http://journal.nafo.int
J. Northw. Atl. Fish. Sci., Vol. 3: 93-104

Aspects of the Biology of *Ammodytes americanus* from the St. Lawrence River to Chesapeake Bay, 1972-75, Including a Comparison of the Long Island Sound Postlarvae with *Ammodytes dubius*

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Abstract

Juvenile and adult *Ammodytes americanus*, ranging in length from 49 to 235 mm, were collected in 1972-75 between the St. Lawrence River and Chesapeake Bay. Those from inshore tended to be younger than those from offshore and the zero year-class by the end of the first year ranged in length from 80 to 115 mm. Weight increased isometrically, with variations between geographical areas and between seasons of the year. An inter-specific cline in meristic index was evident between *A. americanus* and *A. dubius*, and an inshore-offshore intraspecific cline occurred within the range of *A. americanus*. Postlarval *A. americanus* from Long Island Sound differed in pigmentation from *A. dubius* from the Scotian Shelf. *A. americanus* rapidly developed a solid line of stomach pigment, but preanal, supradorsal and subdorsal melanophores, prominent in postlarval *A. dubius*, developed more slowly in *A. americanus*.

Introduction

Two species of the genus *Ammodytes* exist in the Northwest Atlantic region, *Ammodytes dubius* and *A. americanus*. They are usually separated on the basis of distributional range, overall size, and meristic and morphological characters (Scott, 1972a, 1973b; Reay, 1970; Richards *et al.*, 1963; Meyer *et al.*, 1979). *A. dubius*, the large northern species with high meristic counts, ranges from Greenland to the Scotian Shelf, whereas *A. americanus*, the smaller species with lower meristic counts, ranges from Labrador to Virginia. Both species resemble and exhibit behavior patterns similar to *A. marinus* of the Northeast Atlantic region (Macer, 1966, 1967; Reay, 1970; Winslade, 1974). Along the North American coast, the genus *Ammodytes* appears to be divided into isolated groups with different meristic characters (Scott, 1972a) that show clines in both latitude and distance offshore (Richards *et al.*, 1963; Winters, 1970). Separation of these groups into the two species is difficult, not only in the adult stage but particularly as postlarvae (Richards, 1965; Scott, 1972b; Richards and Kendall, 1973; Sherman *et al.*, 1981).

Considerable research on *A. dubius* in Canadian waters has been reported by Scott (1968, 1972a, 1972b, 1973a, 1973b) and Winters (1970, 1981), but little has been done on the biology of *A. americanus* over its entire range during a short period of time to reduce annual variations. Therefore, an effort was made in 1972 and 1973 to collect *A. americanus* of all sizes from many locations, both inshore and offshore, throughout as much of its range as possible. In addition, spawning adults, eggs and planktonic stages were collected in Long Island Sound during the winters of 1972-75, for comparison with results of similar studies on *A. dubius* in Nova Scotian waters (Scott, 1968, 1972a, 1972b, 1973a, 1973b).

Materials and Methods

The offshore samples (more than 9 km from the coast) of *A. americanus* in 1972-73 were collected during spring and autumn bottom-trawl surveys by research vessels of the Northeast Fisheries Center, Woods Hole, USA, conducted according to the groundfish survey program described by Grosslein (1969). Scattered collections between 1955 and 1967 were provided by the Northeast Fisheries Center, Woods Hole, and by Dr J. S. Scott of the St. Andrews Biological Station, New Brunswick. These were useful for comparison but the data were, for the most part, not included here. Inshore collections from beaches and estuaries were provided by several individuals and organizations and by the Little Harbor Laboratory. The locations of all collections of sand lance during 1955-75 are shown in Fig. 1. The seasons, areas and size of collections since 1970 are summarized in Table 1. The majority of the specimens were collected offshore from Georges Bank to Chesapeake Bay and inshore from the south side of Cape Cod and in Long Island Sound.

The sand lance specimens from the offshore region between Browns Bank off southern Nova Scotia to Chesapeake Bay were taken in a Yankee 36 bottom

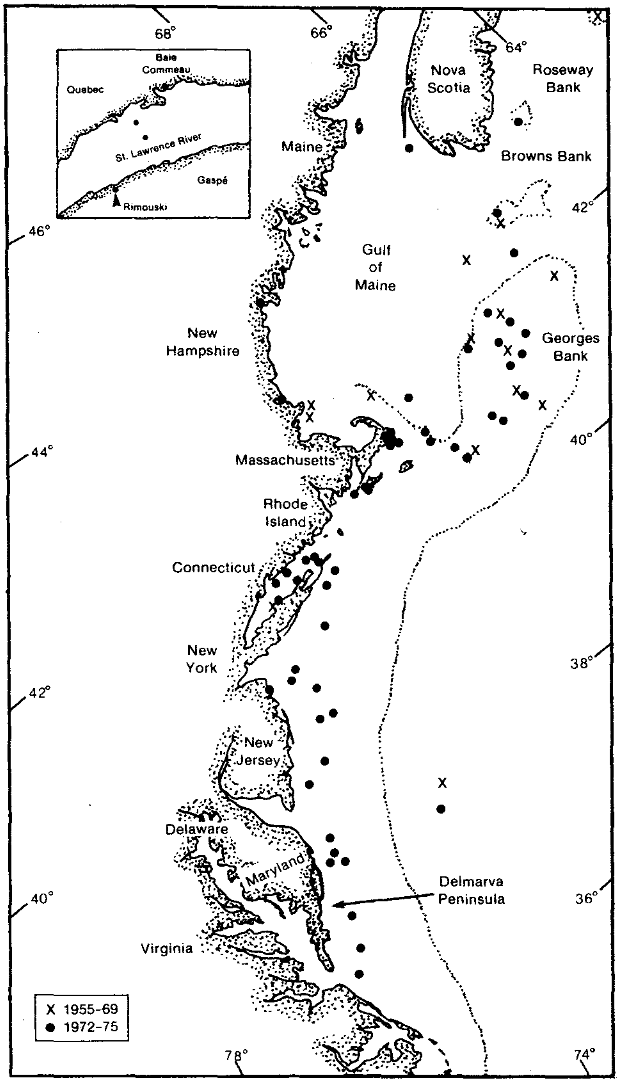

Fig. 1. Locations of collections of *A. americanus* in the Northwest Atlantic during 1955-69 and 1972-75. (Only the latter collections are considered in this paper.)

otter-trawl with a codend liner mesh size of 12.5 mm (stretched). Samples from coastal beaches and estuaries were taken in a variety of gears: bag and beach seines with 6.3 mm mesh size, gillnets with 6.3 and 9.5 mm meshes, Japanese elver trap of 10 meshes per 12.5 cm throughout (Topp and Raulerson, 1973), Danish sandeel trawl with 6.3 mm mesh codend liner, and 0.5 and 1.0 m plankton nets with 0.158 and 0.366 mm meshes. Some specimens from Long Island Sound were caught by common and roseate terns, and a large collection from Yarmouth Flats on the south side of Cape Cod was the result of a natural kill due to high temperatures on the incoming tide during an extremely hot afternoon (Ian Nesbit, Massachusetts Audubon Society, pers. comm.).

