6	0.16	17.8			0.00	0.0			0.00	0.0
1970			0.00	0.0	0.02	99.8			0.00	0.0			0.00	0.0
1971			0.00	0.0	0.00	0.0			0.03	99.7			0.00	0.0
1972			0.02	80.8	0.16	48.2	0.26	51.5	0.00	0.0	0.06	32.7	0.05	99.9
1973			0.00	0.0	0.04	61.3	0.00	0.0	0.00	0.0	0.00	0.0	0.02	99.9
1974			0.00	0.0	0.03	99.8	0.00	0.0	0.00	0.0	0.01	99.4	0.10	70.4
1975			0.04	57.6	0.50	24.4	0.02	92.0	0.03	99.8	0.08	56.4	0.02	99.9
1976			0.00	99.6	0.07	33.2	0.00	0.0	0.00	0.0	0.04	34.4	0.04	60.1
1977			0.00	0.0	0.10	36.2	0.96	14.8	0.12	61.2	0.22	41.2	0.56	38.7
1978			0.01	74.2	0.43	16.9	0.19	75.3	0.08	87.7	0.04	64.0	0.13	84.7
1979	0.00	0.0	0.03	45.5	0.44	12.7	0.60	20.7	0.11	46.7	0.22	14.8	0.34	36.9
1980	0.00	0.0	0.15	52.3	0.55	29.1	0.93	93.9	0.23	99.8	0.04	55.2	0.28	60.0
1981	0.00	0.0	0.03	99.7	0.81	17.7	1.93	10.1	0.24	41.6	0.07	64.8	0.52	25.1
1982	0.00	0.0	0.14	68.3	0.52	26.7	1.71	43.3	0.00	0.0	0.11	36.5	0.37	34.7
1983	0.00	0.0	0.00	0.0	0.04	51.0	0.89	22.7	0.04	70.7	0.19	31.3	0.10	58.3
1984	0.00	0.0	0.03	71.0	0.14	30.6	0.97	40.7	0.02	99.9	0.00	0.0	0.07	73.2
1985	0.51	9.0	0.01	54.4	0.65	20.0	1.13	29.3	0.11	71.6	0.05	49.6	0.04	73.4
1986	0.00	0.0	0.01	99.6	0.57	23.6	0.18	81.1	0.08	99.9	0.06	49.9	0.06	99.9
1987	0.00	0.0	0.00	0.0	0.34	33.9	0.00	0.0	0.00	0.0	0.02	81.8	0.16	80.4

spring and autumn offshore means were near zero until 1979 and then indices increased through 1981 (Fig. 2). Inshore Gulf of Maine indices showed a similar increase in spring but not in autumn. In the Georges Bank region, mean numbers-per-tow were low prior to the mid-1970s in spring and autumn but increased to generally higher levels through the 1980s (Fig. 2). The inshore and offshore areas of the Southern New Eng-

land region and Middle Atlantic region (Fig. 3) exhibited trends similar to the Georges Bank region. A decline in the abundance index occurred in all regions from 1982 through 1985-87. An increase was evident again from 1987 to 1988. Although the summer and winter time series were abbreviated (9 and 7 years, respectively), similar abundance trends were observed for all regions.

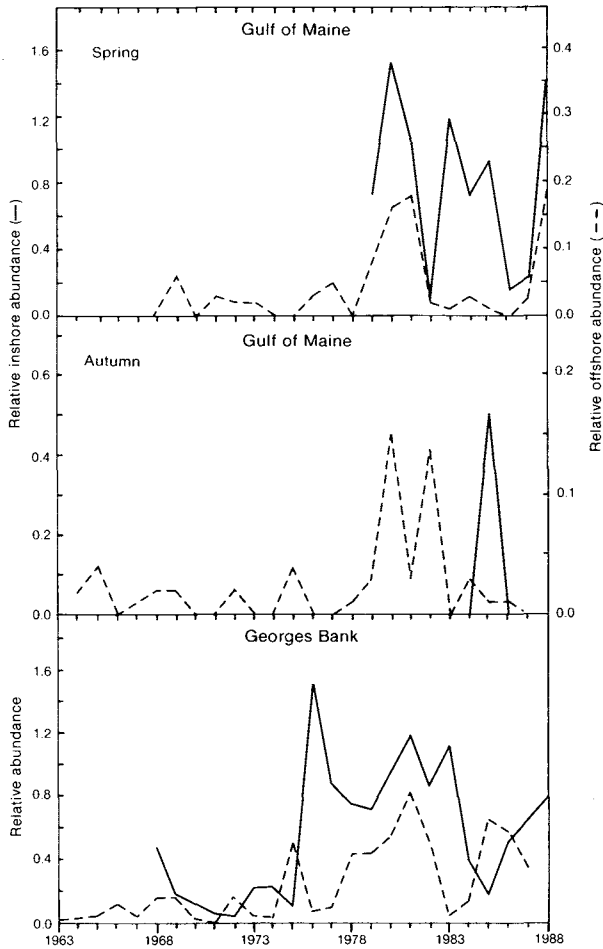


Fig. 2. Indices of relative abundance for *A. dubius* from the inshore and offshore areas of the Gulf of Maine and Georges Bank in spring and autumn.

Sand lance catches were generally highest in the shallowest sampling strata (IN and D1), and declined with depth (Table 2). A possible seasonal offshore movement was indicated in the Middle Atlantic, as abundance shifted from IN in winter and spring to D1 in summer and autumn (Table 2). A similar shift was evident in the Gulf of Maine data, although Kruskal-Wallis results were slightly different in autumn (Table 2).

Sand lance were captured at a wide range of bottom water temperatures ( $0^{\circ}$  to  $24^{\circ}$  C) throughout the year. The fish occurred more frequently at depths with temperatures of  $2^{\circ}$  to  $7^{\circ}$  C during winter ( $\bar{x} = 3.4^{\circ}$  C) and spring ( $\bar{x} = 5.2^{\circ}$  C), and  $7^{\circ}$  to  $15^{\circ}$  C during summer ( $\bar{x} = 11.5^{\circ}$  C) and autumn ( $\bar{x} = 13.2^{\circ}$  C). These results indicate that the shift in depth distribution may be a behavioural response to changing water temperatures, as suggested by Winters (1983).

