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*ECOLOGY OF YOUNG  
WINTER FLOUNDER  
IN AN ESTUARY*

**BULLETIN**

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Ecology of an Estuarine  
Population of Winter Flounder,  
*Pseudopleuronectes americanus*  
(Walbaum) · Parts I-IV

WILLIAM G. PEARCY

*Issued August 1962 · New Haven, Connecticut, U.S.A.*

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*Ecology of an Estuarine Population of  
Winter Flounder Pseudopleuronectes americanus  
(Walbaum)<sup>1,2</sup>*

*I. Hydrography of the Mystic River Estuary*

By

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ABSTRACT

The Mystic River estuary, in eastern Connecticut, is small, only 8.5 km in length, and its tidal prism is 38% of the volume at mean high water ( $11.4 \times 10^6$  m<sup>3</sup>). The recorded temperature in the channel during 1958-59 ranged from -0.8 to 25°C, with seasonal warming and cooling taking place more rapidly in the upper than in the lower estuary. Salinity at the mouth averaged 30‰ and decreased toward the head. Vertical salinity stratification became more pronounced landward, indicating a well developed two-layer transport system in the upper estuary. Current profiles also displayed vertical differences that reflected two-layer transport. The exchange ratio for the upper estuary during the spring, calculated from net current velocities, volume of freshwater influent, and morphometric measurements, is estimated to be 0.16.

*Introduction.* Although the problems of hydrography are often similar among estuaries, generalizations regarding their basic physical features are encumbered by the inherent variability of this biotope (*e.g.*, Ketchum, 1952). Consequently, knowledge of the physical environment, a fundamental part of many ecological studies, must often be gained through direct observation in a particular estuary. This paper provides a brief descriptive account of certain hydrographic features of the Mystic River estuary which may be useful in an interpretation of the distribution or abundance of estuarine animals. Temperature, salinity, and circulation are considered.

<sup>1</sup> Contribution No. 16 from the Marine Research Laboratory, University of Connecticut.

<sup>2</sup> These four papers represent the major portion of a dissertation presented to the Faculty of the Graduate School of Yale University in candidacy for the degree of Doctor of Philosophy.

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*Acknowledgments.* I wish to thank Gordon A. Riley and Sarah W. Richards of the Bingham Oceanographic Laboratory for their assistance in all phases of these studies. Constructive criticism of the manuscripts by Daniel Merri-man, E. F. Thompson, and L. M. Passano is appreciated. G. B. Deevey and Pierre Brunel helped to identify copepods and amphipods respectively. Field work was conducted at the University of Connecticut Marine Research Laboratory, Noank, Connecticut, through the cooperation of its director, J. S. Rankin, Jr. Charles Rogers constructed the beam trawl and maintained much of the equipment used in the field. Also, I acknowledge the assistance of my wife with field work and preparation of the manuscript.

U.S. Public Health Service (EF-10, 632), The Wendell Anderson Fellowship, the Bingham Oceanographic Laboratory, and the Office of Naval Research provided financial support.

*Methods.* Area-depth relationships were derived from planimeter measurements of the depth contours from U.S. Coast and Geodetic Survey Chart 358. Additional sounding data were provided through the courtesy of the U.S. Corps of Engineers.

Water samples for salinity determinations were taken at least monthly, generally at high or low water. They were collected from July 1958 to September 1959 with a Kemmerer water bottle at Sts. 0.4, 2.1, 3.7, 5.1, 6.2, and 7.5 (numbered according to the distance in kilometers from the head of the estuary). Over 500 salinity analyses were made, mostly by chlorinity titration, but hydrometers were used occasionally. Temperature was measured by means of a bucket thermometer or a thermistor when the water was sampled. The standard Winkler method was used for oxygen determinations.

Currents were measured by the method of Pritchard and Burt (1951). Net currents were estimated for six complete tidal cycles at Sts. 2.1, 3.7, or 6.2 in the spring of 1959. Duplicate readings were made every 0.5, 1, or 2 hours at each one-meter depth interval.

Estimation of freshwater drainage into the estuary was possible from data on the watershed area (U.S. Geological Survey, personal communication) and run-off volumes from the nearby Great Brook (Borough of Groton, Department of Utilities; personal communication). Direct current measurements were also made in the Mystic River by the flotation method (Welch, 1948).

*Hydrography.* The Mystic River estuary (Fig. 1) is located in eastern Connecticut and opens into Fishers Island Sound, the northern boundary between Long Island and Block Island sounds. The estuary, presumably a drowned river valley in origin, is 8.5 km in length (4.6 nautical miles). It is a relatively simple one-channel system which runs perpendicular to the coast. On the basis

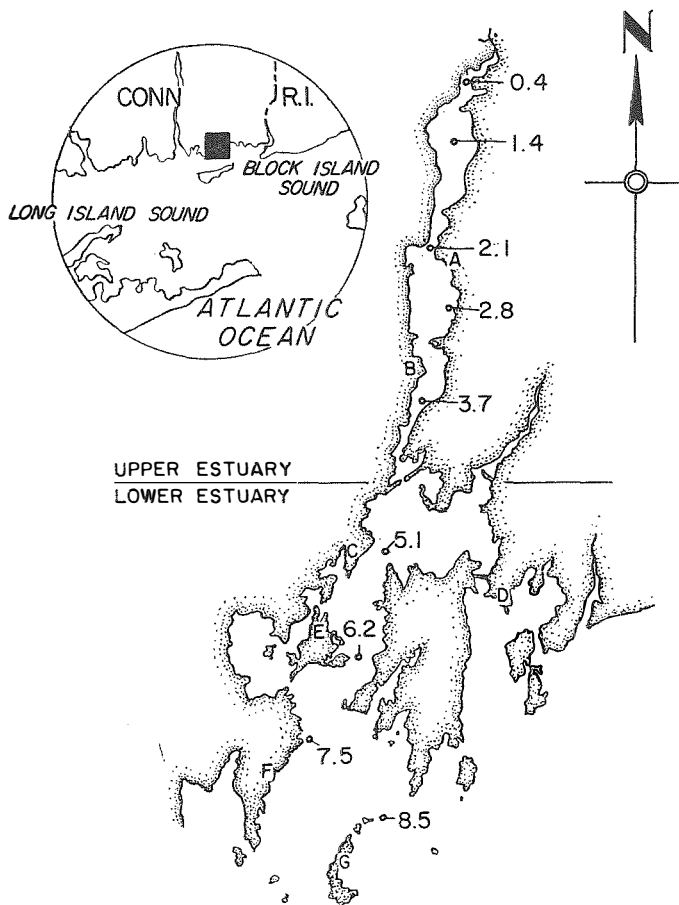


Figure 1. The Mystic River estuary. Station numbers designate their location in kilometers distance from the head of the estuary. Seine stations along the shore are shown by letters.

of morphometry, the estuary is divided into two major regions: the elongated landward extension (*upper estuary*), and the widened seaward portion (*lower estuary*).

The area-depth relationships are summarized in a hypsograph (Fig. 2). The total area of the estuary is 5.4 km<sup>2</sup> at mean low water (MLW). About half of this area is less than one meter in depth. The volume of the estuary at MLW, calculated from the formula of Welch (1948), is  $7.1 \times 10^6$  m<sup>3</sup>. With a mean tidal amplitude of 0.8 m (Tide Tables, U.S. Coast and Geodetic Survey), the volume at mean high water (MHW) is approximately  $11.4 \times 10^6$  m<sup>3</sup>. The intertidal volume is about 38% of the volume at MHW.

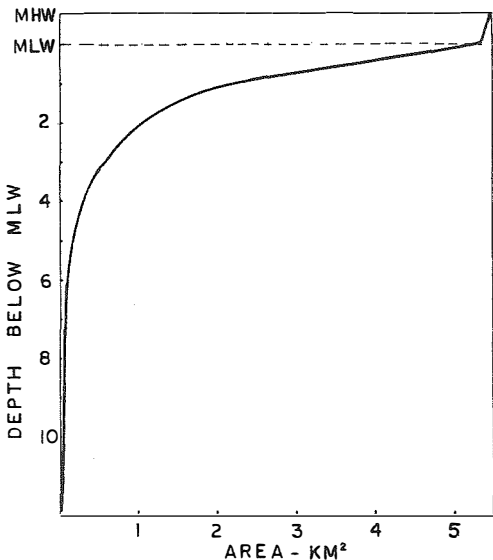


Figure 2. Hypsograph (area and depth) of the Mystic River estuary.

*Temperature.* The averaged temperature data for two stations, one in the upper and one in the lower estuary, demonstrate the large amplitude of the annual temperature cycle (Fig. 3). Water temperatures were the lowest in January, when individual readings were as low as  $-0.8^{\circ}\text{C}$ , and highest in July and August when some readings were over  $25^{\circ}\text{C}$ . (Greatest temperature extremes occurred on the shallow flats where anchor ice may form in the winter and where temperatures of over  $30^{\circ}\text{C}$  were observed in the summer). The temperatures in the shallower upper estuary were more extreme than those in the deeper lower estuary, the former having a lower winter minimum and a higher summer maximum. Since cooling in the fall and warming in the spring were more rapid in the shallow waters, average temperatures there were below those of the lower estuary from October to February and above from March to September.

Thermal stability for both stations was greatest during the spring warming period and in the summer. In the fall, temperature inversions were common. During fall and winter, isothermal profiles were typical, often being associated with strong winds.

Temperature inversions were also found at St. 0.4 during the summer, when the freshwater influent was cooler than the underlying estuarine water.

The temperature regime for June 1959–March 1960 was about  $1^{\circ}$ – $4^{\circ}\text{C}$  warmer than for the same period a year earlier. Only during the first winter was solid ice formed over the upper estuary.