Total, standard and head lengths (mm) and total weight (g) were measured. These were transformed to

TABLE 1. Collections of *A. americanus* from various offshore and inshore areas of the Northwest Atlantic.

Region (Season)	Area	No. of samples	No. of specimens
Offshore (Oct-Dec 1972)	Off SW Nova Scotia	2	18
	Georges Bank area	5	121
	Delmarva Peninsula	1	7
Offshore (Mar-Apr 1973)	Georges Bank area	12	61
	New York Bight	9	166
	Delmarva Peninsula	6	197
Inshore (Jun-Aug 1972-73)	St. Lawrence River[a]	2	38
	Maine (mid-coast)	2	96
	Cape Cod (south)	8	450
	Long Island Sound	4	203
	New York Bight	1	9
Inshore (Autumn 1972)	Long Island Sound	1	20
Postlarvae (Dec-Apr 1972-75)	Long Island Sound	104	1131

[a] Summer 1974.

$\log_{10}$, and regressions of head length and total body weight on standard length for each area were compared by testing whether the standard error of the distance between pairs of lines differed from zero.

Stomach contents were examined, stomach fullness was noted, and food contents were identified generally by groups of species, e.g. copepods, mysids, etc. Developed gonads were weighed to determine the gonadosomatic index from the ratio of gonad weight to total body weight. Mature ovaries were preserved in Gilson's fluid (Simpson, 1951), and eggs were counted when the interovarian tissue had disintegrated sufficiently to allow the eggs to be teased apart easily. Counting eggs in aliquot portions by volume was accurate to within 5%, based on counting eggs in all aliquots of three ovaries.

Counts of dorsal and anal fin rays and of vertebrae were made, as have traditionally been done to separate species of *Ammodytes* (Richards *et al.*, 1963; Macer, 1966; Reay, 1970; Scott, 1972a; Kitaguchi, 1979). The numbers of dorsal and anal fin rays and vertebrae were positively correlated, i.e. sand lance with high vertebral numbers also had high numbers of fin rays, and vice versa (Richards *et al.*, 1963), and a meristic index based on the sum of all three counts for each fish was used. The range, mean and standard deviation of this index were used to define a population from a geographical area. Tests for significant differences between pairs of populations were made by the standard Student's t-test.

Postlarval pigmentation was examined as soon as possible after capture (before fading), using the pigment nomenclature of Macer (1967). Additional terms were used for pigment not included in the descriptions by Macer (1967) and Scott (1972b). Melanophores were counted and their occurrence on different parts of the body compared with descriptions of *A. dubius* postlarvae by Scott (1972b).

Results and Discussion

Length frequencies

Standard lengths of *A. americanus* examined in different seasons and locations ranged from 49 to 235 mm, the larger specimens being more common in offshore than in inshore samples (Table 2). Very few zero-year specimens were found in the offshore collections from the spring and autumn bottom trawl surveys in 1972 and 1973. Two specimens (94 and 108 mm long) were taken on the northern edge of Georges Bank in October 1972. Pre-1970 collections included four specimens (54–88 mm) from Georges Bank east of Cape Cod in July 1961. Zero-year specimens of *A. dubius* have been caught frequently offshore on the Scotian Shelf (J. S. Scott, pers. comm.).

Sand lance from the beaches and estuaries along the coast tended to be shorter than those taken offshore (Fig. 2). Many specimens larger than 100 mm were taken offshore with bottom trawl, but a few were obtained in coastal areas of Maine with elver trap, Cape Cod during a fish kill, and Long Island Sound with trawl and gillnet. Sand lance larger than 155 mm were not taken in coastal waters (except one specimen in the St. Lawrence River estuary), although they have occasionally been seen (Carolyn Griswold, Natl. Mar. Fish. Serv., Narragansett Laboratory, Rhode Island, pers. comm.), but they were common on the shelf from Browns Bank to Chesapeake Bay in spring and autumn. None longer than 235 mm occurred in the collections analyzed in this paper, but *A. dubius* as

TABLE 2. Standard lengths (range and mean, mm) of *Ammodytes americanus* from various areas of the Northwest Atlantic.

Region (Season)	Area	No.	Range	Mean
Offshore	Off SW Nova Scotia	18	124–184	162
(Autumn 1972)	Georges Bank area	121	94–211	143
	Delmarva Peninsula	7	131–175	154
Offshore	Georges Bank area	61	115–235	167
(Spring 1973)	New York Bight	166	126–214	162
	Delmarva Peninsula	197	124–195	142
Inshore	St. Lawrence River[a]	38	75–183	85
(Summer 1972–73)	Maine (mid-coast)	96	75–155	102
	Cape Cod (south)	160	59–155	93
	Long Island Sound	203	62–141	82
	New York Bight	9	49–67	53
Inshore (Autumn 1972)	Long Island Sound	20	80–141	109
All areas		1,096	49–235	

[a] Summer 1974.

large as 372 mm total length (about 345 mm standard length) occurred in the 1967–70 collections by Scott (1968, 1972a) from the Scotian Shelf.