**Size structure.** Regression analyses indicated a statistically significant decline in the maximum length but not

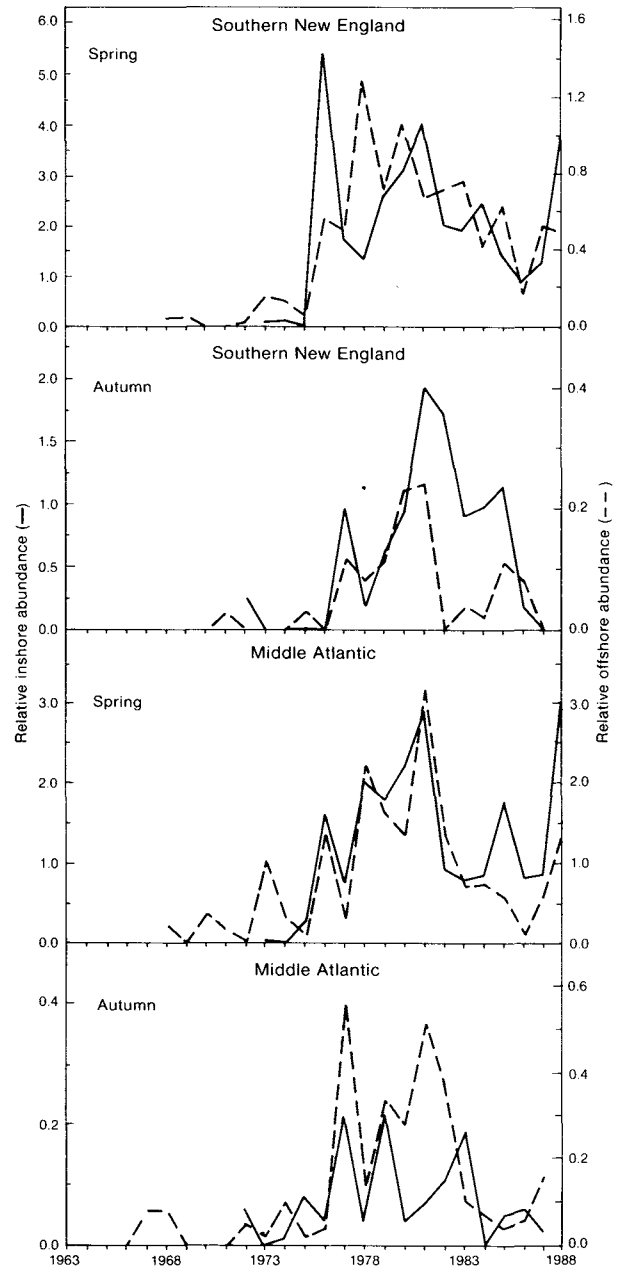


Fig. 3. Indices of relative abundance for *A. dubius* from the inshore and offshore areas of Southern New England and Middle Atlantic Bight in spring and autumn.

in mean length, of *A. dubius* captured from 1963 to 1988 for Gulf of Maine in spring and Georges Bank in both spring and autumn (Fig. 4). No significant relationships were found for Southern New England or Middle Atlantic data (slopes:  $P > 0.25$ ). Similarly, Spearman's coefficient of rank correlation showed the same significant negative relationship between maximum length and calendar years for the Gulf of Maine and Georges Bank in the same seasons, but not for Southern New England or Middle Atlantic ( $P > 0.05$ ).

TABLE 2. Depth zone comparisons of *Ammodytes dubius* transformed stratified means numbers-per-tow from spring 1972 to spring 1988 in the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions by season. If the Kruskal-Wallis ANOVA indicated a significant difference between depth zone means, a Z statistic for Multiple Comparisons of Mean Ranks (Gibbons, 1976) was calculated to show the direction of the difference. Depth zones are: <27 m = (IN), 27-55 m = (D1), 56-110 m = (D2), 111-185 m = (D3), and 186-366 m = (D4).

Kruskal-Wallis ANOVA <sup>a</sup>	
<b>Gulf of Maine</b>	
Winter <sup>b</sup>	IN=D2
Spring	IN>D2>D3>D4
Summer <sup>b</sup>	IN=D2
Autumn	IN<D2>D3
<b>Georges Bank</b>	
Spring	D1>D2>D3>D4
Summer <sup>b</sup>	D1>D2=D3
Autumn	D1>D2>D3
<b>Southern New England</b>	
Winter <sup>b</sup>	IN=D1>D2
Spring	IN=D1>D2>D3
Summer <sup>b</sup>	IN=D1
Autumn	IN=D1>D2
<b>Middle Atlantic</b>	
Winter <sup>b</sup>	IN=D1
Spring	IN=D1>D2>D3
Summer <sup>b</sup>	IN<D1>D2
Autumn	IN<D1>D2>D3

<sup>a</sup> Symbols represent directions of differences as follows: "=" - no significant difference between depth zones; ">" or "<" - preceding depth zone is greater or less than the following one at p<0.05.

<sup>b</sup> Depth zones D2-D4 were not always sampled during the winter and summer cruises.

The decline in maximum length suggests that an event such as a decreasing growth rate or an increasing predation rate upon larger individuals may have occurred over time. The former mechanism would suggest a density-dependent response to increasing population size. If this hypothesis is correct, the maximum length should reflect the abundance level at some past time of the fishes' life. Spearman's coefficient of rank correlation was used to test for the existence of a relationship between relative abundance indices and maximum length at 0-3 year time lags. No significant correlations were found for any region or season (P>0.05). This suggests that the decline in maximum length was probably not the result of an increasing population. Thus, the decrease in size may be associated with higher rates of demersal juvenile and adult mortality.

**Biology**

**Length-weight relations.** No significant differences in length-weight equations were observed between sexes in any season or region, so all data were pooled for the

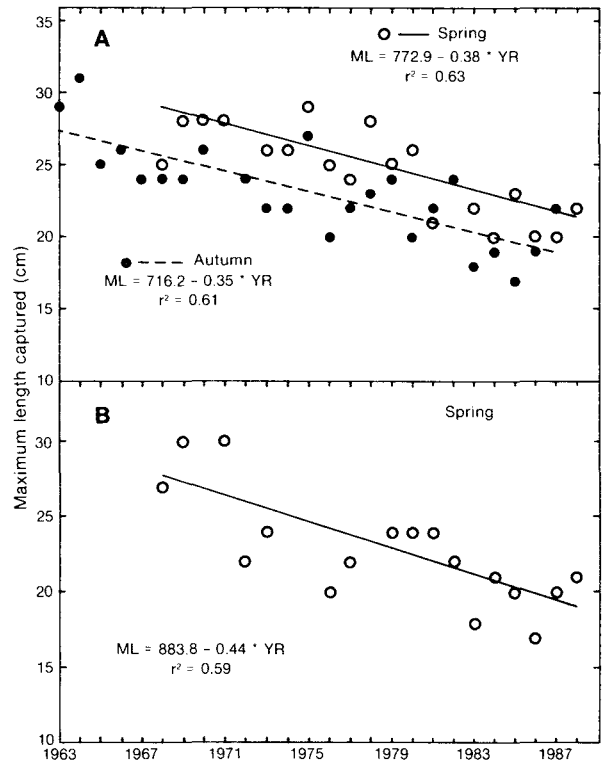


Fig. 4. Regressions of maximum length (ML) of *A. dubius* captured in the NMFS otter trawl vs calendar year for (A) Georges Bank in spring (n=20) and autumn (n=24) and (B) Gulf of Maine in spring (n=17).

subsequent analyses. Seasonal length-weight regression equations for combined sexes are listed in Table 3. Regression slopes were significantly different between all seasons for Georges Bank (P<0.001; Table 4). The regression slope was the highest in summer, which indicates that sand lance gain more weight per unit increase in length during this season than in spring and autumn. Prespawning sand lance from Georges Bank in autumn were heavier than those in spring. Weight loss of 1.5% at 140 mm TL to 16.5% at 220 mm TL occurred during spawning. In the Middle Atlantic region, the autumn regression was not significantly different to spring, probably due to the absence of sand lance >120 mm in those samples. Multiple comparisons revealed regression slopes were significantly different between all regions in spring (P<0.05) except for the Gulf of Maine - Southern New England comparison; adjusted means in this case were significantly different from each other (Table 4).

**Age determination.** Examination of monthly percentages of otoliths with opaque edges showed that an opaque ring is formed only once a year in *A. dubius*. Deposition of opaque material began as early as March (5.8% of those otoliths examined) in the Middle Atlantic and as late as May in the Gulf of Maine (Table 5). On Georges Bank, deposition peaked in June at 31% and it

TABLE 3. Seasonal regression statistics of total weight (TW in g) vs total length (TL in mm) for the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions. The regressions take the form:  $\log_{10}(\text{TW}) = \log_{10} a + b \cdot \log_{10}(\text{TL})$ . All slopes and intercepts were significantly different ( $P < 0.05$ ) from zero.