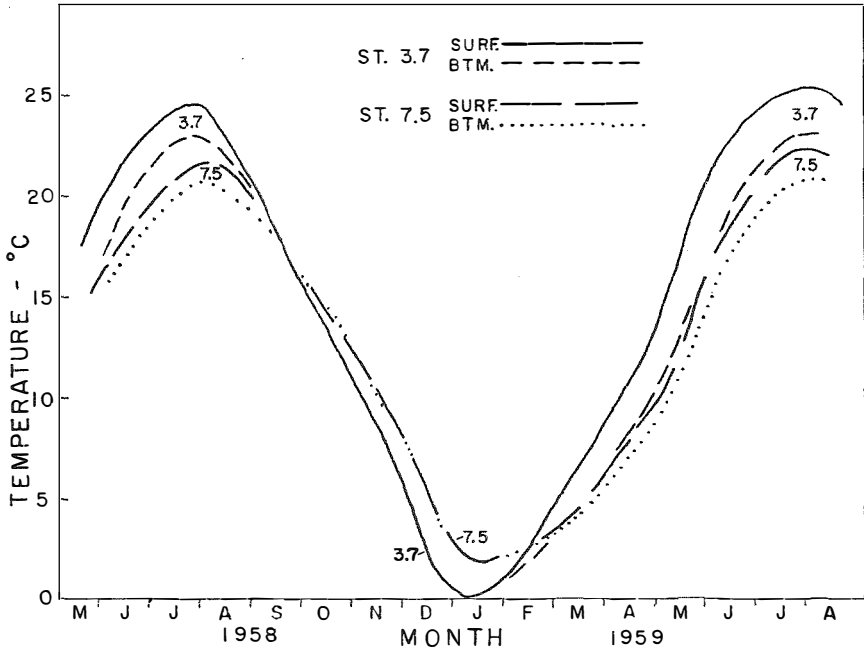


Figure 3. Seasonal distribution of surface and bottom temperatures at a station in the upper and lower Mystic River estuary.

Sediment temperatures lagged behind rapidly changing water temperatures, and in the fall, for example, temperatures under several centimeters of mud were as much as  $2^{\circ}\text{C}$  warmer than the bottom water temperature.

*Oxygen.* Although untreated domestic wastes are discharged directly into the Mystic River estuary, no deleterious effects from them were noted. The oxygen content of water samples collected during midsummer in the deepest water along the length of the estuary ranged from 2.95–3.80 ml/l, and all were above 50% saturation. There was also little difference in the concentration of oxygen in the bottom water at 1700 EST and then 12 hours later (3.85 vs. 3.07 ml/l), both samples taken at low tide at the town of Mystic on September 7, 1959.

*Salinity.* Although average salinities have been calculated, it should be emphasized that these values have no meaning in a static sense, since variations were continuous, often extreme and unpredictable. The wide range of salinity at each station is apparent in Table IA. Variations presumably result from the interaction of tidal forces, stability structure, and wind stress.

The plot of salinity variations over a complete tidal cycle consisted of asymmetrical oscillations, with the greatest difference between surface and bottom

TABLE I. SALINITIES AND DENSITIES AT SIX STATIONS IN THE MYSTIC RIVER ESTUARY.

	STATION											
	Lower						Upper					
	7.5		6.2		5.1		3.7		2.1		0.4	
A. Annual salinity range (‰)												
Surface	23.1-30.7	21.0-30.3	19.4-27.8	12.6-25.9	4.1-25.5	0 - 7.9						
Bottom	29.9-30.7	27.6-30.4	24.5-29.7	22.8-29.4	18.1-28.9	3.2-21.4						
B. Average salinity profiles for high and low water												
Depth (m)	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW
0	28.3	30.1	26.2	27.6	25.1	27.5	19.2	23.0	15.6	17.7	4.3	1.9
1	29.2	29.9	26.4	28.3	25.4	27.5	19.9	23.7	17.9	21.5	13.6	12.1
2	29.5	30.0	26.9	28.7	26.2	27.7	21.3	24.9	19.5	23.5	-	18.4
3	29.8	30.2	27.4	29.0	26.6	28.7	23.7	26.1	22.2	24.6	-	-
4	29.9	30.3	27.9	29.1	27.6	28.6	25.0	26.6	23.9	26.2	-	-
5	30.2	30.4	27.9	28.9	-	-	-	27.7	26.5	25.6	-	-
6	-	30.6	28.8	29.8	-	-	-	-	-	-	-	-
C. Differences between surface and bottom densities ( $\Delta\sigma_t$ )												
Ann. Mean	1.10	1.87	1.94	3.52	6.72	-						
March-May	2.70	3.10	3.90	5.16	8.75	-						

occurring at slack water and the least difference during half tide when mixing was pronounced. The average high and low water salinities (Table IB) as well as the salinity ranges (Table IA) indicate that variations are greater in the upper estuary. No consistent seasonal trends in salinity were evident.

Average salinity profiles for each station (Fig. 4) illustrate the "positive" structure of the estuary, with salinities increasing from head to mouth. Strong vertical gradients, present in the upper estuary, diminished seaward to a nearly

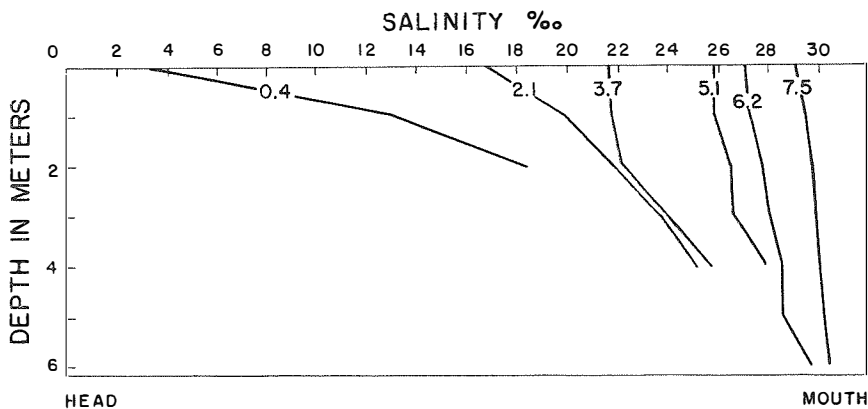


Figure 4. Average salinity profiles for the Mystic River estuary. Each profile is designated by a station number (0.4-7.5).

isohaline profile near the mouth. Such horizontal variations in the vertical salinity structure paralleled density ( $\sigma_t$ ) differences (Table IC) and therefore indicated increasing vertical stability in the landward direction.

This structure allows certain inferences on net transport; namely, a well defined two-layer transport system in the upper estuary with its resultant net seaward flow near the surface and a landward countercurrent near the bottom. The decreased stability near the mouth reflects greater vertical mixing in this area (perhaps due to increased wind stress) and less differentiation on the two-layer system.

The density differences between the surface and bottom fluctuated, depending upon local conditions, but high values often occurred during the spring (Table IC), perhaps because of the thermal stratification and accelerated freshwater run-off during this season. However, the greatest density gradient,  $\Delta\sigma_t = 15$ , was found under solid ice at St. 2.1 in January 1959. It is noteworthy that density inversions, due to salinity differences of over 0.5‰, were common at mid-depths at St. 2.1; possibly they were related to "tidal over-mixing" (Burt and Queen, 1957).

*Freshwater Influent.* The quantity of fresh water entering the estuary influences the salinity distribution and is an important consideration in the quantitative analysis of net transport. The volume of freshwater influent was determined indirectly by comparing the area of the watershed of the Mystic River estuary with that of the neighboring Great Brook for which monthly stream flow was available. The drainage area of the Mystic River system, 16.8 km<sup>2</sup>, is about 1.9 times that of the other watershed. This factor was multiplied by the stream flow volumes for Great Brook, thereby providing approximations for the amount of fresh water entering the Mystic River estuary. The mean annual volume was 1/59th of the intertidal volume per tidal cycle. For the spring period (March–June), with its higher run-off, the value was 1/44th of the intertidal volume, which is equal to about  $97 \times 10^3$  m<sup>3</sup>.

Direct current measurements in the Mystic River, although variable, corroborated the indirect estimates above.

*Tidal Currents.* Tidal forces, which effect the exchange of the intertidal volume and supply the energy for mixing processes in the estuary, were measured with the current drag. The mean flood velocities for a complete tidal cycle generally exceeded the mean ebb velocities, but the ebb phase was often of longer duration. The current profiles indicated both flooding and ebbing at all depths, with maximum velocities (up to 0.74 m/sec.) associated with flooding at lower depths. (One series, taken during a moderate up-estuary wind, however, demonstrated maximum flooding near the surface.) Ebbing tended to be largely restricted to the upper water layers, especially in the upper estuary. These observations are in general agreement with those of LeLacheur and Sammons (1932).

The range of the tide, measured at both the head (St. 0.4) and the mouth (St. 7.5) on two occasions, was nearly equal. Tidal phases, on the other hand, were later at the head of the estuary.

*Net Transport.* Net current velocity, or nontidal drift, represents the difference between the flood and ebb current velocities over an entire cycle. In Fig. 5, net transport in the surface waters is in a seaward direction (ebb) whereas the net velocities in the lower half of the water column show transport in a landward direction (flood). Both of these net current profiles reflect two-layer transport.

The net velocity and transport data for three tidal cycles at St. 3.7 are summarized in Table II. The net velocities were calculated from the difference between the sum of ebb and the sum of flood velocities divided by the number of observations for each tidal cycle. The net velocities for each depth interval were then averaged for the three tidal cycles. The product of a mean net velocity and its respective planimeted cross-sectional area gives an estimate of net transport.