The length frequencies of juvenile sand lance from the coastal areas, arranged chronologically by month, indicate progressive increase in size from June to November (Fig. 3). The specimens in the small sample from New York Bight in June 1972 were considerably smaller than those taken in June 1973 from the southern New England area. The difference in size between years may have been the result of environmentally-induced variation in, for example, time of spawning

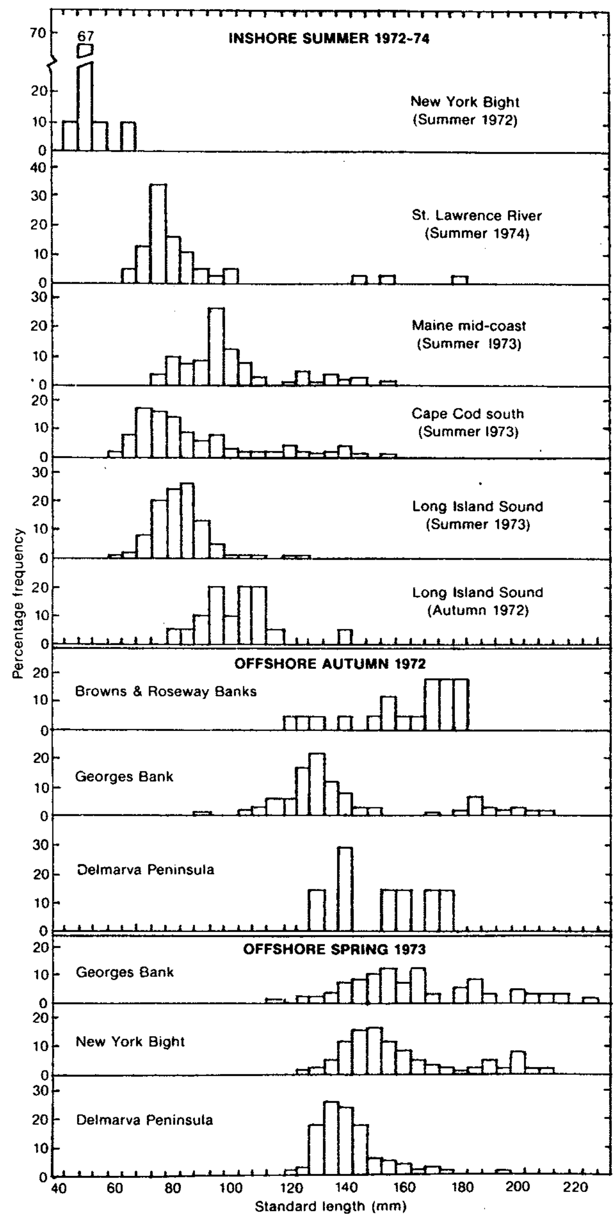

Fig. 2. Length (standard) frequencies of *A. americanus* from various areas of the Northwest Atlantic, 1972–75.

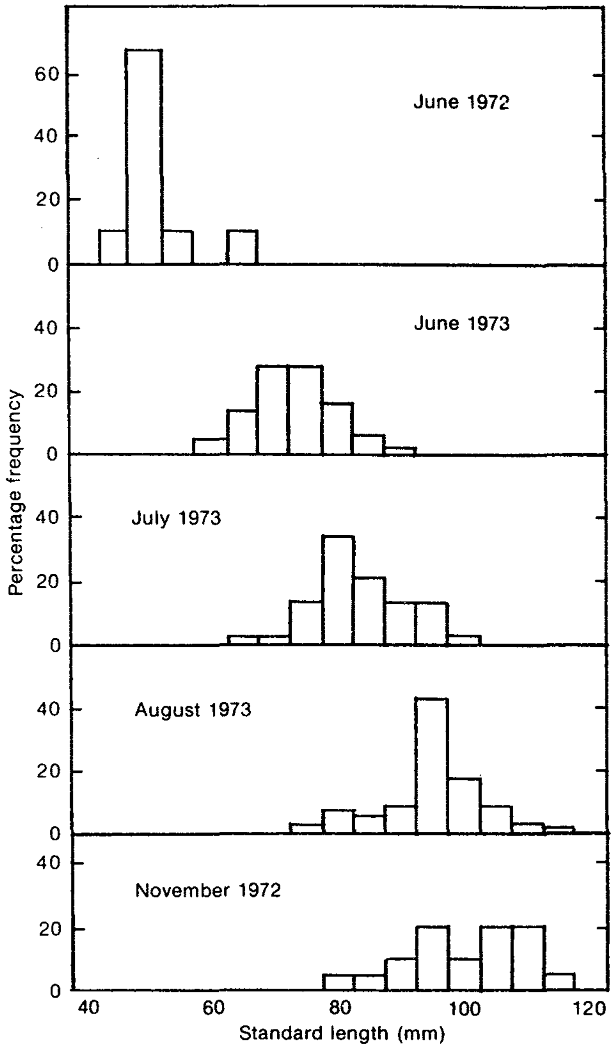

Fig. 3. Length (standard) frequencies of juvenile *A. americanus* from inshore areas, arranged by month to show seasonal growth of 0-group fish.

and subsequent growth. Winters (1981) observed that variation in temperature strongly affects growth in *A. dubius* during the first year of life. However, the inshore length-frequency data for juveniles in 1973 (Fig. 3) indicate an increase in modal length from 70-75 mm in June to 80 mm in July and to 95 mm in August. The small sample of November 1972 juveniles, which were determined to be age-group 0 from otolith examination, ranged in length from 80 to 115 mm, with a mean length of 100 mm. This is considerably less than the mean length of 120 mm for *A. dubius* from Nova Scotia (Scott, 1968) but within the back-calculated range of 80-110 mm for the same species from the Grand Bank (Winters, 1981). As noted above for the June samples, this November 1972 sample may not be fully representative of juvenile sizes in late autumn. Seasonal growth of older sand lance could not be discerned from the length frequencies, and this must await examination of the entire collection of otoliths.

Morphological characteristics

The ratio of standard length to total length, expressed as percentages, for the 1972-73 collections of *A. americanus* from various inshore and offshore areas (Table 3), ranged from 86.8 to 95.5% with an overall mean of 91.8%. Scott (1972a) reported that the percentages for *A. dubius* from Nova Scotia ranged from 92.6 to 93.7%.

Previously, Richards *et al.* (1963) indicated that the head length, expressed as percentage of standard length, was a poor character for separating groups of *Ammodytes* and that there was evidence of allometric growth of the head. This latter indication was examined further by computing, after $\log_{10}$ transformation of the variables, regressions of head length on standard length for all collections of *A. americanus* in

TABLE 3. Percentage standard length of total length for *A. americanus* from various areas of the Northwest Atlantic.