	Estimate	Standard error	No.	r <sup>2</sup>
<b>Gulf of Maine</b>				
Spring				
a	-4.988	0.137		
b	2.722	0.062	154	0.926
<b>Georges Bank</b>				
Spring				
a	-5.452	0.105		
b	2.929	0.048	693	0.845
Summer				
a	-6.444	0.015		
b	3.390	0.015	394	0.992
Autumn				
a	-6.157	0.066		
b	3.261	0.030	377	0.968
<b>Southern New England</b>				
Spring				
a	-4.891	0.086		
b	2.664	0.040	479	0.904
<b>Middle Atlantic</b>				
Spring				
a	-6.228	0.045		
b	3.301	0.021	983	0.962
Autumn				
a	-6.607	0.140		
b	3.502	0.070	145	0.946

was completed, or nearly so, by September in the Middle Atlantic and October on Georges Bank. From these results, a south to north trend in timing of opaque material deposition was evident.

A single regression equation adequately characterized the otolith length (OT) to fish length (TL) relationships for sand lance >62 mm, all seasons combined:

$$\log_{10}(\text{OT}) = -1.471 + 0.846 \cdot \log_{10}(\text{TL});$$

$$r^2 = 0.901,$$

$$n = 2130.$$

Age determination was based on a total of 1,840 sand lance (54–226 mm TL). Seasonal age composition of sand lance from each region was derived through application of the appropriate age-length keys to seasonal length data (Fig. 5–8). Ages in spring ranged from I–IV years in the Gulf of Maine, on Georges Bank and in Southern New England, and from 0–V years in the Middle Atlantic (Fig. 5–8). Ages  $\geq$ III in the Gulf of Maine and Georges Bank and age  $\geq$ II in Southern New England and Middle Atlantic appeared fully represented in the catches during spring. Very few fishes of ages IV and V were captured in any region. In summer, age 0 sand lance were recruited into the otter trawl on Georges Bank and, by July, this age class comprised the highest proportion of the catches (Fig. 6). Age I+ and older constituted the majority of the autumn samples on Georges Bank, but only ages 0+ and I+ were captured in the Middle Atlantic.

TABLE 4. Tukey's test results for the (A) intra- and (B) interregional multiple comparisons of the  $\log_{10}$  weight- $\log_{10}$  length equations.  $q$  = Tukey's test statistics; degrees of freedom are in brackets. The null hypothesis ( $H_0$ ) tested was slopes (b) of the regression lines were equal. If  $H_0$  was not rejected, adjusted means were tested for equality. (ns = not significant.)

<b>A. Intra-regional comparisons</b>			
$H_0: b_1 = b_2$			
	Spring	Summer	Autumn
Georges Bank			
Spring	—	$q[1083] = -13.33^a$	$q[1066] = -8.51^a$
Summer	—	—	$q[767] = 5.23^a$
Middle Atlantic			
Spring	—	—	$q[1124] = -2.57\text{ns}^b$
<b>B. Inter-regional comparisons</b>			
$H_0: b_1 = b_2$			
	Georges Bank	Southern New England	Middle Atlantic
Gulf of Maine	$q[843] = 6.27^a$	$q[629] = -1.57\text{ns}^b$	$q[1133] = -15.28^a$
Georges Bank	—	$q[1168] = 6.03^a$	$q[1672] = -10.02^a$
Southern New England	—	—	$q[1458] = -20.17^a$

<sup>a</sup>  $p < 0.001$

<sup>b</sup> Adjusted means were significantly different at  $p < 0.001$ .



Seventy-one percent of the 259 individual vertebrae aged were in accordance with their respective otolith ages. Of those ages in disagreement, 41 vertebrae were aged older than the corresponding otolith, while 34 were younger. No significant bias was directed towards a particular ageing error ( $X^2 = 0.68$ ;  $df = 1$ ).

**Sex ratios, maturity and fecundity.** Sex ratios did not deviate significantly from unity in any season except for those from the Middle Atlantic in spring, which were skewed significantly towards females at 60% ( $X^2 = 26.570$ ,  $P < 0.001$ ,  $n = 560$ ); this trend was not apparent

TABLE 5. Monthly percentages of otoliths with opaque edges and total number of otoliths examined for the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions.

Month	% Opaque	Total No.
<b>Gulf of Maine</b>		
Apr	0.0	87
May	3.5	57
<b>Georges Bank</b>		
Apr	3.2	386
May	10.9	92
Jun	31.7	41
Jul	19.0	179
Sep	0.0	49
Oct	4.4	202
<b>Southern New England</b>		
Mar	0.0	157
Apr	8.1	123
May	17.4	23
<b>Middle Atlantic</b>		
Mar	5.8	292
Apr	14.4	355
Sep	0.0	71

in the same region in autumn. Analyses of the regional sex ratios at size, with length subdivided into 5 mm intervals, revealed significant deviations toward females lengths  $< 132.5$  mm from the Middle Atlantic region in spring (Table 6). Males were the largest individuals sampled in all regions and seasons except on Georges Bank in summer.

Onset of gonadal maturation, indicated by changes in maturity stages, began on Georges Bank in late July when one female was classified as stage II (Table 7). By September, 11% of all individuals were developing. In October, both stage II and stage III individuals comprised 79% of the Georges Bank samples. Forty-nine percent of the September samples from Middle Atlantic were comprised of developing young-of-the-year (YOY) individuals (the smallest individual was 89 mm) which indicated some *A. dubius* mature at the end of their first year of life. Stage IV and V individuals were identified in March to May in all regions. The majority of individuals captured during the spring and summer months were classified as either stage 0 or 1 in all regions.

Seasonality of reproduction was also indicated by monthly changes in the GSIs of all mature (stages I-V) sand lance over time. The mean GSIs for females and males were  $< 0.36\%$  during the spring and summer months in all regions (Table 8); females GSIs were higher than those of males during this period. In autumn, mean GSI for males increased more rapidly than females in the Georges Bank and Middle Atlantic regions, and by October male mean GSI (the highest individual GSI was 18.63%) was significantly different ( $P < 0.05$ ; t-test for means with unequal variances) from the mean GSI for females on Georges Bank (Table 8). This suggests male sand lance mature earlier each year than females. Maximum GSI and peak spawning time

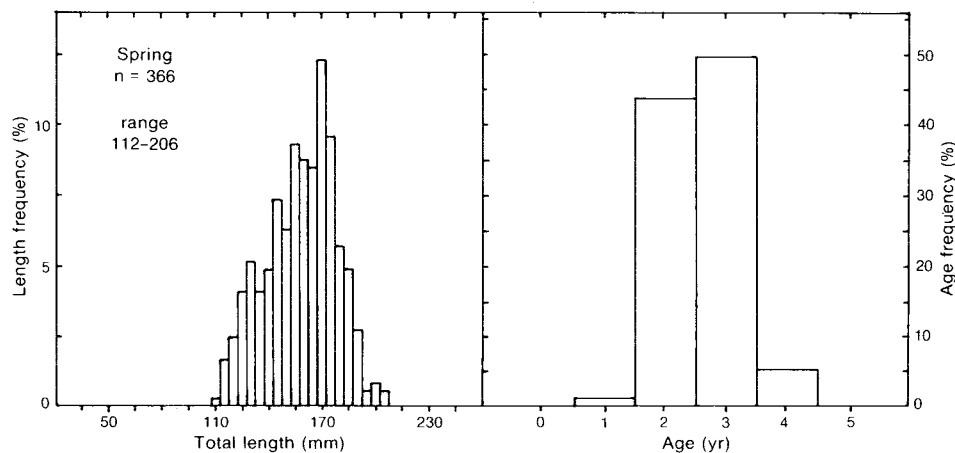


Fig. 5. Length and age frequency distributions of samples of *A. dubius* from the Gulf of Maine region in spring, 1986-88.