The current measurements at St. 3.7 resulted in an average profile with net flooding at all depths, a situation obviously inconsistent with continuity requirements. The salt balance equation of Riley (in press), which was modified for a single tidal cycle and applied to the high and low water average salinity profiles (Table IB), also gave excessive values for landward transport. Both of these approaches indicate the difficulty of reliably describing transport parameters from a few observations. Exchange is apt to be complex, transient, and nonsinusoidal. Fluctuations among tidal ranges are common, and observations on consecutive tidal cycles would be necessary to approximate a so-called average situation. In addition, data were obtained at a linear series of stations

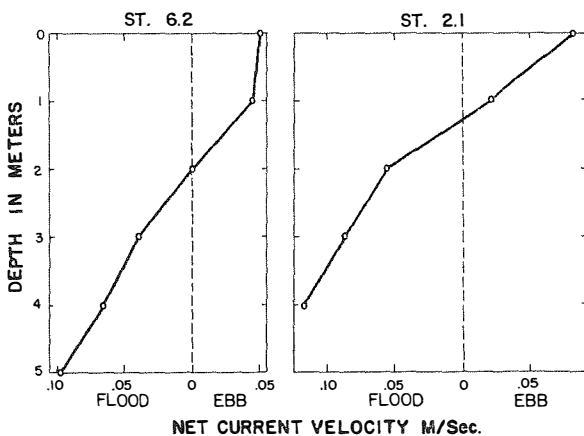


Figure 5. Net current profiles for two stations in the Mystic River estuary, April 24, 1959.

TABLE II. AVERAGE NET TRANSPORT FOR THREE TIDAL CYCLES AT ST. 3.7 DURING THE SPRING OF 1959<sup>1</sup>. ALL VELOCITIES ARE IN THE FLOOD OR LANDWARD DIRECTION.

Depth (m)	Mean net Velocity (m/sec)	Cross-sectional Area (m <sup>2</sup> )	Transport (m <sup>3</sup> /sec)
0.0-0.5 .....	.0075	69.5	0.522
0.5-1.5 .....	.0188	73.9	1.389
1.5-2.5 .....	.0104	57.4	0.597
2.5-3.5 .....	.0536	47.0	2.519
3.5-4.5 .....	.0432	41.0	1.771
4.5-5.5 .....	.0032	18.0	0.058

<sup>1</sup> One series that was interrupted by marked changes in wind velocities is not included.

The mean net velocity for each tidal cycle was estimated by  $(\Sigma F_v - \Sigma E_v)/n$ , where

$F_v$  = tidal velocity of flood

$E_v$  = tidal velocity on ebb

$n$  = no. observations per tidal cycle series.

along the length of the estuary, requiring a two-dimensional analysis. This is valid only if lateral uniformity is assumed. However, currents and salinities may vary across the estuary due to changes in morphometry and to frictional effects of the bottom. Lateral salinity gradients of 1 ‰, observed across the estuary at St. 3.7, offer direct evidence for the lack of lateral uniformity. Also, currents and salinities at each meter depth interval may not have been representative of the vertical interval  $\pm 0.5$  m, in which case linear interpolation between depths is not justified. Finally, sampling intervals may not have adequately represented the time between observations; this would be especially true if asymmetrical tidal phases existed. These limitations, including criticism of the current drag method, are discussed by Pickard and Rodgers (1959).

Estimation of the exchange ratio by the following simplified equation was attempted for the upper estuary where, in spite of the directional anomaly in net velocities at St. 3.7, both salinity and current observations consistently indicated a two-layer system:

$$r = \frac{\sum (\bar{V}_d A) + I}{V_h}, \quad (1)$$

where  $r$  is the exchange ratio, or the fraction of total volume permanently transported seaward per tidal cycle (Ketchum, 1951),  $\bar{V}_d$  the average net landward velocity per tidal cycle at depth  $d$ ,  $A$  the cross-sectional area corresponding to  $\pm 0.5$  m on each side of the depth  $d$  at mean tidal level,  $I$  the volume of fresh water added to the estuary per tidal cycle, and  $V_h$  the volume of the upper estuary at high water.

The dividend in eq. (1) is then the sum of the net landward transport plus the volume of fresh water entering per tidal cycle. The volume,  $I$ , was previ-

ously calculated to be  $97 \times 10^3$  m<sup>3</sup>. Since the major portion of the net landward transport was at depths greater than two meters (Table II, Fig. 5), this depth is assumed to be the layer of no-net-motion, and only transport below this depth is considered. The mean net transport so calculated is  $207 \times 10^3$  m<sup>3</sup>. Substituting these values into the equation, the exchange ratio equals  $304/1925$  or 0.16.

If the zero net velocity reference line is drawn to intersect the current profile for St. 3.7 at two meters depth, landward transport will still be too high. Therefore, any error in the average exchange ratio as calculated above is likely to be in excess. It is noted, however, that eq. (1) consists of several terms and does not magnify error in current velocities. Also, the above estimates are not inconsistent with the intertidal volume of  $881 \times 10^3$  m<sup>3</sup> for the upper estuary. Thus, the above value for  $r$  appears to be a reasonable approximation of the exchange parameter for the upper estuary.

Currents in the adjoining Sound are relevant, since they affect the disposition and eventual fate of plankton that drift out of the estuary. Surface tidal currents in Fishers Island Sound are strong (averaging almost one knot) and run parallel to the coastline; the nontidal drift is eastward toward Block Island Sound and the Atlantic Ocean (LeLacheur and Sammons, 1932; Riley, 1952). As a result of these currents, very little water and plankton leaving the estuary are thought to return during subsequent tidal cycles.

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Вильям Г. Перси

Экология предустьевой популяции зимней камбалы  
*Pseudopleuronectes americanus* (Walbaum)

I. Гидрография эстуария реки Мистика.

#### Краткий Обзор

Эстуарий реки Мистика в восточной части штата Коннектикут длиной всего в 8.5 километров. Объему его приливо-отливочной воды составляет 38% объема воды во время прилива средней высоты ( $11.1 \times 10^6 \text{ m}^3$ ). Температура русла зарегистрированная в 1958–59 г. колебалась между  $-0.8^\circ$  и  $+25^\circ\text{C}$ . Сезонное повышение и понижение температуры происходит быстрее в верхней чем в нижней части эстуария. Соленость у устья равнялась в среднем 30‰ и уменьшалась с удалением от устья. Вертикальное расслоение солености становилось более резким с удалением от устья, что указывает на хорошо развитую систему двухслойного передвижения. Разрезы течения тоже проявили вертикальные различия указывающие на двухслойное передвижение. Коэффициент обмена (0.16) был подсчитан по скорости течения, объему втекающей пресной воды и морфометрическим измерениям.

*Ecology of an Estuarine Population of  
Winter Flounder, Pseudopleuronectes americanus  
(Walbaum)*

*II. Distribution and Dynamics of Larvae*<sup>1</sup>

By

William G. Percy

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ABSTRACT

In weekly plankton collections of winter flounder larvae from February through June 1959 at seven stations in the Mystic River estuary, larvae were common from March to June. They were most abundant in the brackish waters of the upper estuary during March and April when densities were often over 10/m<sup>3</sup>; later in the spring, the bulk of the population was found in the lower estuary.

Vertical distribution studies revealed that larval densities near the bottom were about six times those near the surface; and laboratory observations disclosed that the larvae have a mixed planktonic and benthonic behavior. On the basis of larval distribution and estuarine circulation, it has been calculated that currents removed 3% of the population per day from the upper estuary, about one-third the loss that would be expected if there were uniform vertical distribution. The concentration of larvae near the bottom and in the upper estuary, where a countercurrent was apparent, is believed to be a major factor in reducing offshore dispersal. Variations in vertical and size distribution are explained by differences in circulation and by the weaker swimming ability of small larvae.

The post-recruit catch curve, constructed from the size-frequency distribution of over 3000 larvae and growth data, is concave, indicating high losses early in larval life followed by gradually decreasing loss rates with age. The estimated loss rate for small larvae is 20% per day as compared to only 4% for postlarvae. Both natural mortality and translocation are higher for young larvae. Natural mortality, however, is deduced to be the major component of total losses and of the age-specific differences in the loss rates.

*Sarsia tubulosa* medusae preyed on flounder larvae, and their distribution in time and space was similar to that of the larvae. Assuming a lesser ability of small larvae to evade and escape the medusae, a differential predation rate is postulated that helps to explain the relatively high mortality rates for small larvae.

Since the adult winter flounder spawns in estuaries and inlets along the coast and since the young stages are nondispersive, the breeding and nursery grounds are localized in the

<sup>1</sup> Contribution No. 17 from the Marine Research Laboratory, University of Connecticut.



same area. Several ecological relationships concerning the inshore breeding habits of this species are discussed. In addition, similarities in the biology of other flatfish known to lay demersal eggs are pointed out.

*Introduction.* Relatively little is known about the population dynamics of the young stages of animals in nature. This is especially true about species with a high fecundity, where early stages are abundant. During the early life history of such species, important and dramatic changes in population parameters (such as natural mortality) may occur, and slight changes in early survival can result in significant changes in later abundance. Most of the literature on marine fish populations concerns large or adult fishes. There are only a few quantitative studies on the larval or juvenile stages, and none are known that treat the entire early life history. Major reasons for this lack are associated with the location of spawning, the type of eggs laid, and the distribution of early stages. Fecund species, including most fishes of commercial importance, usually lay buoyant or pelagic eggs offshore and over large areas; this results in wide dispersal of young stages, which greatly increases the problems of sampling and assessing population parameters.

However, the winter flounder, *Pseudopleuronectes americanus*, is unusual in that it has a high fecundity while its eggs are demersal, that is, they sink and are nondispersive. This results in a concentration of young near the spawning grounds. Since breeding takes place in shallow, semi-isolated inlets and estuaries along the coast, localized and independent populations are formed (Perlmutter, 1947). Such is the case in the Mystic River estuary, thus providing a rather unique opportunity to study a population of young marine fish.