Region (Season)	Area	No.	Range	Mean	SD
Offshore	Off SW Nova Scotia	18	90.7-92.7	92.1	0.5
(Autumn 1972)	Georges Bank area	121	90.1-93.5	91.9	0.6
	Delmarva Peninsula	7	91.1-93.1	92.2	0.7
Offshore	Georges Bank area	58	90.0-95.3	92.8	0.8
(Spring 1973)	New York Bight	166	88.1-95.1	92.3	1.0
	Delmarva Peninsula	117	88.0-95.0	91.9	1.0
Inshore	St. Lawrence River[a]	38	89.5-93.5	91.1	0.9
(Summer 1972-73)	Maine (mid-coast)	62	86.8-95.5	91.9	1.2
	Cape Cod (south)	450	88.5-95.0	91.8	1.2
	Long Island Sound	203	88.3-94.1	91.0	1.2
	New York Bight	9	90.4-94.6	91.7	1.5
Inshore (Autumn 1972)	Long Island Sound	20	90.6-94.4	92.0	0.9
All areas		1,269	86.8-95.5	91.8	0.8

[a] Summer 1974.

1972-73 (Table 4) and applying an analysis of covariance. Except for the low value of 0.58, based only on 7 specimens, the regression coefficients ranged from 0.68 to 0.84. Graham (1956), for sand lance from Narragansett Bay, has previously reported a regression coefficient of 0.82. Despite differences in variation about the regression lines, head length was highly correlated with standard length. No significant differences were found between the regression coefficients for the collections, whether inshore or offshore, with the exception of the autumn collection from Georges Bank relative to those from New York Bight and Delmarva Peninsula in the spring, due obviously to the large numbers of specimens in the collections with consequent small standard errors. It is therefore considered that head-length growth was isometric throughout the range of *A. americanus* represented by the collections.

Seasonal variation in weight was noticeable (Table 5). Although the autumn pre-spawning groups showed greater variation in weight for a given length than the spring post-spawning groups ($P = 0.02$), they were also significantly heavier ($P = 0.01$). The difference in weight between the two seasons was particularly evident in the Georges Bank collections ($P < 0.01$). Comparison of the plotted regression lines indicated that autumn prespawners were 5 g heavier, on the average, for a given length than spring postspawners. Previous work on other species of *Ammodytes* showed seasonal variation in body weight (Reay, 1970; Sekiguchi *et al.*, 1976). Indeed, Scott (1972a) found that prespawning

TABLE 4. Regressions of log head length (H) on log standard length (L) for *A. americanus* from various areas of the Northwest Atlantic. (a = intercept, b = regression coefficient, SE = standard error, r = correlation coefficient.)

Region (Season)	Area	No.	a	b	SE_b	$\bar{H}$	$\bar{L}$	r
Offshore	Off SW Nova Scotia	18	-0.31	0.81	0.05	1.48	2.21	0.97
(Autumn 1972)	Georges Bank area	75	-0.35	0.84	0.02	1.47	2.16	0.98
	Delmarva Peninsula	7	+0.21	0.58	0.12	1.49	2.19	0.91
Offshore	Georges Bank area	61	-0.17	0.77	0.04	1.54	2.22	0.94
(Spring 1973)	New York Bight	157	-0.13	0.75	0.02	1.53	2.21	0.94
	Delmarva Peninsula	117	+0.04	0.68	0.04	1.50	2.16	0.82
Inshore	St. Lawrence River[a]	38	-0.31	0.82	0.05	1.27	1.93	0.95
(Summer 1972-73)	Maine (mid-coast)	62	-0.29	0.80	0.08	1.32	2.01	0.81
	Cape Cod (south)	160	-0.34	0.83	0.02	1.30	1.97	0.94
	Long Island Sound	100	-0.16	0.74	0.04	1.25	1.92	0.87
Inshore (Autumn 1972)	Long Island Sound	20	-0.08	0.70	0.11	1.35	2.04	0.84
All Areas		815	-0.04	0.70		1.35	2.00	

[a] Summer 1974.

TABLE 5. Regressions of log weight (W) on log standard length (L) for *A. americanus* from various areas of the Northwest Atlantic. (a = intercept, b = regression coefficient, SE = standard error, r = correlation coefficient.)

Region (Season)	Area	No.	a	b	SE_b	$\bar{W}$	$\bar{L}$	r
Offshore	Off SW Nova Scotia	18	-5.66	3.03	0.12	1.04	2.21	0.99
(Autumn 1972)	Georges Bank area	75	-5.43	2.97	0.08	0.99	2.16	0.97
	Delmarva Peninsula	7	-6.13	3.29	0.18	1.06	2.19	0.99
Offshore	Georges Bank area	61	-4.62	2.57	0.13	1.08	2.22	0.94
(Spring 1973)	New York Bight	157	-4.72	2.65	0.07	1.13	2.21	0.95
	Delmarva Peninsula	117	-4.46	2.52	0.11	0.99	2.16	0.90
Inshore	St. Lawrence River[a]	38	-5.62	3.08	0.15	0.32	1.93	0.96
(Summer 1972-73)	Maine (mid-coast)	96	-5.80	3.18	0.08	0.56	2.00	0.97
	Cape Cod (south)	160	-5.87	3.21	0.06	0.45	1.97	0.97
	Long Island Sound	100	-5.72	3.13	0.30	0.27	1.92	0.73
Inshore (Autumn 1972)	Long Island Sound	20	-4.88	2.70	0.33	0.62	2.03	0.89
Autumn samples		120	-5.22	2.87	0.27	0.94	2.15	
Spring samples		335	-4.48	2.53	0.15	1.07	2.19	
Summer samples		394	-5.86	3.20	0.17	0.42	1.96	

[a] Summer 1974.

A. dubius (205–242 mm SL) were as much as 10 g heavier, on the average, than postspawners of the same length.

Disregarding seasonal variation in weight, the overall relationship between body weight (W) and standard length (SL) can be expressed as

$$\log W = 2.84 \log SL - 5.16$$

with standard error of the regression coefficient (b) being 0.24. The coefficient (b = 2.84) is slightly less than 2.99 and 2.94 for *A. dubius* from Emerald Bank and Newfoundland respectively (Scott, 1972a) and 3.07 for the closely related *A. marinus* from the North Sea (Macer, 1966).

Meristic index

Three samples of *Ammodytes*, obtained in years prior to 1972, were used to test the meristic index, defined as the sum of the counts of vertebrae and dorsal and anal fin rays. In a sample of 20 *A. dubius* from Emerald Bank on the Scotian Shelf in 1967, the index ranged from 165 to 176 (mean, $\bar{x} = 171$; standard deviation, SD = 4). The index for 70 *A. americanus* from Georges Bank in 1955 ranged from 156 to 171 ($\bar{x} = 163$, SD = 3), and the index for 20 *A. americanus* from Long Island Sound in 1963 ranged from 143-153 ($\bar{x} = 148$, SD = 3). As expected from past experience (Richards *et al.*, 1963; Scott, 1968), these averages were significantly different from each other.