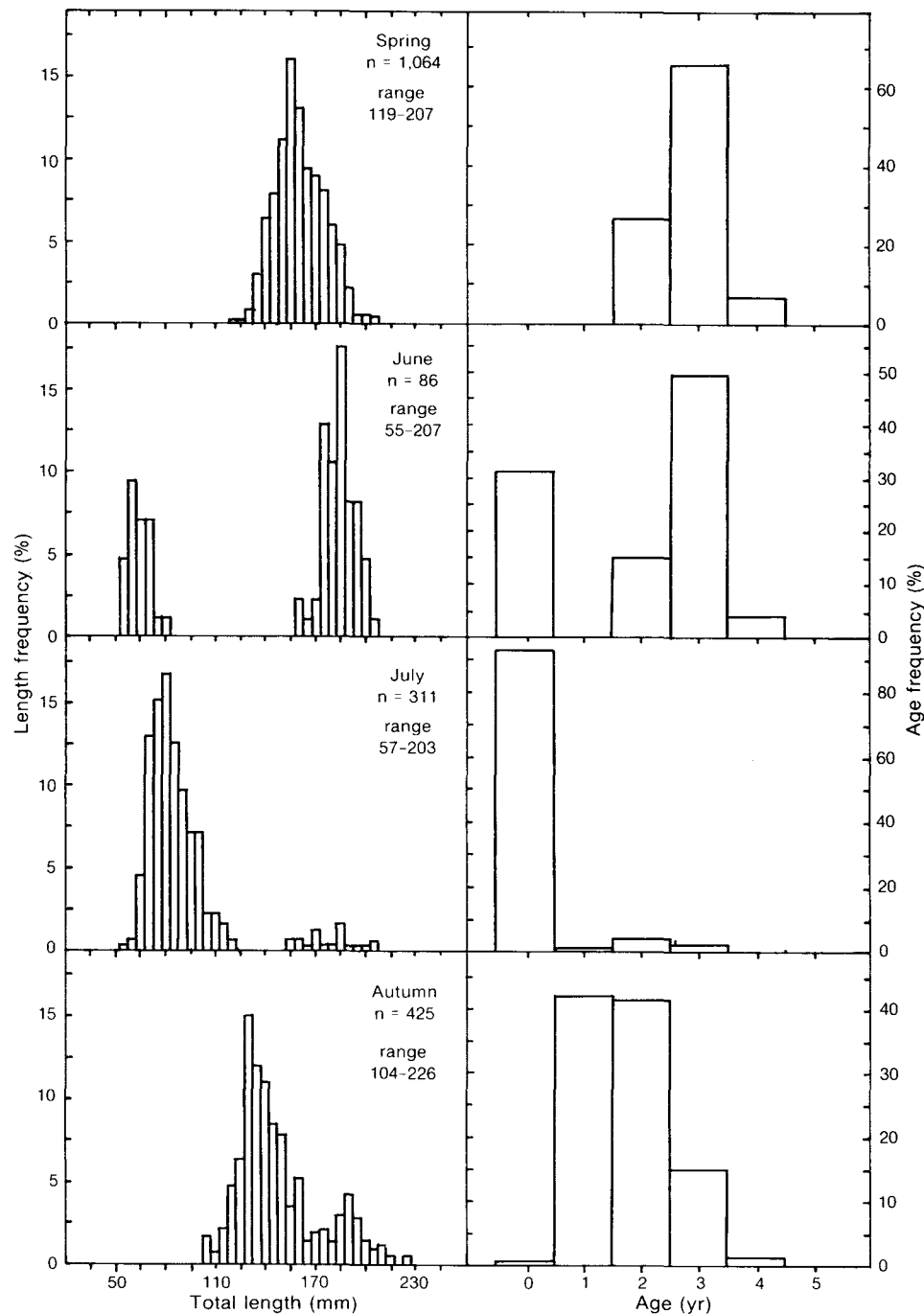


Fig. 6. Length and age frequency distributions of samples of *A. dubius* from Georges Bank in spring, summer (June and July) and autumn, 1986-88.

for sand lance were not determined because samples were not collected further into the reproductive season.

Probit analysis estimates of length at 50% maturity were 150 mm, 154 mm, 144 mm and 147 mm for Georges Bank in spring and autumn, Southern New England and Middle Atlantic in spring, respectively. Age at 50% maturity was 11 years in spring for all regions

and 1+ years in autumn for Georges Bank. As stated by Winters (1989), autumn values are probably most reliable because these samples include first time and repeat spawners, while first time spawners will be classified immature in spring.

Fecundities for 21 individuals were estimated. Coefficients of variation of the replicated fecundity

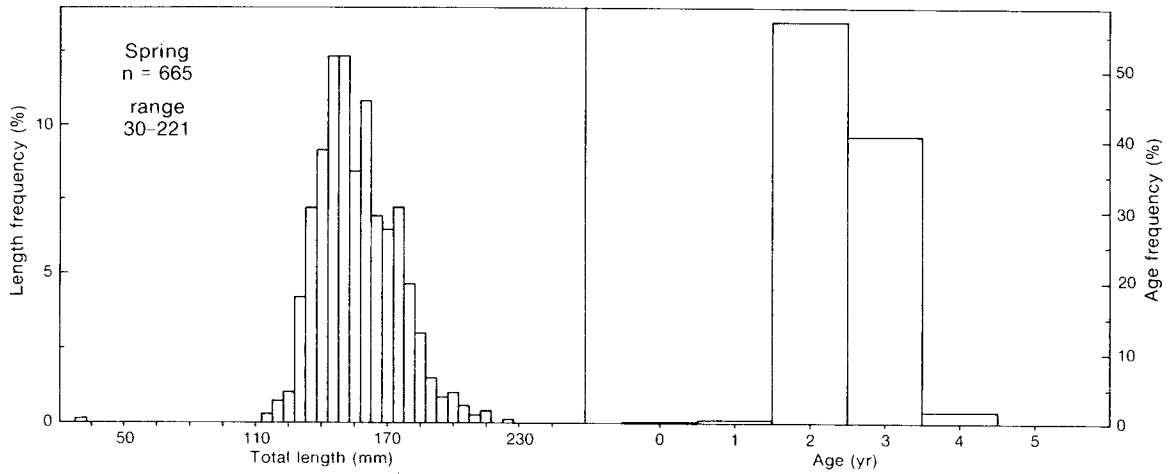


Fig. 7. Length and age frequency distributions of samples of *A. dubius* from the Southern New England region in spring, 1986-88.