The general life history of the winter flounder has been reviewed by Bigelow and Schroeder (1953). Information from the present study on the location and time of spawning in the Mystic River estuary and on characteristics of its eggs pertains to larval distribution and abundance. The spawning migration of adults into the estuary was determined by catches in a trapnet set at the mouth of the estuary; there was a five-fold increase in the catch per day between January 10 and February 12, 1959, and ripe adults were common until April. The number of adults captured by otter trawling showed that the principal spawning grounds were in the upper estuary. Catches there, which were almost as high as 1.0 fish/m<sup>2</sup> in March, averaged 16 times the catches in the lower estuary during the breeding season. The number of ripe and spent individuals indicated that spawning commenced about mid-February, reached peak activity in March, and extended through April 1959. Bottom temperatures in the upper estuary for this period ranged from 1–10°C, with peak spawning at about 2–5°C. (In the milder winter of 1960, adults were common earlier in the winter, and spent females were recovered in January.) Over 100 flounder eggs were collected in plankton tows, mainly from the upper estuary. The eggs were small, 0.75–0.96 mm, and usually adhered to each other, forming clusters. The specific gravity of individual fertilized

eggs, as determined with gum arabic and seawater, was 1.085–1.095 compared to *in situ* estuarine water of 1.010–1.024.

The high densities of young winter flounder in the Mystic River estuary, then, are due to the high fecundity of adults, the location of spawning within the estuary, and the nondispersive nature of the eggs. This paper is mainly concerned with another factor affecting larval abundance: losses of the population from the estuary due to net currents and natural mortality.

*Materials and Methods.* Larvae from over 200 plankton tows formed the basis for this study. Weekly collections were made from February to June 1959 at Sts. 0.4, 1.4, 2.1, 3.7, 5.1, 7.5, and 8.5. Samples were also taken at these stations biweekly during the summer, and monthly during January and February 1960. The plankton net was 47 cm in diameter; No. 2 mesh was selected to preclude escapement of even the smallest larvae through the mesh. A Clarke-Bumpus meter wheel was mounted in the center of the net, and the volume of water filtered was calculated directly from the relative area of openings and from measured volume passing through the meter. The average tow filtered about seven cubic meters of water. Horizontal surface tows were confined to the upper meter of water; horizontal bottom tows, in the bottom meter of water, were achieved by attaching a weighted cord to the bridle of the net, sinking the net vertically, and towing so that the weight dragged along the bottom.

Oblique tows were made by bringing the weighted net from the bottom to the surface at a uniform rate.

Plankton collections were preserved immediately in the field with formalin in seawater. All of the larvae were sorted from the total plankton and counted, except for three collections, where they were very numerous and subsamples were aliquoted. Larvae were measured to the nearest 0.1 mm in length from the tip of the maxilla to the end of the notochord (standard length) with the aid of a dissecting microscope and an eyepiece micrometer. Although most of the larvae were measured within a week of capture, some were measured several months later. The average difference in length between replicate measurements of the same larvae, remeasured eight months later, was  $\pm 0.05$  mm, indicating little shrinkage during preservation.

Although a study of catch variation is not intended as an objective in this paper, the following statistics provide information on the reliability of subsequent data. Ten pairs of plankton tows, taken at the same station and within several minutes of each other, gave coefficients of variation,  $C$ , for the catch/ $m^3$  ranging between 1.2–57% (mean 23%). The variation of catch within a tidal cycle at a station was considerably higher than for duplicate tows. Collections taken periodically (usually at two-hour intervals) during four tidal cycles at St. 3.7 gave  $C$ 's ranging from 52–146% (mean 96%) for similar types of tows. Catch/ $m^3$  was usually highest during low water at this station,

probably because of the incursion of water from up-estuary which contained higher densities of larvae during the sampling dates.

In view of the additional variability associated with time between tows, including tidal and perhaps diurnal effects, it was desirable to make all collections under conditions that were as nearly uniform as possible. Consequently, collections were usually taken at high water. As tidal phases progressed gradually up the estuary, collections could be made at all stations at approximately the same tidal stage.

Catch/m<sup>3</sup> of day and night tows taken during single tidal cycles at St. 3.7 showed no consistent differences that were independent of tidal variations. The sizes of larvae captured during the day and night were similar. Thus there was no evidence for greater avoidance of the plankton net during daylight than at night.

The catch/m<sup>3</sup> for all types of tows taken at a station during a cruise was averaged by

$$\frac{(\text{surface catch/m}^3 + \text{bottom catch/m}^3)/2 + \text{oblique catch/m}^3}{2} \quad (1)$$

Comparison of data for oblique catches with the average for surface and bottom catches gave a mean coefficient of variation of 40%. Even though this was higher than the *C* for duplicate oblique tows, it is believed that all available data should be included in the estimates of the average density of larvae.

*Drift and Distribution of Larvae.* The problem of retention of an endemic population of plankton in an estuary having a net seaward transport is apparent. Seaward dispersal is basically a result of the direction and speed of net currents. If these vary horizontally and vertically, then the distribution of plankton relative to these diverse currents may have a critical bearing on their rates of removal (Ketchum, 1954, *et al.*). Behavior may also modify the translocation rates since many so-called planktonic animals are not completely at the mercy of the currents. Active orientation, such as tactic responses, as well as passive physical factors, such as specific gravity, etc., may be important (Bishai, 1960). The duration of larval life for meroplankton is also directly related to the degree of offshore translocation (Thorson, 1950).

The exchange ratio for the upper Mystic River estuary has been estimated to be 0.16 (Pt. I); in other words, about 30% of the volume is removed seaward per day. The winter flounder, which hatches at a small size, has a larval period lasting about two months before metamorphosis. Considering the rather long larval period and the possibility that exchange regularly removes a percentage of the extant population during each of 120 tidal cycles, maintenance of the larval population in the rigorous estuarine environment appears

tenuous. The question of how the population is retained leads us to an examination of the larval distribution within the estuary.

**VERTICAL DISTRIBUTION.** Information on the vertical distribution of the larvae was derived from 61 paired surface and bottom plankton tows, each pair being made at the same station several minutes apart. The proportion of larvae near the bottom,  $B$ , was calculated for each pair of collections by the following equation:

$$B = \frac{C_b}{C_b + C_s}, \quad (2)$$

where  $C_b$  and  $C_s$  are the catch/m<sup>3</sup> for the bottom and surface tows respectively. The results, summarized in Table I, show that the catch/m<sup>3</sup> is nearly always greater for the bottom tow. The mean  $B$  is 0.85, showing that the vertical distribution was not even: densities of larvae near the bottom were about six times those near the surface.

In the estuary, seaward transport was reduced towards the bottom, and both current and salinity profiles indicated two-layer transport, especially in the upper estuary. If we assume that all net seaward transport occurred in the upper half of the water column, then the percentage of larvae removed seaward (the translocation rate) is a product of exchange and the percentage of larvae in the surface waters. Exchange, or that proportion of water volume removed per tidal cycle above 2 m, equals 0.19 for the upper estuary ( $304 \times 10^3$  m<sup>3</sup>/1591  $\times 10^3$  m<sup>3</sup>; see Pt. I). The translocation rate, then, is  $0.19 \times (1-0.85)$ , or .03. In other words, about 3% of the larval population was dispersed seaward per tidal cycle. This estimate is appreciably less than the exchange ratio, and it is less than one-third the loss that would be expected if there were no differences in vertical distribution of the larvae. Thus the high concentrations of larvae in deep water appear to be of major significance in reducing offshore dispersal.

Laboratory observations on the swimming behavior of the larvae are informative at this time in interpreting the gradient in depth distribution found in the estuary. Winter flounder larvae are nonbuoyant. Live pro-larvae have

TABLE I. VERTICAL DISTRIBUTION OF DIFFERENT LENGTH CATEGORIES OF LARVAE AS DETERMINED BY PAIRED SURFACE AND BOTTOM PLANKTON TOWS. THE RATIO  $B$  IS AN ESTIMATE OF THE PROPORTION OF LARVAE FOUND NEAR THE BOTTOM.

Larval Length (mm)	B	Larval Length (mm)	B	Larval Length (mm)	B
2.5-2.8	.83	4.3-4.6	.99	6.1-6.4	.96
2.8-3.1	.81	4.6-4.9	.98	6.4-6.7	.93
3.1-3.4	.80	4.9-5.2	.97	6.7-7.0	.91
3.4-3.7	.82	5.2-5.5	.97	7.0-7.3	1.00
3.7-4.0	.88	5.5-5.8	.97	7.3-7.6	.95
4.0-4.3	.94	5.8-6.1	.99		

a passive sinking rate of about 4 mm/sec in sea water having a specific gravity of 1.022. These small larvae are feeble swimmers; they swim in a vertical 90° climb, and when they stop they rotate 180° and passively sink in a head-down attitude. Swimming ability increases with size, and the large larvae are not restricted to these vertical movements. Frequently the small larvae, and the large ones as well, sink to the bottom of the aquarium and come to rest (see also Sullivan, 1915; Bigelow and Welsh, 1925). These observations are of special interest since they reveal that the winter flounder larvae are partially benthic animals; thus an explanation is offered for their high concentrations in bottom waters.

Comparison of the vertical distribution of different sizes of larvae was made after measuring 1242 specimens from surface and bottom tows. The number in the 0.3-mm length categories was recorded for each tow, and these numbers were made proportional to the catch/m<sup>3</sup> by the following ratio:

$$\frac{(\text{no. measured in each size category}) (\text{tow catch}/\text{m}^3)}{\text{total no. measured from the collection}} \quad (3)$$

The adjusted numbers in each 0.3-mm size category were then summed, and the percentage of larvae taken in bottom tows was calculated (omitting size categories with less than five individuals). The results are given in Table I. Consistent differences are evident between the vertical distribution of small and large larvae. The lowest percentages are for the small ones; that is, small larvae are less common near the bottom and more common near the surface.

If these size-depth differences are due to the weaker swimming ability of small larvae and to their greater susceptibility to transfer into surface waters by vertical turbulence, then a lower percentage would be expected both in the lower estuary, where vertical mixing is greater, and early in the larval season, when the average size is minimal. As is seen in Table II, such is the

TABLE II. PROPORTION OF LARVAE CAPTURED IN BOTTOM TOWS, B, PLOTTED FOR SEVERAL LOCATIONS DURING THE SPRING.