Further comparisons of the means, standard deviations and ranges of the meristic index were made for the 1972-73 collections of *A. americanus* from inshore and offshore areas (Fig. 4). Index values for collections from coastal waters ranged from 140 to 166 ($\bar{x} = 150$), whereas those for offshore sand lance ranged from 145 to 174 ($\bar{x} = 160$), with considerable variation within groups (Table 6). The high values from Browns and Roseway banks, resembling the earlier counts for *A. dubius* from Emerald Bank, were significantly different from all other counts for the 1972-73 samples ($P<0.01$). The average meristic index for Georges Bank samples was very similar to values for offshore samples from areas farther south, but the means for all offshore samples were significantly higher than those for the inshore samples ($P<0.01$).

Among the inshore collections, only the index for the Maine sample ($\bar{x} = 154$) was significantly different ($P<0.1$). This collection appeared to be a mixture of inshore and offshore groups. However, some variation in the index for coastal populations would be expected, because water temperatures may decrease from 9° to 1°C during the long hatching period from early December to late February or early March (Wheatland, 1956; Richards and Kendall, 1973).

Food

The stomach contents of *A. americanus* from the St. Lawrence River were not examined, and those from Southeast Nova Scotia, Maine and Delmarva Peninsula were all empty (Table 7). Food was found in many of the stomachs from Georges Bank, Cape Cod, Long Island Sound and New York Bight, although the degree of stomach fullness varied widely. During the autumn, sand lance from Georges Bank and Long Island Sound concentrated on copepods (mainly *Labidocera aestiva*) and mysids, *Neomysis americana*. Small snails were common while cumaceans and small crabs occurred infrequently in the Georges Bank specimens. In the spring samples, although copepods were still important, at least one third of the fish contained hydroids and cumaceans, indicative of feeding near the bottom. The diversity of prey increased, with polychaetes, small clams, cyprids, amphipods and mysids occurring in more than 5% of the fish. Copepods and small snails occurred in the few fish with food from New York Bight, along with ostracods, amphipods and mysids in small numbers. In summer, along the coast, copepods were the favorite prey, although there was indication of benthic feeding by the presence of small snails, cumaceans, isopods, amphipods and small crabs.

Previous studies have shown that copepods form an important part of the diet of *A. americanus*. Collections from Long Island Sound in the 1950's indicated concentrated feeding on copepods (primarily *Temora longicornis* and *Acartia* sp.) and cyprids, *Balanus balanoides*, (Richards, 1963), whereas fish from Stellwagen Bank in Massachusetts Bay during the 1960's and 1970's consumed copepods almost exclusively, with the addition of a few *Sagitta elegans*, *Meganyctiphanes norvegica*, amphipods and mysids (Meyer *et al.*, 1979). Copepods were by far the most important prey of *A. dubius* from the Scotian Shelf, followed by other crustacean larvae, polychaete larvae, fish eggs, and *M.norvegica* (Scott, 1973a).

Winslade (1974) reported that *A. marinus* in European waters fed only during daylight. Analysis of the offshore samples of *A. americanus* from North American waters by 6-hour periods indicated that food was present in 66% of the specimens caught between midnight and 0600 hr, in 42% of the fish caught between 0600 and 1200 hr, in 25% of the fish caught between 1200 and 1800 hr, and in 37% of the fish caught between 1800 and 2400 hr. Thus, *A. americanus* apparently feeds during day and night.

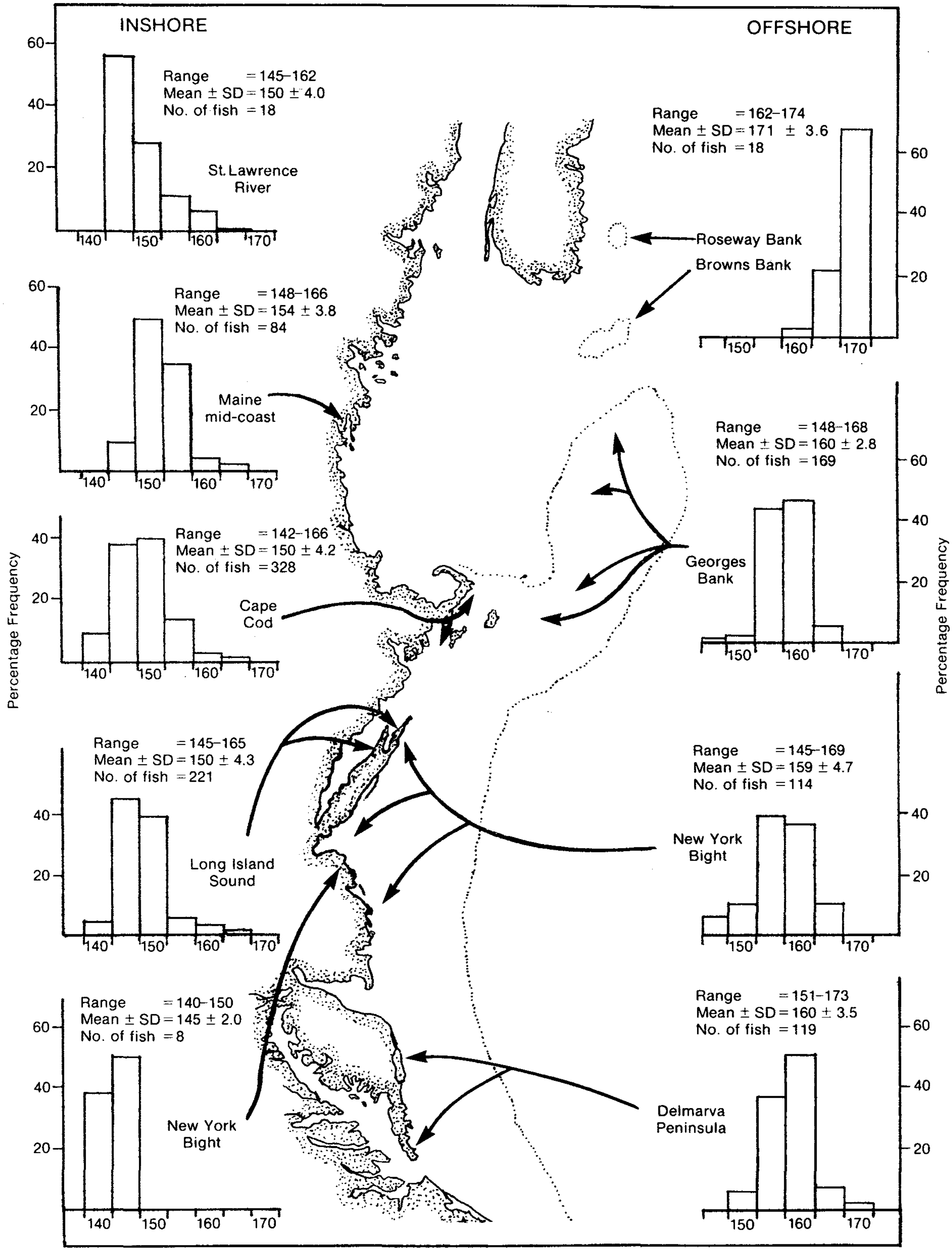

Fig. 4. Meristic index frequencies for *A. americanus* from various inshore and offshore areas of the Northwest Atlantic, 1972–75.