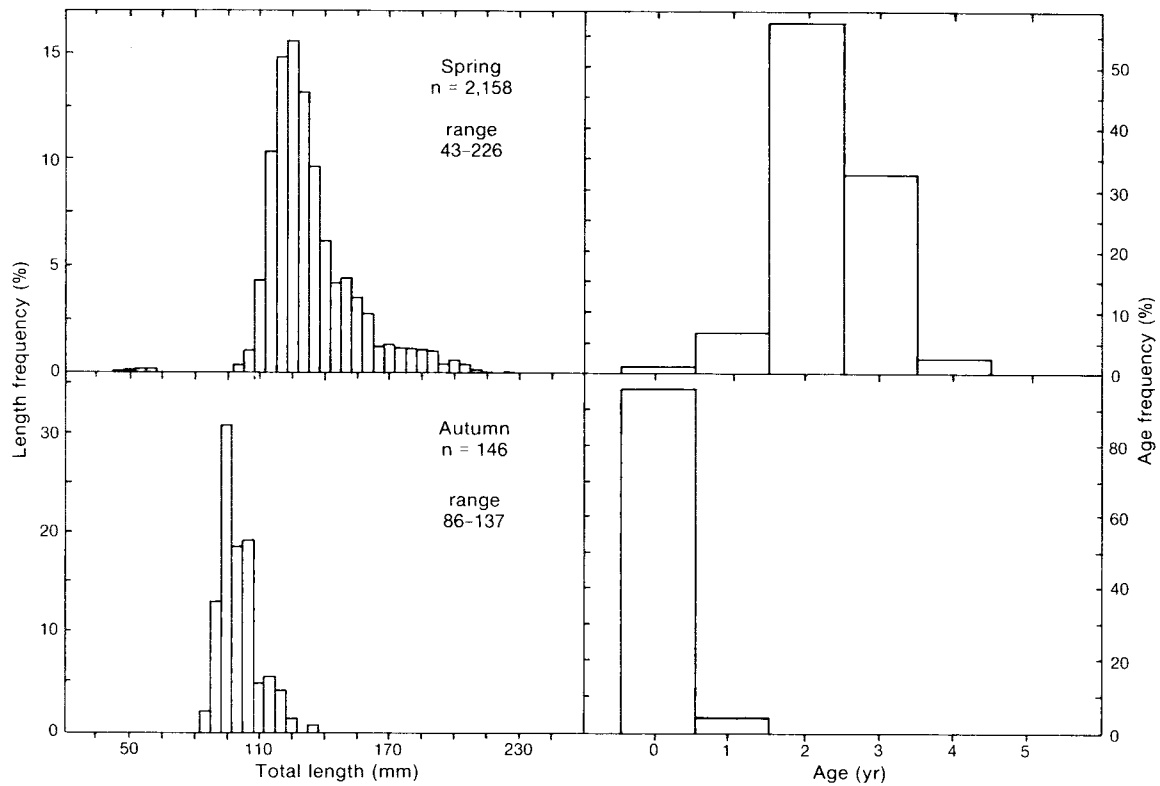


Fig. 8. Length and age frequency distributions of samples of *A. dubius* from the Middle Atlantic region in spring and autumn, 1986-88.

counts were low and ranged from 0.007 to 0.07 with a mean of 0.04. These results indicate that the Folsom splitter was an adequate subsampling device for sand lance eggs. Fecundity estimates ranged from 1,169 to 22,904 ova per female for sand lance 137 to 213 mm TL, 5.07 to 28.82 g TW and ages I-IV+. Least squares regression analyses showed that fecundity (F) was related best to total weight, total length and age (A) as follows:

$$F = -683.651 + 709.632 \cdot TW$$

$$r^2 = 0.816, n = 21$$

$$\log_{10} F = -4.728 + 3.867 \cdot \log_{10} TL$$

$$r^2 = 0.748, n = 21$$

$$F = -6759.560 + 5582.750 \cdot A$$

$$r^2 = 0.724, n = 19$$

TABLE 6. Spring sex ratios (female:male) by length, of *Ammodytes dubius* from the Middle Atlantic. Deviations from unity were tested using  $\chi^2$ .

Length <sup>a</sup> interval (mm)	Ratio
102.5	4:0 ( $p \leq 0.05$ )
107.5	10:4
112.5	23:12
117.5	36:14 ( $p \leq 0.01$ )
122.5	42:30
127.5	45:23 ( $p \leq 0.01$ )
132.5	37:19 ( $p \leq 0.05$ )
137.5	24:16
142.5	30:18
147.5	24:19
152.5	11:14
157.5	21:20
162.5	4:8
167.5	7:1 ( $p \leq 0.05$ )
172.5	8:2
177.5	1:3
182.5	3:3
187.5	3:4
192.5	2:3
197.5	3:1
202.5	2:2
207.5	1:0
212.5	0:1
217.5	0:1
222.5	
227.5	0:1
Total	341:219 ( $p \leq 0.001$ )

<sup>a</sup> Midpoint of length interval (>100 to  $\leq 105$ , etc.).

Number of ova-per-g of non-gonadal body weight did not change as body length increased (slope = 0;  $P > 0.10$ ). Mean ova-per-g was 706.

**Growth analyses.** Seasonal mean lengths- and weights-at-age were similar between years in all regions. Length ranges of each age class were similar to those reported by Scott (1973) for *A. dubius* from the Scotian Shelf, Westin *et al.* (1979) for *A. americanus* and Macer (1966) for *A. marinus*. No significant differences in mean length-at-age between sexes were found; thus, age data for each sex were combined for analyses of growth.

Asymptotic length of Gulf of Maine and Georges Bank sand lance, based on fits to the Von Bertalanffy growth model, were slightly higher than the observed maxima of 206 and 226 mm, respectively, while that of Southern New England was lower than the observed maximum length of 221 mm (Fig. 9). A growth curve for Middle Atlantic fishes is not presented due to high variance around the model parameters.

A logistic growth function (Moreau, 1987) was fitted to monthly mean total length and age (months) values for larval and juvenile (age 0) sand lance listed in

TABLE 7. Percentages of *Ammodytes dubius* classified into maturity stages by month for the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions. Maturity stages were 0=immature, I=resting, II=developing, III=ripe, IV=spent, V=recovering.

Month	Maturity stages					Total No.	
	0	I	II	III	IV		V
<b>Gulf of Maine</b>							
Apr	58.6	27.6				13.8	29
May	25.4	74.5					55
<b>Georges Bank</b>							
Apr	30.0	64.3			0.3	5.3	303
May	27.5	68.1				4.4	91
Jun	17.5	82.5					40
Jul	86.9	12.1	0.9				107
Aug <sup>a</sup>			100.0				10
Sep	40.8	42.8	16.3				49
Oct	15.1	6.0	73.3	5.6			232
<b>Southern New England</b>							
Mar	18.7	60.4			2.8	18.0	144
Apr	40.8	52.5				6.7	120
May	45.4	54.5					22
<b>Middle Atlantic</b>							
Mar	52.9	35.5				11.6	225
Apr	51.4	47.9			0.6		317
Sep	1.3	49.3	49.3				75

<sup>a</sup> An incidental sample of 10 *A. dubius*, ranging in size from 192 to 221 mm, was captured from a sea scallop cruise in August of 1988. Only visual maturity information were obtained from these individuals.

Potter and Lough (1987) for December, February, April, and May, and calculated in this study for June, July, and October (Fig. 10). Standard length measurements given by Potter and Lough (1987) were converted to total length using a conversion factor of 1.09 (Richards, 1982).

## Discussion

### Historical data

**Abundance.** The historical data show abundance of *A. dubius* has fluctuated significantly throughout the Gulf of Maine to Cape Hatteras range. Meyer *et al.* (1979) and Winters (1983) noted increases in abundance on Stellwagen and Newfoundland Banks during the late-1970s and early-1980s, respectively, that were similar to our observations. Smith *et al.* (1978) suggested favourable water circulation and bottom temperatures enhanced survivorship of larval sand lance, allowing the populations to increase during the mid to late-1970s. However, Sherman *et al.* (1981) dismissed environmental conditions as factors regulating sand lance abundance and further demonstrated that the apparent increase in abundance was probably an opportunistic response (competitive release) of sand lance due to the

TABLE 8. Monthly mean ( $\bar{x}$ ) gonadosomatic indices (%)  $\pm$  95% confidence interval (CI) of *Ammodytes dubius* by sex from the Gulf of Maine, Georges Bank, Southern New England and Middle Atlantic regions.