	STATION NUMBER			
	7.5	5.1	3.7	2.1
May .....	.95	1.00	1.00	1.00
	.89	1.00	.94	.65
April .....	1.00	.79	.90	.85
	1.00	1.00	.96	.84
	.72	—	.99	.94
	.69	.82	.89	.92
	—	—	.90	—
March .....	.40	.78	.94	.84
	.55	.47	.53	.89

case. Here ratios for dates and stations are plotted against each other, using the most complete time-station data available. Note the general trend for small ratios or low catches near the bottom toward the lower left of the table, *i. e.*, near the mouth of the estuary and early in the spring. Individual ratios differ significantly from the mean ratio for March and for Sts. 7.5 and 5.1 in the lower estuary, suggesting that early in the larval season larvae were common in surface waters of the lower estuary, where they would be most vulnerable to net seaward currents.

**HORIZONTAL AND SEASONAL DISTRIBUTION.** Horizontal and seasonal variations in larval abundance are shown in Fig. 1, where the average catches for the upper and lower estuary are plotted on a log scale against time. The seasonal occurrence of the larvae in both areas is similar. Low catches of less than

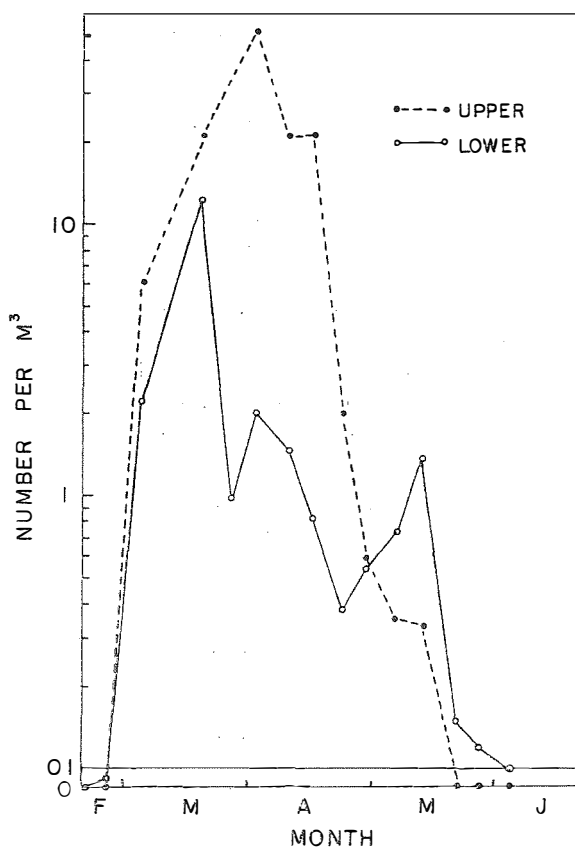


Figure 1. Average Densities of Flounder Larvae in the Upper and Lower Mystic River Estuary from February to June 1959.

0.2/m<sup>3</sup> occur prior to March, peak catches of 10–50/m<sup>3</sup> between mid-March and mid-April (with individual catches as high as 150/m<sup>3</sup>), and low or zero catches by June. Metamorphosing larvae were taken from early May into June; this change to benthic habits, where they were not sampled by plankton tows, explains some of the decline after mid-May.

Comparison of the two areas of the estuary (Fig. 1) reveals definite gradients in the horizontal distribution of the larvae. Early in the larval period, densities in the brackish waters of the upper estuary are greater than those in the lower estuary by about 15 times. Late in the spring an interesting change takes place. There is an abrupt decline of densities in the upper estuary, so that by May the densities there are below those of the lower estuary; and by mid-May no larvae are found in the upper estuary. Zero catches were first observed at St. 0.4 early in May and were found subsequently at the other stations down the upper estuary.

There was no evidence from plankton or trawl collections that these variations in the horizontal distribution were caused by *in situ* changes, such as late hatching of larvae in the lower estuary or early metamorphosis in the upper estuary. Movement of the larvae down the estuary is thought to be the explanation for the change from high catches. Note in Fig. 1 that the decline in catches in the upper estuary corresponds to an increase in the catches in the lower estuary, lending circumstantial support for a transfer of larvae down the estuary. Reasons for such a change in distribution are unknown. Since larvae were common throughout the estuary early in spring, a minimum salinity tolerance was not indicated. Perhaps the shift in the center of the population was in some way related to the earlier warming of waters in the upper estuary.

Average lengths of larvae in Fig. 2 (each average based on at least 50 measurements) show horizontal and seasonal variations. Although there is little difference in average length at different stations early in the season when larvae are small, during late March and early April an inverse relationship is indicated between larval length and distance from the head of the estuary; at this time the smallest average sizes were found in the lower estuary. During mid-April, on the other hand, this trend was reversed, with the largest larvae being taken in the lower estuary.

Possibly the weaker swimming ability of small larvae and differences in net transport explain these size variations. Early in the spring relatively large larvae were found in the upper estuary where retention would be high in countercurrent waters. Small larvae, being more common near the surface, may have been preferentially drifted into the lower estuary by accelerated seaward drift in surface waters. Once they were in the lower estuary, increased vertical mixing and weakened two-layer transport may have hastened their seaward translocation, this resulting in a relatively short residence time in the estuary and a small average size. The changes in size later in the season are probably related

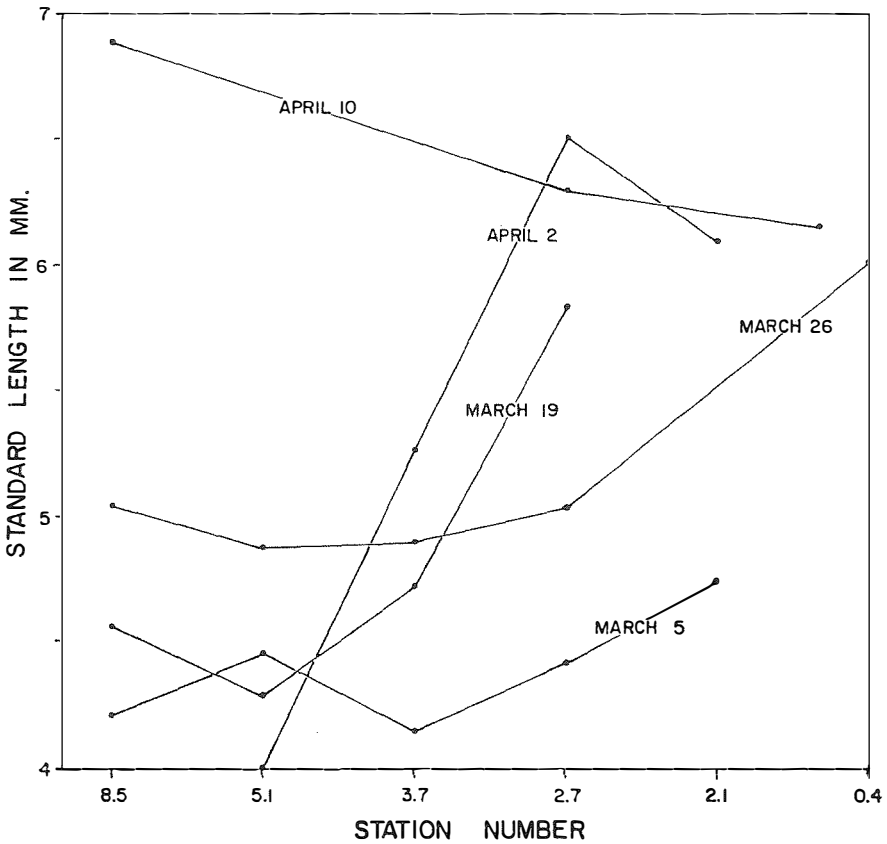


Figure 2. Variations in Average Length of Flounder Larvae with Station Location and Date.

to the apparent movement of the population down the estuary, which at that time was made up of large larvae that were presumably better able to maintain themselves in the lower estuary than small larvae. There is no evidence that different locations of spawning account for these observed changes in size distribution.

The most interesting conclusion emerging from the analysis of vertical and horizontal distribution is the fact that the bulk of the larval population was located near the bottom and in the upper estuary, the area where a two-layer transport system was pronounced and where minimal seaward losses would be expected from net currents. Later in the spring the population was found in the lower estuary, but at this time individuals were large and better able to maintain themselves within the estuary in spite of a weakened countercurrent near the bottom.



*Population Dynamics.* The foregoing considers only translocation losses from the estuary. The parameters of total loss and its two components, translocation and natural mortality, will be treated next through an analysis of the age-specific statistics of the larval population.

Data on size-frequency distribution were derived from measurements of 3128 specimens collected over the entire larval period. The numbers of larvae in each 0.3-mm length category were summed, and these totals were made proportional to the catch/m<sup>3</sup> for each collection by formula (3). In order to make the catch/m<sup>3</sup> proportional to the catch below one square meter of surface area, an adjustment was necessary to compensate for the greater depth of water in the lower estuary. The mean depth at stations in the lower estuary was therefore divided by the mean depth of stations in the upper estuary; the resulting quotient of 1.5 was multiplied by the average densities in the lower estuary.

Length was converted to age using information on larval growth derived from the average length of prolarvae of a known age (reared in the laboratory) and from length-frequency progressions for the estuarine population. Additional growth data on winter flounder larvae have been given by Williams (1902), Sullivan (1915), and Bigelow and Schroeder (1953).