TABLE 6. Range and mean values of meristic index for *A. americanus* from various areas of the Northwest Atlantic. (SD = standard deviation.)

Region (Season)	Area	No.	Range	Mean	SD
Offshore	Off SW Nova Scotia	18	162-174	171	4
(Autumn 1972)	Georges Bank area	121	155-164	160	2
	Delmarva Peninsula	5	160-163	161	2
Offshore	Georges Bank area	56	148-167	160	5
(Spring 1973)	New York Bight	114	145-169	159	5
	Delmarva Peninsula	194	151-173	160	4
Inshore	St. Lawrence River[a]	18	145-162	150	4
(Summer 1972-73)	Maine (mid-coast)	84	148-166	154	4
	Cape Cod (south)	328	142-166	150	4
	Long Island Sound	188	140-164	149	5
	New York Bight	8	140-150	145	2
Inshore (Autumn 1972)	Long Island Sound	20	144-157	148	4
All areas		1,154	140-174	155	6

[a] Summer 1974.

TABLE 7. Percentage occurrence of various groups of food items in *A. americanus* stomachs by season from different areas in the Northwest Atlantic.

				Percentage occurrence in all fish examined												
Season	Area	Stomachs examined	Percent empty	Hyd-roids	Poly chaetes	Small clams	Small snails	Cope-pods	Ostra-cods	Cyp-rids	Cuma-ceans	Iso-pods	Amphi-pods	My-sids	Small crabs	Sand
Autumn	Off SW Nova Scotia	18	100	—	—	—	—	—	—	—	—	—	—	—	—	—
	Georges Bank area	102	1	—	—	—	49	98	—	—	9	—	—	99	1	7
	Long Island Sound	20	15	—	—	—	—	80	—	—	—	—	—	80	—	5
	Delmarva Peninsula	7	100	—	—	—	—	—	—	—	—	—	—	—	—	—
Spring	Georges Bank area	61	28	34	5	5	—	30	—	10	34	—	16	15	—	5
	New York Bight	144	78	1	—	—	7	14	2	—	—	—	1	3	—	—
	Delmarva Peninsula	117	100	—	—	—	—	—	—	—	—	—	—	—	—	—
Summer	Maine (mid-coast)	34	100	—	—	—	—	—	—	—	—	—	—	—	—	—
	Cape Cod (south)	455	92	—	—	1	—	23	—	7	—	1	2	2	—	—
	Long Island Sound	203	44	—	1	—	18	40	—	—	5	—	1	4	3	1

Spawning

The ranges of the gonadosomatic index for *A. americanus* from offshore areas (Table 8) indicate that gonads were maturing in early October at the southern end of the range and that some were nearly ripe by late October. The Southwest Nova Scotia specimens were almost ripe in mid-November, with gonads averaging 15% of body weight. In inshore waters (Long Island Sound), maturing gonads were found in two fish (79 and 131 mm) in August, and ripe and running fish were found as early as 20 November, some with gonads approaching 25% of body weight. Thus, inshore spawning may commence earlier than offshore spawning. Judging from the size and abundance of postlarvae collected during December-April, spawning in both coastal and offshore areas peaked in December-January and terminated in February. This spawning season is similar to that of *A. dubius* off Nova Scotia (Scott, 1968) and *A. marinus* in the North Sea (Macer, 1966).

The smallest fish from Long Island Sound with maturing gonads (8% of body weight) was 89 mm, with the majority in the collection being in the range of 102-114 mm, entering their second year. Offshore, the smallest fish with maturing gonads was 94 mm from Georges Bank. Early maturity, at the end of the first year of growth, was not exceptional. Macer (1966) noted that some *A. marinus* matured at the end of the their first year at a total length near 100 mm. Scott (1968), on the other hand, found that *A. dubius* matured at the end of their second year.

Egg counts for eight females from Long Island Sound (89-141 mm) varied from 1,855 to 5,196, with a mean of 3,475. Except for the minimum estimate for the 89 mm specimen, no clear relationship between egg count and fish length was obvious in this small sample. These counts are within the range of those for the closely related *A. marinus* in fish less than 2 years old (Macer, 1966).

Eggs of *A. americanus*, collected from the bottom of Goldsmith Inlet in Long Island Sound during November-December 1975, ranged in diameter from 0.72 to 1.10 mm, slightly larger, on the average, than those (0.67-0.91 mm) collected farther westward in the

TABLE 8. Range and mean values of gonadosomatic index (gonad weight as percent of body weight) for *A. americanus* from offshore and inshore areas of the Northwest Atlantic.

Region	Date	Area	No.	Range	Mean
Offshore	4 Oct	Delmarva Peninsula	18	0.6-4.1	1.9
	21-26 Oct	Georges Bank area	122	1.6-17.3	6.4
	11-14 Nov	Off SW Nova Scotia	18	10.7-19.1	15.2
Inshore	20 Nov	Long Island Sound	18	0.1-23.8	15.2

Sound near Stony Brook Harbor. Most of the eggs in both samples were smaller than eggs of *A. dubius* off Nova Scotia, which were 0.97-1.02 mm in diameter (Scott, 1972b).

Both Winslade (1974) and Sekiguchi *et al.* (1976) mentioned that *A. marinus* and *A. personatus* entered a dormant state. *A. marinus* apparently remains buried in the sand after spawning in December-January until April and again from July to November. *A. personatus*, in Japan, apparently remains buried from June to November. Such behavior has not been shown for *A. americanus* due to the lack of attempts to collect inshore samples in the autumn. However, terns in Long Island Sound catch sand lance in the water column in August, and there is a commercial fishery at the mouth of the Merrimack River, Massachusetts, in October (Pellegrini, MS 1976). Further observations on predation of sand lance from the water column by birds and whales (Overholtz and Nicolas, 1979) during autumn migration are needed to determine whether seasonal aestivation is typical of American sand lances.