Month		Gulf of Maine		Georges Bank		Southern New England		Middle Atlantic	
		Female	Male	Female	Male	Female	Male	Female	Male
Mar	x	—	—	—	—	0.34%	0.22%	0.32%	0.18%
	95% CI	—	—	—	—	$\pm 0.024$	$\pm 0.022$	$\pm 0.041$	$\pm 0.032$
Apr	x	0.31%	0.17%	0.31%	0.20%	0.27%	0.19%	0.22%	0.15%
	95% CI	$\pm 0.071$	$\pm 0.062$	$\pm 0.017$	$\pm 0.016$	$\pm 0.026$	$\pm 0.022$	$\pm 0.023$	$\pm 0.021$
May	x	0.30%	0.25%	0.32%	0.20%	0.21%	0.12%	—	—
	95% CI	$\pm 0.064$	$\pm 0.060$	$\pm 0.029$	$\pm 0.025$	$\pm 0.095$	$\pm 0.062$	—	—
Jun	x	—	—	0.36%	0.21%	—	—	—	—
	95% CI	—	—	$\pm 0.037$	$\pm 0.039$	—	—	—	—
Jul	x	—	—	0.32%	0.17%	—	—	—	—
	95% CI	—	—	$\pm 0.132$	$\pm 0.040$	—	—	—	—
Sep	x	—	—	0.37%	2.99%	—	—	0.91%	1.37%
	95% CI	—	—	$\pm 0.187$	$\pm 0.414$	—	—	$\pm 0.173$	$\pm 0.641$
Oct	x	—	—	3.04%	6.03%	—	—	—	—
	95% CI	—	—	$\pm 0.489$	$\pm 0.102$	—	—	—	—

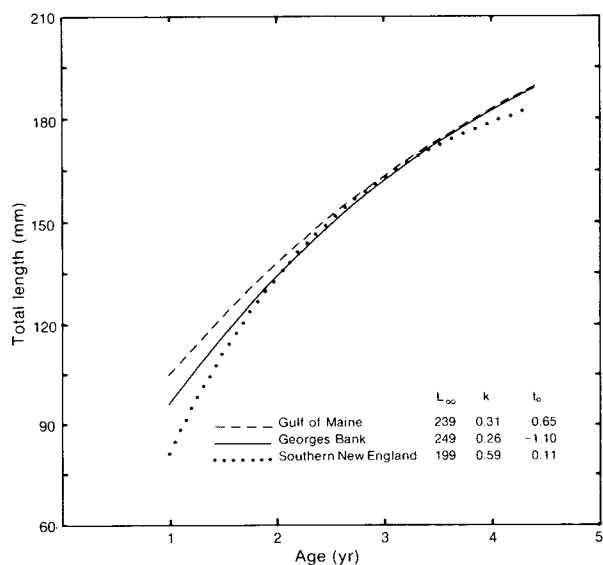


Fig. 9. Von Bertalanffy growth curves for *A. dubius* collected from the Gulf of Maine, Georges Bank and Southern New England regions in spring 1986 to spring 1988.

fishery-induced collapse of Atlantic mackerel and herring stocks in the Northwest Atlantic in the late-1970s.

Bowman *et al.* (1984b) showed that the diet composition of mackerel, herring and sand lance overlap substantially. Additionally, mackerel, and to a lesser extent herring, feed upon sand lance larvae, juveniles and adults. They hypothesized that consumptive competition with, and predation by, mackerel and herring may regulate sand lance abundance. Further, they predicted a decline in sand lance if mackerel biomass recovered. In fact, mackerel biomass increased from an

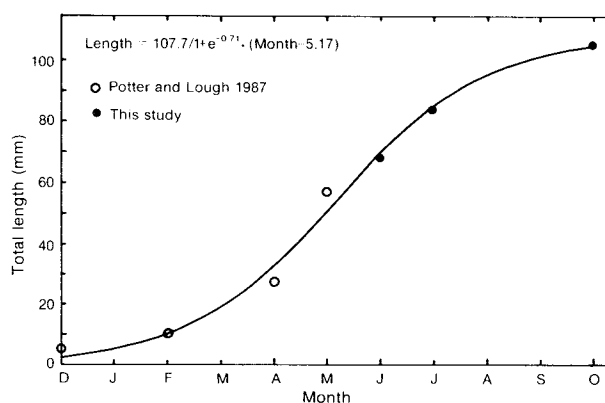


Fig. 10. Age-length relationship of age 0 sand lance from Georges Bank. The curve was fitted using the logistic function.

estimated average of 485,000 tons during 1977–81 to 1.6 million tons in 1987 (NMFS/NEFC, 1988) and, as shown in this study, sand lance abundance declined concurrently from 1982 to 1986–87. The interspecific interactions between mackerel and sand lance seem most important in the regulation of sand lance abundance, since Atlantic herring populations have only recently begun to recover (NMFS/NEFC, 1988).

Our study showed that the abundance of *A. dubius* shifts from coastal to deeper offshore waters during the summer, but it did not return to shallow waters during autumn, as previously noted by Winters (1983) for *A. dubius* on the Grand Banks.

**Size structure.** The maximum length of *A. dubius* captured in the NMFS trawl has decreased over time in the Gulf of Maine and on Georges Bank. We suspect that this decline was indirectly related to the aforemen-

tioned collapse of Atlantic herring. Prior to the mid-1970s, herring were a significant component of many piscivores diets in the Gulf of Maine and Georges Bank. As herring abundance declined, sand lance numbers rose, and adult *A. dubius* became increasingly important as food for many piscivores (Langton and Bowman, 1980; Bowman *et al.*, 1984a). The occurrence of sand lance in the Atlantic cod stomachs, for example, increased from approximately 1% in 1969–72 to 13.9% in 1981–84. Predation mortality upon large adults, thus, appeared to increase as herring became progressively scarce, and this affected the longevity of sand lance.

## Biology

**Length-weight relations.** Seasonal and regional differences in length-weight relationships can be attributed to variations in body growth influenced by fluctuating abiotic and biotic factors, such as temperature and food availability. On Georges Bank, seasonal mean bottom temperatures increase from a range of 5.0–6.6°C in spring to 10.1–11.5°C in autumn. At any given time, offshore mean bottom temperatures are generally highest in the Middle Atlantic followed by Southern New England, Georges Bank, and/or the Gulf of Maine (NMFS trawl survey data from 1970–87). Abundance of copepods, the primary dietary items of sand lance (Meyer *et al.*, 1979), appear more abundant in the Middle Atlantic during early spring than in northern regions (Sherman and Jones, 1980). Therefore, body growth should be greatest in the season or region exhibiting higher temperatures and temporally more abundant food resources. This would explain the heavier weight-at-length of sand lance during summer on Georges Bank and, similarly, in spring for Middle Atlantic fishes.

Length-weight relationships may also be influenced by reproductive maturity cycle. During autumn, gonad weight of both sexes increased and this resulted in a length-weight relationship close to that of summer. Weight differences between pre- and post-spawners demonstrate the effect of maturation on these relationships. Scott (1968) found a 30% difference between 240–250 mm pre- and post-spawners from Emerald Bank, whereas a 16.5% difference was calculated for Georges Bank fishes at 220 mm.

**Age determination.** Deposition of opaque material in the sagittal otoliths of *A. dubius* occurs over a protracted spring to early autumn period on Georges Bank (this study) and the Scotian Shelf (Scott, 1973), but it peaks during the summer. In contrast, Reay (1972) showed that in *A. tobianus*, deposition is a fairly rapid process occurring over a short time period in spring.

Vertebrae of *A. dubius* were used as an alternative, comparative ageing structure for the first time. These

structures were slightly more suitable for age determination than otoliths — only 10% were considered unreadable, compared to 13% for otoliths. However, preparation time was 1–2 minutes longer than otoliths because soft tissue had to be removed from the vertebral centra. If time is not a constraint, we recommend the use of vertebrae as, at least, a secondary ageing structure in age validation. This should be appealing to biologists given the less well-defined growth patterns of scales and problems associated with back-calculation using sand lance otoliths (Scott, 1973; Winters, 1981).

**Sex ratios, maturity and fecundity.** Deviations in sex ratios have been attributed to many factors, including differential growth rates between sexes (Shepherd and Grimes, 1983) and temperature effects (Conover and Kynard, 1981). The former can be ruled out because mean lengths-at-age did not differ between sexes. Temperature on the other hand may influence sex determination in sand lance from the warmer Middle Atlantic waters; however, Conover and Kynard's (1981) data support skewed deviations towards males, not females, at higher temperatures.