Lengths ranging from 2.8–8.0 mm are plotted on a logarithmic scale against time (Fig. 3). (Even the largest larvae collected, 8.0 mm and 53 days of age, showed no signs of metamorphosis. Beyond this age, but before completing transformation, they were not frequently captured in plankton nets). The growth curve is basically parabolic, representing reduced (nonisometric) growth in length with age. Two straight lines are fitted to the data, one with a steep slope for the small larvae, the other with a gentle slope for postlarvae. The lines intersect between 5 and 6 mm, a size after which fin formation and increased body depth were often apparent. The two slopes of the growth curve (b), calculated from

$$b = \frac{\log L_2 - \log L_1}{\text{no. days}}, \quad (4)$$

give values of 0.014 (0–25 days of age) and 0.004 (26–53 days of age). Since these estimates are based on modal values rather than on growth of individual larvae, the data are considered to be minimal for describing growth.

As growth increments vary with larval size, adjustments must be made when converting length to age. The average postembryonic age of each length category is computed from

$$\text{age (in days)} = (\log L_2 - \log L_1)/b \quad (5)$$

(Sette, 1943), where  $L_1$  is the mean size at hatching (2.9 for laboratory animals);  $L_2$  the size category's median length; and  $b$  the increase in log length per day.

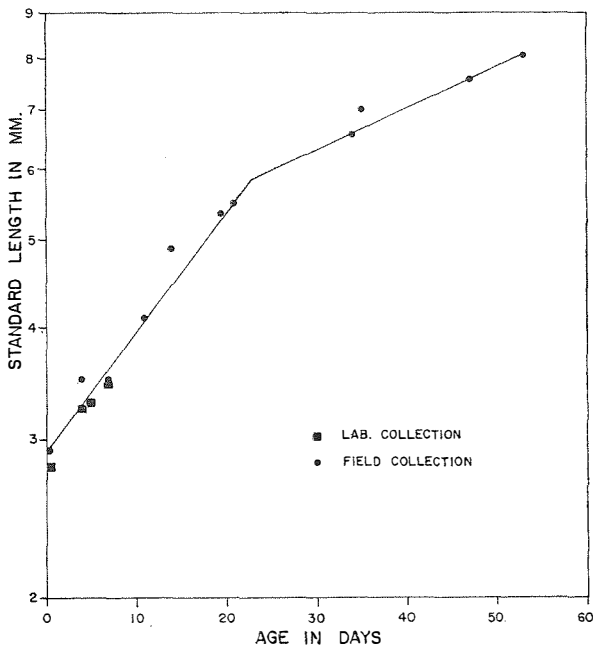


Figure 3. Growth Curve for Larval Winter Flounder from the Mystic River Estuary, 1959. Length Plotted on a Logarithmic Scale.

The catch curve (Fig. 4, solid line), drawn by inspection through the observed frequencies, consists of two basic parts: the ascending or convex pre-recruit portion, and the descending or concave post-recruit portion. The fit of the curve to the points is good, especially for the young age categories. The increased variation for the later ages may be due to sampling small heterogeneous groups of larvae.

The pre-recruit portion of the curve (prior to 9 days of age) obviously does not represent the true age structure of the population. Although this ascending limb is common in many catch curves where net selection or escapement is appreciable, measurement of head diameters of even the smallest larvae have indicated that they would be retained in the net. There was no evidence for either reduced availability of small larvae or immigration of other larvae into the estuary.

These low catches of small larvae are believed to be due to variations in the size at hatching or recruitment. Although newly hatched larvae in the laboratory ranged from 2.7–3.05 mm, individuals as small as 2.3 mm were taken from the estuary. A maximum size at hatching, up to 3.5 mm, has been cited by other authors (Williams, 1902; Sullivan, 1915; Bigelow and Schroeder,

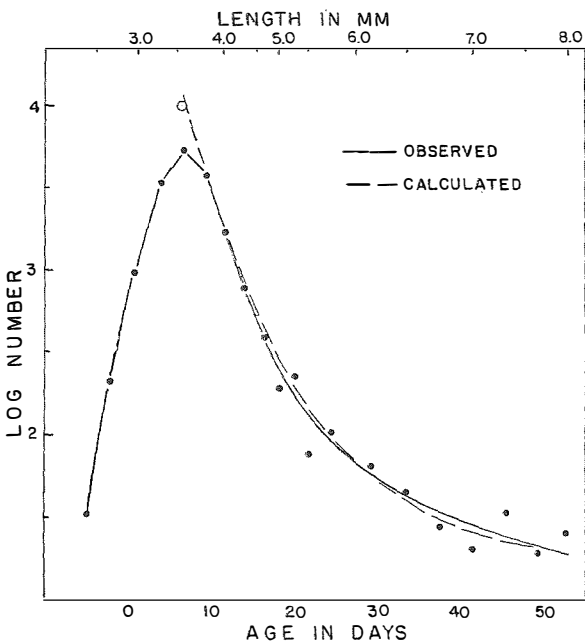


Figure 4. Catch Curve for Larval Winter Flounder. The Calculated (Retention) Curve Computed by Equation (7). Open Circle = Composite, Pre-recruit Frequency.

1953). Therefore, recruitment throughout the first nine days of age probably accounts for the ascending limb of the catch curve.

If it is assumed that each point on the pre-recruit portion of the curve represents frequencies of newly hatched larvae, then summation of all these numbers gives a composite neonate frequency (open circle, Fig. 4) which eliminates the ascending limb and results in a consistent curve of negative and decreasing slopes. This composite frequency logically underestimates the real zero age-frequency since some losses are expected between hatching and growth to 3.55 mm. In the subsequent analyses, accordingly, only the post-recruit structure of the catch curve (9.3–53 days) is considered.

Differences among the age-frequencies are believed to be largely independent of net escapement or avoidance. There was no evidence that night catches were consistently higher than daylight catches or that night tows sampled larger larvae than day tows. Furthermore, the concave post-recruit portion of the catch curve itself suggests no decreased availability of the large postlarvae. Consequently, it is assumed that the plankton collections sampled all sizes of larvae in proportion to their density in the estuary during the larval period. With this basic provision in mind, the post-recruit portion of the curve represents changes in the population age structure. Hence the slopes of the curve,

which can now be called a "retention curve", provide information on age-specific loss rates of larvae from the estuary.

The retention curve indicates that total loss during the larval period (9.3–53 days in Fig. 4) is 99.47%; however, it is clear from the curve's concave form that loss rates are much higher for young than for old larvae. Calculated from the slope, the initial loss rate at nine days of age is 28% per day, 14 times greater than the loss rate of 2% per day at 53 days of age. Another important feature of this curve is the continuous and gradual changes in loss rates with age; no discontinuities or sharp changes in slope are apparent. Thus the expectation for survival within the estuary gradually increases with age. (Although there are no sharp breaks in the retention curve, it should be noted that accelerated mortality during any one short period of development would be difficult to detect since it would be attenuated over several sizes due to growth variations.)

These basic features of the retention curve are fairly well described by the following equation in which the steep initial slope is moderated by a unit change in slope with age:

$$dN/dt = N(-a+bt), \quad (6)$$

or integrating,

$$N_t = N_0 e^{-at + \frac{1}{2}bt^2}, \quad (7)$$

where  $N$  is log number at any age;  $-a$  the initial slope of the retention curve; and  $b$  the change in slope with time,  $t$ . The instantaneous rate of change of population number,  $dN/dt$ , is a function of the high initial loss rate for the young larvae,  $a$ , and a positive rate,  $bt$ , which increases with larval age. Observed frequencies were substituted into eq. (7), giving average values for  $a = -0.045$  and  $b = 0.001$ . These estimated rates were applied to the initial number,  $N_0$ , this resulting in a calculated curve (broken lines, Fig. 4) similar to the one for the observational data.

The above equation was also used to estimate the initial larval number by extrapolation. This estimate, seen above the observed data in Fig. 4, agrees fairly well with the previous estimate based on the summation of pre-recruit numbers and suggests that the pre-recruit loss rates are about the same as those for young post-recruits.

Preliminary inspection of the retention curve has disclosed gradual and continual changes in the age incidence of larval loss rates. Since a continuation in the loss rates of the young larvae would result in almost complete attrition of the larval population before metamorphosis, these changes are vital to the survival of the estuarine population. The question naturally arises whether these changes are due to differences in translocation losses or to natural mortality losses. This is treated next.

**ANALYSIS OF LOSS RATES.** Retention cannot be equated to survival, nor loss rates to mortality, due to the magnitude of net seaward transport and the

TABLE III. FREQUENCY OF LARVAE OF DIFFERENT AGE CATEGORIES FOUND IN THE UPPER ESTUARY AND CALCULATION OF THE SLOPE OF THE RETENTION CURVE FOR SMALL LARVAE (9-25 DAYS OF AGE) AND LARGE LARVAE (26-53 DAYS OF AGE).

Age (days)	Log. frequency		Age (days)	Log. frequency
9.3	3.53	} $b = -0.121$	29.2	1.56
11.7	3.21		33.6	1.08
14.0	2.87		37.8	1.31
16.2	2.59		41.8	0.99
18.2	2.22		45.7	0.49
20.0	2.23		49.4	0.0
21.8	1.76		53.0	0.79
24.6	1.82			} $b = -0.048$

concomitant drift of larvae out of the estuary. The loss rates derived from the retention curve include both translocation losses and natural mortality losses within the estuary. Since estimates of total loss rates are available, evaluation of either component, translocation or natural mortality, permits the derivation of the complementary rate.

In order to evaluate these parameters, a catch curve was constructed from the size-frequency distribution of larvae in the upper estuary (Table III); data on currents there are available for this period. Total loss rates for the upper estuary were calculated from the slope of the retention curve by fitting two straight lines to the curve, first according to the best fit by eye, then by least squares. These two discontinuous exponentials provide a basis for the gross comparison of rates. Since the center of larval abundance was generally found in the upper estuary, the retention curve based on data in Table III is similar to the curve for the entire estuary, and, as is seen in Fig. 4, a fit of two lines intersecting at 25 days would give reasonable approximation of the steep and gradual portion of the curve.