Postlarval pigmentation and growth

Postlarvae of *Ammodytes*, although easily distinguishable from other related genera, are difficult to identify to species. Those of *A. marinus*, *A. dubius* and *A. americanus* are remarkably similar (Macer, 1967; Scott, 1972b; Richards, 1965), but only the last two species occur in the Northwest Atlantic. An attempt to determine differences between these two species was undertaken in this study by comparing postlarvae of *A. americanus* taken in Long Island Sound during the winters of 1972-73 with Scott's (1972b) descriptions of *A. dubius* from Nova Scotia. The differences were based primarily on Scott's (1972b) method of counting black melanophores in various size categories of postlarvae (Fig. 5).

In Long Island Sound, larvae hatched as small as 3.6 mm long, just slightly shorter than previously noted for *A. hexapterus* (=*americanus*) by Williams *et al.* (1964) and for *A. dubius* by Scott (1972b). At this size, there were a few stomach melanophores, a line of preanal melanophores, and usually a few caudal melanophores (see fig. 1E of Williams *et al.*, 1964), but no obvious differences between the two species were evident.

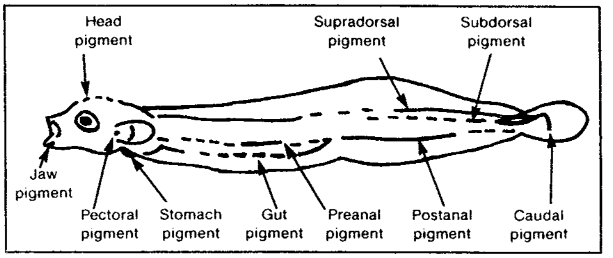

Fig. 5. Nomenclature of pigmentation in postlarval *Ammodytes* (from Macer, 1967), including the addition of "jaw" and "pectoral" pigments for the present study.

As the postlarvae grew in length, slight differences in pigmentation appeared. Frequently, the "stomach" (Scott's "ventral") pigment in *A. americanus* was amalgamated into a solid line (Table 9). A greater number of "preanal" (Scott's "lateral") melanophores developed earlier in *A. dubius* than in *A. americanus*, whereas the numbers of "postanal" melanophores were similar in both species throughout the postlarval period. "Caudal" pigment, present in all specimens at hatching, developed rapidly in both species. *A. dubius* greater than 13 mm appeared to have a slightly greater number of caudal melanophores than *A. americanus*.

Dorsal pigmentation appeared late in both species. "Supradorsal" (Scott's "dorsal") pigment, located above the musculature but beneath the fin fold, usually consisted of a large single melanophore, just posterior to the head, in postlarvae greater than 12 mm. A slightly greater number of these occurred in *A. dubius* 13-17 mm long (Table 9). By 25-30 mm, the melanophores extended all the way to the caudal region in both species. The number of "subdorsal" (Scott's "vertebral" melanophores, buried beneath the musculature just above the vertebral column, differed greatly between the two species. They first appeared in *A. dubius* at 6.0-8.9 mm, but they were not present in *A. americanus* until 13.0-16.9 mm. At that size, *A. dubius* had already developed an average of 40 subdorsal melanophores. Such large differences persisted throughout the remainder of postlarval life.

"Head" (Scott's "cranial") pigment was nonexistent in both species shorter than 9 mm in length. *A. dubius* 9.0-12.9 mm long nearly always had at least one melanophore and 15.0-16.9 mm specimens had two or three. Occasionally, *A. americanus* shorter than 23 mm

TABLE 9. Comparison of *A. americanus* from Long Island Sound with *A. dubius* from Emerald Bank, Nova Scotia, based on numbers of melanophores in postlarvae. (*A. dubius* data from Scott, 1972b.)

Body area (Fig. 5)	Species (% occurrence of melanophores)	Numbers of melanophores (range, mean and SD) by length group of larvae					
		3.0-5.9 mm	6.0-8.9 mm	9.0-12.9 mm	13.0-16.9 mm	17.0-22.9 mm	⩾23 mm
Stomach	*A. americanus* (100%)	3-12(76[a])	3-12(28[a])	3-10(15[a])	5-9 (12[a])	4 (4[a])	2 (2[a])
	A. dubius	4-7 (5)	2-11(6)	0-14(6)	0-11(6)	5 (5)	2-7 (5)
Preanal	*A. americanus* (100%)	0-16(9±2)	0-16(10±3)	6-17(11±2)	7-15(11±3)	10-19(15±3)	14-14(14)
	A. dubius	11-19(15)	10-21(16)	8-23(17)	13-21(17)	17-26(20)	19-30(26)
Postanal	*A. americanus* (100%)	0-15(8±4)	4-19(12±4)	10-23(17±3)	11-28(18±4)	16-25(22±4)	28-28(28)
	A. dubius	4-11(9)	5-22(15)	12-25(18)	14-24(19)	16-26(21)	24-35(30)
Caudal	*A. americanus* (100%)	0-8 (3±2)	2-11(5±2)	4-12(7±2)	4-11(8±2)	1-10(3[a])	2 (2[a])
	A. dubius	1-7 (4)	2-15(7)	4-19(9)	7-25(11)	5-24(14)	7-20(15)
Supradorsal	*A. americanus* (4%)	0	0	0-1	0-2 (1)	0-2 (2±1)	13
	A. dubius	0	0	0-2	0-8 (3)	1-22 (9)	1-60(30)
Subdorsal	*A. americanus* (9%)	0-8(<1)	0	0	2-16(5±6)	6-10(6±4)	7
	A. dubius	0	0-1	0-52	11-65(40)	40-78(60)	41-100(62)
Head	*A. americanus* (4%)	0	0	0-2	0-1	0	1-2
	A. dubius	0	0	1-3	2-3	0	0
Jaw	*A. americanus* (<1%)	0	0-1	0	0	0	0
	A. dubius	0	0	0	0	0	0
Gut	*A. americanus* (1%)	1	0-1	0-2	0	0-1	0
	A. dubius	0	0	0	0	0	0
Pectoral	*A. americanus* (51%)	0-1	0-1	0-1	0-2	0-1	0-3
	A. dubius	0	0	0	0	0	0
Numbers of *A. americanus* examined		114	62	49	15	4	2

[a] Solid line of pigment rather than separate melanophores.

possessed one or two melanophores on the top of the head. "Jaw" and "gut" pigments were rare in *A. americanus* and were presumably absent in *A. dubius*. A melanophore on the jaw occurred in a 7.3 mm specimen. Gut pigment, when present, usually consisted of one melanophore at the anus. Only two *A. americanus* (4 and 20 mm) showed gut pigment, as illustrated by Macer (1967) for a 19 mm *A. marinus* and all *Gymnammodytes semisquamatus*.