Based on our observations on maturity and ova size, *A. dubius* from Georges Bank are once-a-year, mid-autumn to early-winter spawners, as concluded previously for *A. dubius* from Scotian Shelf waters (Scott, 1968, 1972), *A. americanus* (Westin *et al.*, 1979), and *A. marinus* (Macer, 1966). Sexually developing young-of-the-year *A. dubius* were identified from Middle Atlantic samples. Macer (1966) observed some *A. marinus* maturing within their first biological year of life, as did Richards (1982) for *A. americanus* in Southern New England waters. It is unknown whether these individuals will actually spawn, but if they do, contribution to recruitment would be insignificant because of their low potential fecundity (at length 99 mm, backcalculated fecundity is 984 ova per female).

Differences in timing of gonadal development and magnitude of GSI by sex were observed. In females the mean GSIs were always higher than in males in spring and summer. The converse was true in autumn, which suggested that males mature earlier than females in a reproductive season. Annual gonadal maturation has been shown to occur earlier in males for the yellow perch, *Perca fluviatilis*, (le Cren, 1951) and marine dab, *Limanda limanda*, (Htun-Han, 1978). While testes of the males of these species gained weight more rapidly and reached peak development slightly earlier, female ovaries eventually attained a greater weight. We could not conclude this for *A. dubius* because samples were lacking from the peak spawning period.

Fecundity values presented here are the first described for *A. dubius* in the Northwest Atlantic. Compar-

TABLE 9. Comparison of estimated fecundity (ova/female) between *Ammodytes dubius* from Georges Bank (this study), *A. americanus* from coastal New England (Westin *et al.*, 1979) and *A. marinus* (Macer, 1966) from the Outer Dowser Banks.

Total length (mm)	Fecundity		
	<i>A. dubius</i>	<i>A. americanus</i> <sup>a</sup>	<i>A. marinus</i> <sup>b</sup>
120	2,094	4,821	4,054
130	2,848	6,559	5,177
140	3,787	8,723	6,493
150	4,938	11,376	8,016
160	6,239	14,853	9,763
170	7,991	18,416	11,749
180	9,956		13,991
190	12,258		16,504
200	14,932		19,304
210	18,015		22,407
220	21,547		25,829

<sup>a</sup> Only fishes up to 168 mm were used by Westin *et al.* (1979) to generate the fecundity-length relationship.

<sup>b</sup> The length was not specified, so total length was assumed the proper measure.

ison of *A. dubius* fecundity-at-length to predictions for *A. americanus* from coastal New England (Westin *et al.*, 1979) and *A. marinus* on the Dowser Banks (Macer, 1966) showed that female sand lance from Georges Bank produce less ova than females of the other species at the same size (Table 9). Our estimate of relative fecundity (706 ova-per-g) was substantially lower than 973 ova-per-g calculated for *A. americanus* by Morse (1982).

**Growth analyses.** Sand lance examined in this study were younger ( $\leq 5$  years) and smaller in length ( $\leq 226$  mm) than *A. dubius* from coastal Newfoundland, Grand Banks and Nova Scotia; maximum age and length for these regions were 9 years and 280 mm (Winters, 1989), 10 years and approximately 288 mm (maximum size was not listed; Winters, 1983) and 9 years and 372 mm (Scott, 1968; 1973), respectively. Consequently, size at 50% maturity was lower (150 mm vs 170 mm) for Newfoundland fishes. Growth curve comparisons (Fig. 11) show *A. dubius* collected from Georges Bank also grow slower than those fishes from the northern regions, except on Banquereau Bank. These comparisons imply a decrease in maximum size, age, length-at-maturity and growth rate of *A. dubius* with declining latitude, a pattern observed in several temperate marine fishes such as the weakfish, *Cynoscion regalis* (Shepherd and Grimes, 1983). Such clinal variations have been attributed to temperature, energetic costs of reproduction (Leggett and Carscadden, 1978) and variable prey availability (Jones and Johnston, 1977). Although Scott (1973) and Winters (1981) attributed variations in *A. dubius* growth characteristics to areal disparities in temperature, the role of factors such as predation or competition should not be discounted. Such patterns are presumably not produced by a single factor but

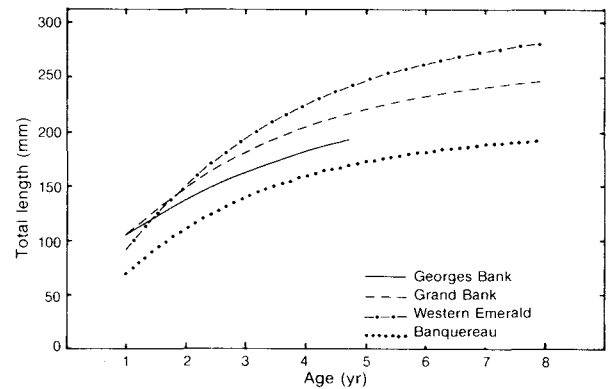


Fig. 11. Comparison of *A. dubius* growth curves derived for Georges Bank (this study), Scotian Shelf banks (Scott, 1973) and Newfoundland Grand Bank (Winters, 1981).

rather by a combination of factors acting synergistically and, given the historical fluctuations in *A. dubius* abundance, the influence of these factors probably changes from year to year.

## Acknowledgements

The authors extend thanks to S. A. Murawski, M. D. Grosslein, and L. A. Deegan for helpful guidance throughout all aspects of this project. J. Boreman reviewed earlier drafts of this paper. M. G. Draft provided encouragement throughout this study. We also thank the staff of the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, Massachusetts, and the Massachusetts Division of Marine Fisheries for assistance in the collection of sand lance specimens. Funding for this project was provided in part by NMFS (Contract No. 43-EANF-732522), and in part through the UMASS/NOAA Cooperative Marine Education and Research Program (NOAA Cooperative Agreement NA89EAN-00015). Portions of this manuscript were taken from a thesis submitted by the first author in partial fulfillment of the requirements for the Master of Science degree at the University of Massachusetts.

## References

- AZAROVITZ, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. In: Bottom trawl surveys. W. G. Doubleday and D. Rivard (eds.). *Can. Spec. Publ. Fish. Aquat. Sci.*, **58**: 62-67.
- BIGELOW, H. B., and W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *Fish. Bull. U.S.*, **53**: 577 p.
- BMDP. 1981. BMDP Biomedical computer programs. W. J. Dixon and M. D. Brown (eds.). University of California Press, 734 p.
- BOREMAN, J. 1983. Status of bluefish along the Atlantic