The slope of these two lines was converted to a daily loss rate by

$$b \text{ (slope)} = \log (1-y), \quad (8)$$

where  $y$  is the percentage of the larval population lost per day from the upper estuary. The resulting average daily loss rate for the young larvae is 24%, over twice the loss rate of 10.5% for the older larvae (Table IV).

The translocation rates for larvae, to be considered next, vary positively with the estuary's exchange ratio. Differences between the rates of exchange and the rates of translocation depend upon the vulnerability of larvae to seaward transport. Translocation rate, or the percent of the population removed per day,  $t$ , can then be estimated for the upper estuary from the equation,

$$t = 1 - (1-rS)^m. \quad (9)$$

TABLE IV. A. DAILY LOSS RATES AS ESTIMATED FROM THE LENGTH-FREQUENCY DATA FOR LARVAE FROM THE UPPER ESTUARY AND ENTIRE ESTUARY. B. CALCULATION OF NATURAL MORTALITY FROM ESTIMATES OF TOTAL LOSS AND TRANSLOCATION IN THE UPPER ESTUARY.

	Length (mm)	Age (days)	Slope (b)	Loss Rate (y)
A. Upper Estuary . . . . .	3.5-6.0	9-25	-.121	0.24
	6.0-8.0	26-53	-.048	0.105
Entire Estuary . . . . .	3.5-6.0	9-25	-.110	0.22
	6.0-8.0	26-53	-.017	0.04
B.	Age (days)	Loss Rate (y)	Translocation Rate (t)	Natural Mortality (n)
	9-26	0.24	0.041	0.207
	26-53	0.105	0.015	0.091

The exchange ratio,  $r$ , was estimated to be 0.19 per tidal cycle for the two surface meters of the upper estuary.  $S$ , or  $1-B$ , is assumed to represent the proportion of larvae in the upper two meters of water where seaward transport occurred and where larvae are most vulnerable to translocation; this statistic, derived from the study of vertical distribution of larvae (Table I), averaged 0.11 for small larvae (9-25 days) and 0.04 for large larvae (26-53 days of age). The number of tidal cycles per day,  $m$ , equals 2. Solution of eq. (9) results in a translocation rate of 4.1% per day for small larvae and a lower value, 1.5% per day, for large larvae.

With estimates available for both total loss rate and translocation rate, the difference, which is natural mortality within the upper estuary, can now be calculated from the equation,

$$y = n + t - nt, \quad (10)$$

and transposing,

$$n = y - t / 1 - t,$$

where  $n$  is natural mortality rate, and  $t$  translocation rate.

Table IV gives the concluding inter-relationships of these vital statistics for the upper estuary. The rates of both natural mortality and translocation are higher for the small larvae than for the large. Natural mortality, however, is the major component of total losses, being about five times higher than translocation losses.

In order to evaluate the general applicability of these statistics for larvae from the entire estuary, two exponentials were fitted to the points of the retention curve (Fig. 4) in the same manner as for the upper estuary. These results, also included in Table IV, show that, although total losses of the small larvae are similar for both the upper estuary and the entire estuary (22% per day and 24% per day), there is considerable disparity between the loss rates for

large larvae (4% per day and 10.5% per day). Considering the large larvae, the estimate for total loss in the upper estuary gives a natural mortality rate which is higher than the total loss for the entire estuary; thus, the rates for them in the upper estuary are obviously inapplicable as virtual rates to the entire estuary.

A tenable explanation for the high loss rate may be the movement of the population center from the upper into the lower estuary late in the spring (Fig. 1). As previously suggested, this movement may have been an active emigration from the upper estuary. If this were the case, the translocation estimate would not completely explain such a change in larval distribution, which was mainly from upper to lower estuary and not out of the estuary. As a result, the estimate for natural mortality, the difference between total loss and translocation, is probably too high for these larvae.

In spite of the limitations of the data, the magnitude of difference between the statistics permits several general conclusions. Natural mortality is high, especially during early larval life when it averages at least twice that during late larval life (Table IV). There is reason to suspect, therefore, that the form of the retention curve (Fig. 4) is largely due to variations in natural mortality and, furthermore, that the survival curve for winter flounder larvae in the estuary has a concave form of decreasing mortality rates with age.

*Predation.* Little is known about the causal mechanisms affecting early mortality of fecund teleosts, since direct and quantitative evidence for the causes is extremely difficult to collect for natural populations. There is some evidence, however, for larval flounder mortality from predation by *Sarsia tubulosa* (M. Sars), a small hydromedusa that was very abundant in the estuary.

*Sarsia* medusae, which had larval flounder well into their manubria, were taken in plankton tows of about one minute duration. Others were found adhering to the tentacles of *Sarsia*. The predatory behavior of these small medusae was actually observed when medusae in a 13-liter laboratory aquarium succeeded in capturing larvae. Russell (1953), who reported medusae of this species in estuaries during the spring, described them as voracious carnivores.

All other potential predators of flounder larvae were numerically unimportant compared to the *Sarsia* medusae; during the spring of 1959 as many as 3600 were collected per cubic meter. Fig. 5 shows that their distribution was very similar to that of the flounder larvae in time and place: both were most abundant during the spring in the upper estuary. *Sarsia*, like the larval flounder, were also more common in bottom plankton tows. Decreases in larval density in general were associated with high densities of medusae, lending circumstantial evidence for predation.

Peaks in flounder abundance were followed by peaks of *Sarsia*, suggesting the possibility of a classical predator-prey lag oscillation. This was true for both

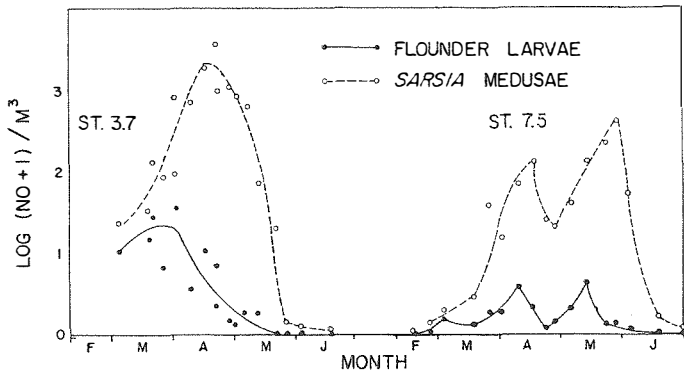


Figure 5. Seasonal Abundance of Winter Flounder Larvae and *Sarsia tubulosa* Medusae at Two Stations in the Mystic River Estuary during the Spring of 1959.

stations even though fluctuations occurred at different times. Coefficients of correlation were calculated from the data as plotted in Fig. 5, and also for flounder density and the observed density of medusae two weeks later; coefficients of 0.43 and 0.73 respectively resulted. Although the probability that these two values are drawn at random from the same population is 0.06, biological evidence for a direct regulatory mechanism is lacking. A density-dependent numerical response—or high larval density leading to an increased reproductive rate for *Sarsia*—is biologically untenable since there is no medusoid budding in *S. tubulosa* (Russell, 1953). As the hydroids are small, with minute tentacles, it is not likely that a response could be mediated through the hydroid stages. A functional response—or increased selection of larvae when their densities are high—seems improbable in view of the limited sensory and locomotory ability of the medusae and their indiscriminate feeding behavior. Consequently, even though a similar distribution of high densities of these species may have resulted in an increased number of larvae captured, there is no evidence for regulatory control. Perhaps synchronous occurrence of both of these meroplankters was related to seasonal changes in hydrographic or basic biological factors.

A feasible explanation for the age-specific variations of larval mortality involves a predation coefficient that is inversely related to larval size rather than to one directly related to age-frequencies. The swimming movements of small larvae were feeble (see p. 21), whereas large larvae, particularly after development of fins, were able swimmers. In the laboratory, large larvae evaded medusae better than small larvae and were able on occasion to survive nematocyst contact, freeing themselves from the tentacles. It seems possible, then, that larvae of different sizes are not equally vulnerable to capture and that small larvae are preyed upon most heavily. Such a differential predation rate would result in lowered survival of young larvae. Moreover, if the degree of



predation depends upon the difference in size between predator and prey, then the small larvae would be subjected to even higher losses, since the population structure of the medusae also consists mostly of small individuals. Parenthetically, a differential predator vulnerability, as hypothesized above, coupled with density-dependent growth, could be an effective regulatory mechanism (Ricker and Foerster, 1948).

*Discussion.* Although the winter flounder is the most common flatfish in the Gulf of Maine (Bigelow and Welsh, 1925) and dominates the demersal fish communities of Block Island Sound (Merriman and Warfel, 1948) and Long Island Sound (Richards, in press), comparatively little is known about the distribution of larval stages. Despite the abundance and high fecundity of this species, no larvae have been reported from either Block Island Sound (Merriman and Sclar, 1952) or the open Gulf of Maine (Bigelow and Schroeder, 1953). In Long Island Sound, the larvae were taken in low numbers (Wheatland, 1956); their scarcity in these waters has been ascribed to the location of spawning grounds inshore and to the concentration of early stages in shallow waters of estuaries and bays.

Movement of adult winter flounder into shallow inshore water prior to spawning and into deep offshore water after spawning has been indicated by Lobell (1939), McCracken (1954), and Saila (1961). An inshore spawning migration has also been inferred from decreased catches in deep water during the fall or winter (Merriman and Warfel, 1948; Richards, in press). The occurrence of eggs in shallow, brackish areas (Scott, 1929) and of larvae near estuaries or in bays (Williams, 1902; Sullivan, 1915; Breder, 1924; Perlmutter, 1939, 1947) offers additional evidence for the location of the spawning and nursery grounds. This study confirms the above observations and offers quantitative evidence for high densities of winter flounder larvae within an estuary.