"Pectoral" pigment, an addition to Macer's (1967) terminology (Fig. 5), was presumably missing in *A. dubius*. Its occurrence in *A. americanus* was intermittant.

Fin-ray development in the postlarvae varied greatly in 21 specimens of both species. They first appeared in *A. americanus* at a length of 12-13 mm, and ranged in number from 0 to 17 in 14-15 mm specimens. Dorsal and anal fins were almost completely developed in 23 mm larvae. In *A. dubius*, fin rays appeared at 14-15 mm but the full complement was not present until after the larvae were greater than 25 mm long. There was such variation about the mean fin-ray counts for each length group that no significant difference between species could be determined.

Growth of postlarvae of *A. americanus* was difficult to estimate because of the influx of recently-hatched cohorts throughout the winter. The length range increased from 3-5 mm in December to 4-16 mm in January (mean 9 mm) and to 3-20 mm in February and March, with means varying from 7 to 12 mm, depending on the sampling date. By April, the length ranges were 8-23 mm in 1972-73 samples and 19-35 mm in 1975. Scott (1972b) determined that *A. dubius* mean lengths increased from 7 to 25 mm during February-May. Further analysis of *A. americanus* postlarval growth must await examination of daily growth increments from the otoliths.

The increase in weight of postlarval *A. dubius* from Long Island Sound was similar in December-January and February-April and also within the size groups 3.5-13.5 mm and 14-25 mm. The regression coefficients of log weight on log length for these size groups were not significantly different. The combined regression for the weight-length relationship, $\log W = 2.94 \log L - 5.94$ ($SE_b = 0.06$), was similar ($P>0.50$) to that for juvenile *A. americanus* from Long Island Sound in summer (Table 5). Apparently, weight increased isometrically in sand lance from inshore waters during the first year of life.

Conclusions

The length range of juvenile and adult *A. americanus* collected in 1972-74 from the St. Lawrence River to Chesapeake Bay was 49-235 mm. Geographical and annual differences in temperature, combined with decreasing temperatures during the hatching period, were presumably mainly responsible for the wide range of length (80–115 mm) near the end of the first growing season. Weight increased isometrically in sand lance with minor variation between areas. Differences in weight of pre-spawning and post-spawning adults were particularly evident in the samples from Georges Bank.

A definite inshore-offshore intraspecific cline of the meristic index was evident for *A. americanus* combined with an apparent north-south interspecific cline for *A. dubius* and *A. americanus*. Such differences may be the result of temperature variation at the time of hatching and larval development, together with the general trend of higher meristic counts with increasing latitude. Larvae hatched in December encountered water temperatures as high as 8°-10° C, whereas those hatched later in the winter encountered considerably lower temperatures (Richards and Kendall, 1973). Differential mortality rates of various cohorts of postlarvae, possibly creating different intraspecific ranges of meristic indices in survivors, may result in separate populations within the total geographical ranges of *A. americanus* and *A. dubius* in the Northwest Atlantic.

A. americanus, which is primarily a pelagic plankton feeder, was found to feed on benthic invertebrates, presumably during times of low zooplankton abundance. Recently-consumed food was found in the stomachs of many specimens throughout the 24-hr day.

The larger of the 0-group *A. americanus* spawned at the end of their first year. Presumably, these were fish which had hatched in the early part of the previous spawning season. Egg numbers, which ranged from 2,000 to 5,000 in eight females (89–141 mm), most of which were 0-group fish, would be expected to increase with age and be comparable to the fecundity of age-groups 2 and 3 of the closely related *A. marinus* (10,000–15,000 eggs, Macer, 1966).

A. americanus postlarvae, larger than 6 mm, from an inshore area, could be distinguished from *A. dubius* postlarvae, described by Scott (1972b), on the basis of melanophore development. However, these tediously-derived differences have not been determined for offshore *A. americanus* and *A. dubius* in areas of suspected overlap, such as the banks off southwestern Nova Scotia. The most obvious differences between the two species are the more rapid development of a solid line of "stomach" pigment in young postlarvae and less rapid development of "preanal", "supradorsal" and "subdorsal" melanophores in slightly older postlarvae of *A. americanus* than in *A. dubius*.

The materials for this paper were collected prior to the period (1976) when an increased abundance of sand lance was accompanied by a major shift southward in the distribution of postlarvae in February and March (Sherman *et al.*, 1981). Expected effects of this shift in the offshore population are changes in spawning time, duration of egg development, subsequent hatching time, meristic indices, and first-year growth, resulting in greater intraspecific differences in morphological and meristic characteristics between estuarine and offshore populations.

Acknowledgements

Many persons helped to provide me with samples of sand lance. I am particularly indebted to Don Flescher of the Northeast Fisheries Center, Woods Hole, who arranged for the collection of specimens from the trawl surveys and who sent me many samples previously; J. S. Scott of the St. Andrews Biological Station, New Brunswick, Canada, provided sand lance from Emerald Bank, William C. Leggett of the Zoology Department, McGill University, Montreal, provided specimens from the St. Lawrence River; and Ian Nesbit, then of the Massachusetts Audubon Society, saved specimens from the Chatham region of Cape Cod. Others, who kindly donated specimens, were Helen Hays of the Ornithology Department of the American Museum of Natural History, George C. Williams of the Marine Sciences Department of the State University of New York at Stony Brook, Long Island, and Donald Dorfman of the Biology Department of Monmouth College, New Jersey. Those who helped to collect for the Little Harbor Laboratory were Alan Poole, Fred Richards, Anita Riedinger, Frank Schley, David Wellman and Richard Wellman. Warren Rathjen, of the National Marine Fisheries Service Gear Development Group in Gloucester, Massachusetts, suggested the use of the Japanese elver trap for catching sand lance. Laboratory work-up of the material was done principally by Cynthia Thomas, Colleen O'Connor and Eileen O'Connor, with help from Joseph A. Walker. J. S. Scott kindly reviewed the manuscript. The editorial assistance of Vincent M. Hodder is appreciated. To all of the above, I am extremely grateful.

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