- coast. *NMFS/NEFC Lab. Ref. Doc.*, No. 28, 66 p.
- BOWMAN, R. E., and W. MICHAELS. 1981. Food habits of seventeen species of northwest Atlantic fish. *NOAA Tech. Memor.* NMFS-F/NEC-28, 183 p.
- BOWMAN, R., R. EPPI, and M. GROSSLEIN. MS 1984a. Diet and consumption of spiny dogfish in the Northwest Atlantic. *ICES C.M. Doc.*, No. G:27, 16 p.
- BOWMAN, R., J. WARZOGHA, and T. MORRIS. MS 1984b. Trophic relationships between Atlantic mackerel and American sand lance. *ICES C.M. Doc.*, No. H:27, 20 p.
- CONOVER, D. O., and B. E. KYNARD. 1981. Environmental sex determination: interaction of temperature and genotype in a fish. *Science*, **213**: 577-579.
- DUTIL, J. D., and J. M. CONTU. 1988. Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence. *Fish. Bull. U.S.*, **86**(2): 197-212.
- FINNEY, D. J. 1971. *Probit Analysis*, 3rd edition, Cambridge University Press, 333 p.
- FOGARTY, M. J. 1985. Statistical considerations in the design of trawl surveys. *FAO Fish. Circ.*, No. 786, 21 p.
- GIBBONS, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart, and Winston, 463 p.
- GROSSLEIN, M. D. 1969. Groundfish survey program of BFC, Woods Hole. *Comm. Fish. Rev.*, **31**(7): 22-35.
- HTUN-HAN, M. 1978. The reproductive biology of the dab *Limanda limanda* (L.) in the North Sea: gonadosomatic index, hepatosomatic index, and condition factor. *J. Fish Biol.*, **13**: 369-378.
- JEARLD, A. 1983. Age Determination. In: Fisheries Techniques. L. A. Nielsen and D. L. Johnson (eds.). American Fisheries Society, p. 301-324.
- JONES, R., AND C. JOHNSTON. 1977. Growth, reproduction, and mortality in gadoid fish species. In: Fisheries Mathematics. J. H. Steele (ed.), Acad. Press, NY, p. 37-62.
- KIMURA, D. K. 1977. Statistical assessment of the age-length key. *J. Fish. Res. Board Can.*, **34**: 317-324.
- LANGTON, R. W., and R. E. BOWMAN. 1980. Food of fifteen Northwest Atlantic gadiform fishes. *NOAA Tech. Rep.*, NMFS, SSRF-740, 23 p.
- LE CREN, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.*, **20**: 201-219.
- LEGGETT, W. C., and J. E. CARSCADDEN. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *J. Fish. Res. Board Can.*, **35**: 1469-1478.
- LEIM, A. H., and W. B. SCOTT. 1966. Fishes of the Atlantic Coast of Canada. *Bull. Fish. Res. Board Can.*, **155**, 485 p.
- MACER, C. T. 1966. Sandeels (Ammodytidae) in the southwestern North Sea; their biology and fishery. *Fish. Invest. Lond.*, Ser. II, **24**(6): 1-55.
- MAYO, C. A., D. K. MATTILA, S. PITTMAN, and L. BARAFF. 1987. Abundance, distribution, and habitat use of large whales in the southern Gulf of Maine: May 1-September 30, 1986. Interim report, Contract No.50-EANF-5-00130. NMFS, NEFC, Woods Hole, MA.
- McEACHRAN, J. D., D. F. BOESCH, and J. A. MUSICK. 1976. Food division within two sympatric species-pairs of skates (Pisces: Rajidae). *Mar. Biol.*, **35**: 301-317.
- MEYER, T. L., R. A. COOPER, and R. W. LANGTON. 1979. Relative abundance, behavior, and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. *Fish. Bull. U.S.*, **77**(1): 243-254.
- MOREAU, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further development. In: Age and Growth of Fish. p. 81-113. R. C. Summerfelt and G. E. Hall (eds.). Iowa State University Press, Ames, Iowa.
- MORSE, W. MS 1982. Spawning stock biomass estimates of sand lance, *Ammodytes* sp., off northeastern United States, determined from MARMAP surveys, 1974-1980. *ICES C.M. Doc.*, No. G:59, 11 p.
- NMFS/NEFC. 1988. National Marine Fisheries Service/Northeast Fisheries Center. Status of the Fishery Resources Off the Northeastern United States for 1988, 135 p.
- NELSON, G. A. MS 1990. Population biology and dynamics of northern sand lance (*Ammodytes dubius*) in the Gulf of Maine to Middle Atlantic Bight region. Master's Thesis. University of Massachusetts, Amherst, MA.
- NIZINSKI, M. S., B. B. COLLETTE, and B. B. WASHINGTON. 1990. Separation of two species of sand lances, *Ammodytes americanus* and *A. dubius*, in the western North Atlantic. *Fish. Bull. U.S.*, **88**(2): 241-255.
- OVERHOLTZ, W. J., and J. R. NICOLAS. 1979. Apparent feeding by the fin whale, *Balaenoptera physalus*, and humpback whale, *Megaptera novaeangliae* on the American sand lance, *Ammodytes americanus*, in the Northwest Atlantic. *Fish. Bull. U.S.*, **77**: 285-287.
- PAYNE, P. M., J. R. NICOLAS, L. O'BRIEN, and K. D. POWERS. 1986. The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel *Ammodytes americanus*. *Fish. Bull. U.S.*, **81**(2): 271-277.
- POTTER, D. C., and R. G. LOUGH. 1987. Vertical distribution and sampling variability of larval and juvenile sand lance (*Ammodytes* sp.) on Nantucket Shoals and Georges Bank. *J. Northw. Atl. Fish. Sci.*, **7**: 107-116.
- POWERS, K. D., and R. G. BROWN. 1987. Seabirds. In: Georges Bank. R. H. Backus and P. W. Bourne (eds.). MIT press, Cambridge, Mass.
- REAY, P. J. 1972. The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. *ICES J. Cons.*, **34**(3): 485-504.
- RICHARDS, S. W. 1982. Aspects of the biology of *Ammodytes americanus* from the St. Lawrence river to Chesapeake Bay, 1972-1975, including a comparison of the Long Island Sound postlarvae with *Ammodytes dubius*. *J. Northw. Atl. Fish. Sci.*, **3**: 93-104.
- SAS INSTITUTE. 1988. The NLIN Procedures. SAS/Stat User's Guide: Release 6.03 Edition, p. 675-712.
- SCOTT, J. S. 1968. Morphometrics, distribution, growth, maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia Banks. *J. Fish. Res. Board Can.*, **25**(9): 1775-1785.
1972. Morphological and meristic variation in Northwest Atlantic sand lances (*Ammodytes*). *J. Fish. Res. Board Can.*, **29**: 1673-1678.
1973. Otolith structure and growth in Northern sand lance, *Ammodytes dubius*, from the Scotian Shelf. *ICNAF Res. Bull.*, **10**: 107-115.
- SHEPHERD, G., and C. B. GRIMES. 1983. Geographic and historic variations in growth of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight. *Fish. Bull. U.S.*, **81**(4): 803-813.
- SHERMAN, K., and C. JONES. MS 1980. The zooplankton component of a northwest Atlantic ecosystem. *ICES C.M. Doc.*, No. L:67, 32 p.



- SHERMAN, K., C. JONES, L. SULLIVAN, W. SMITH, P. BERRIEN, and L. EJSYMONT. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature*, **291**(5815): 486-489.
- SMITH, W. G., L. SULLIVAN, and P. BERRIEN. MS 1978. Fluctuations in production of sand lance larvae in coastal waters off the Northeastern United States, 1974 to 1977. *ICES C.M. Doc.*, No. L:30, 14 p.
- SOKAL, R. R., and F. J. ROHLF. 1981. *Biometry*. W. H. Freeman and Company, New York, 859 p.
- VAN GUELPHEN, L., D. F. MARKLE, and D. J. DUGGAN. 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. *ICES J. Cons.*, **40**: 226-236.
- WESTIN, D. T., K. J. ABERNETHY, L. E. MELLER, and B. A. ROGERS. 1979. Some aspects of biology of the American sand lance, *Ammodytes americanus*. *Trans. Amer. Fish. Soc.*, **108**(3): 328-331.
- WINTERS, G. H. 1981. Growth patterns in sand lance, *Ammodytes dubius* from the Grand Bank. *Can. J. Fish. Aquat. Sci.*, **38**: 841-846.
1983. Analysis of the biological and demographic parameters of northern sand lance, *Ammodytes dubius*, from the Newfoundland Grand Bank. *Can. J. Fish. Aquat. Sci.*, **40**(4): 409-419.
1989. Life history parameters of sand lances (*Ammodytes* spp.) from the coastal waters of eastern Newfoundland. *J. Northw. Atl. Fish. Sci.*, **9**: 5-11.
- WINTERS, G. H., and E. L. DALLEY. 1988. Meristic composition of sand lance (*Ammodytes* spp.) in Newfoundland waters with a review of species designations in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.*, **45**: 516-529.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., 718 p.
-