Certain characteristics of the young stages enhance their retention in these shallow water inlets along the coast. As the eggs are demersal and adhesive, they are localized in the vicinity of the spawning grounds. The larvae are also nonbuoyant. They display a mixed planktonic-benthonic behavior and are most abundant near the bottom. The significance of such depth distribution in an estuary that has vertical differences in net currents is well recognized (Pritchard, 1951; Ketchum, 1954, Bousfield, 1955), and this species appears to be a good example of how the young stages, by virtue of vertical distribution, decrease their dispersal out of an estuary.

Regardless of these adaptations, translocation losses of larvae out of the estuary by seaward drift were significant. *Pseudopleuronectes americanus* larvae have been collected occasionally from open neritic waters (Perlmutter, 1939; Sette, 1943). Although little is known about the actual fate of these individuals, offshore drift of the larvae of other marine teleosts is thought to lead to reduced

survival (Walford, 1938; Sette, 1943; Carruthers, et al., 1951; Wiborg, 1957; for others see Bishai, 1960). It is surmised that conditions for survival of the winter flounder larvae may be less favorable offshore than in shallow nursery grounds. Suitable food, for example, may not be as available in deep water—either for the larvae or for the young metamorphosed flounder.

Since the early stages of this species are nondispersive, the spawning grounds and the nursery grounds are essentially the same. Reproductive success depends largely upon the selection of a spawning site by the adults. Spawning in a fast-flushing or polluted estuary, for example, would probably result in lowered survival of young; natural selection would favor localization of breeding where survival of the young is high. The ability of displaced winter flounders to return to the original area of capture has been reported by Saila (1959), who also noted (1961, and personal communication) the return of individual flounders to the same estuary in successive years. Perhaps this homing behavior enables the flounder to return to its natal estuary where favorable conditions exist for a nursery area. In the Mystic River estuary the densest aggregations of adults during the breeding season—and later the larvae—were found in the upper estuary where the bottom countercurrent was well developed and where minimal seaward drift of the larvae would be expected. Thus currents within the estuary may also be a factor in the location of the spawning site.

In view of the importance of the estuary to the ecology of this commercially important species, a further comment is warranted on the alteration of this habitat by man. Since Greeley (1939) noted the absence of winter flounders in the polluted areas of western Long Island Sound, and since the larval stages of fish are thought to be sensitive to variation in physical factors and effects of contaminants, inshore and estuarine pollution may influence the reproductive success and abundance of this species in New England. Possibly destruction of shallow spawning and nursery grounds by pollution and dredging has been a factor in the past decline of commercial catches of this species since 1930 in New England (Perlmutter, 1947).

Comparison of *P. americanus* with other pleuronectids shows that most flatfish are unlike the winter flounder in that they lay pelagic or buoyant eggs which are widely scattered by currents. With these species, breeding success also depends to a large degree upon the localization of young in shallow nursery areas. We know that adults of some species, such as the plaice and English sole (Wimpenny, 1953; Ketchen, 1956), migrate offshore to deep water spawning grounds and that early stages passively drift with the currents back toward shoal nursery grounds. This interesting theory of contranant migrations of adults and denantant drift of young, first elaborated by Meek (1916), probably will prove to be of a more general nature with our increasing knowledge of fish migrations and ocean circulation.

Among the five species of Pleuronectiformes known to lay demersal eggs (Pearcy, unpublished), definite similarities in breeding biology are apparent.

Spawning is reported as taking place during late winter or early spring, generally in bays or brackish water (Yusa, 1958, 1960; Rass, 1959; T. Abe, personal communication). Comments on two additional characteristics of flatfish larvae from demersal eggs are of special interest since they are related to their dispersal. Two general types of larvae have been distinguished within the flatfish—those with a short pelagic life and early metamorphosis and those with a prolonged larval life (Norman, 1934). Species that lay demersal eggs belong to the first group. The winter flounder, for instance, apparently metamorphoses at one of the smallest sizes for pleuronectids (Bigelow and Welsh, 1925; Kyle, 1898). Since it is generally true that the shorter the larval life the smaller their range of dispersal from the spawning grounds, localized populations of these other species may be expected. Secondly, it is fascinating to learn that the newly-hatched larvae of two other species that lay demersal eggs have the same swimming and planktonic-benthonic behavior as the winter flounder larvae (Yusa, 1958, 1960). It is tempting to speculate that perhaps the larvae of all the demersal egg-laying pleuronectids have a similar behavior which may be ecologically important in decreasing dispersal due to currents.

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### Вильям Г. Перси

#### Экология предустьевой популяции зимней камбалы *Pseudopleuronectes americanus* (Walbaum)

#### II. Распространение и динамика личинок.

#### Краткий Обзор

Еженедельный сбор планктона на семи станциях эстуария реки Мистика делался от февраля до конца Июня 1959 года. Личинки зимней камбалы были обычны от Марта до Июня. Они были наиболее многочисленны в солоноватой воде верховья эстуария в Марте и Апреле, когда их густота

часто превосходила ( $10/m^3$ ); поздней весной большинство личинок было на низовье эстуария.

Исследование вертикального распределения личинок показало что их количество у дна приблизительно в шесть раз больше чем у поверхности, а лабораторные наблюдения установили что образ жизни личинок является смесью планктонного и бентонным. На основании распределения личинок и водообращения в эстуарии было подсчитано что течение воды уносит ежедневно из верховья эстуария 3% популяции, то есть приблизительно одну треть ожидаемой потери личинок если бы их вертикальное распределение оставалось равномерным. Скопление личинок у дна и на верховья эстуария, где противоположное течение ощущаемо, повидимому является главным фактором уменьшающим их забережное распространение. Вариации в вертикальном распределении личинок разной величины объяснимы различиями в скорости течения и меньшей силой плавания у личинок меньшего размера.

Кривая полученная на основании данных по частоте длины и темпу роста у свыше 5000 пойманных личинок оказалась вогнутой в той части, которая включает период сбора следующий за окончанием прироста популяции за счет личинок. Эта вогнутость указывает на большую смертность молодых личинок и ее уменьшение с возрастом. Вычисленный процент потери маленьких личинок равен 20% в день, а постларвальных только 4%. Нормальная смертность и потери, причиняемые перемещением, выше у молодых личинок. Однако нормальная смертность является главной составной частью общих потерь и пропорции потерь причиняемых возрастными различиями.

Медузы *Sarsia tubulosa* пожирают личинок камбалы. Их распределение в пространстве и времени сходны с таковым у личинок. Допуская меньшую способность маленьких личинок избегать похищение медузами мы постулируем дифференциальную скорость похищения что способствует объяснению существования сравнительно высокого процента смертности у маленьких личинок.

Так как взрослая зимняя камбала мечет икру в эстуариях и в бережных бухтах и так как молодые стадии не участвуют в распространении, то размножение и выращивание происходят в той же местности. Некоторые экологические соотношения этого вида рыб с его обычаями бережного размножения подвергнуты обсуждению. Кроме того указаны сходства с биологией других видов камбалы, для которых установлено метание демерсальной икры.

*Ecology of an Estuarine Population of  
Winter Flounder, Pseudopleuronectes americanus  
(Walbaum)*

*III. Distribution, Abundance, Growth, and  
Production of Juveniles; Survival of  
Larvae and Juveniles<sup>1</sup>*

By  
William G. Pearcy

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ABSTRACT

The juvenile flounder of age-groups 0 and 1 in the Mystic River estuary were sampled quantitatively by trawling. The average population density was high, reaching values of over 1/m<sup>2</sup> for age-group 0 in the spring. Juvenile growth was rapid during the warm seasons. Variations in density and growth were calculated on a monthly basis and were used to estimate net productivity. Production for both age-groups was maximal in late summer and fall, and minimal in the winter when both density and growth were low. Annual juvenile production was high, 3.7 g/m<sup>2</sup>; the average biomass was 1.44 g/m<sup>2</sup>.

Average monthly mortality, estimated from a catch curve for periods of comparable availability, equaled 31% for age-group 0 and 8% for age-group 1. The data for mortality of both larvae and juveniles are summarized in a survival curve. The lowest survival rates are for early larval stages followed by gradually increasing survival rates throughout the remainder of the early life history. Total mortality during the larval and juvenile stages was approximated at 99.98–99.99%.

The "critical period" concept is discussed; it has limited usefulness in a description of mortality, especially during the early life history of the winter flounder.

*Introduction.* The parameters of survival and productivity, which are fundamental to an understanding of the population ecology of a species, have rarely been measured for juvenile stages of marine fishes. The purpose of this paper is to estimate the seasonal abundance and growth of the juvenile winter flounder in the Mystic River estuary preliminary to computation of production. Another objective is to estimate juvenile survival rates. These estimates along

<sup>1</sup> Contribution No. 18 from the Marine Research Laboratory, University of Connecticut.

with those for larval survival are used to construct a survival curve for the early life history of this flounder.

Computation of both survival and production is contingent upon unbiased estimates of flounder abundance within the estuary. The difficulties in making such estimates of natural populations are numerous and are well recognized by the ecologist. A reliable measure of juvenile density is basic to production calculations. Survival estimates furthermore depend on the additional assumption that the population within the estuary is stable and homogeneous during the sampling period (Ricker, 1958); this is often complicated by seasonal changes in the recruitment or distribution of animals.

Certain aspects of the winter flounder's behavior are important in evaluating the sampling problems associated with this species; they indicate that the difficulties of quantitative study are not excessive, especially when compared to schooling species of pelagic fishes. After metamorphosis the winter flounder is strictly a benthic animal, notably different from the larva in morphology and habits. It is basically sedentary and spends most of its time lying motionless on the bottom (Bigelow and Schroeder, 1953). The young flounder, limited mainly to shoal waters of bays and estuaries during the first year of life, is thought to be a product of local spawning (Perlmutter, 1947). From tagging studies, populations of winter flounder are known to be relatively stationary. Perlmutter, for example, reported that 93.6% of the tagged fish recovered from inshore waters of New England were from the same area in which they were tagged. He concluded that the population "is comprised of many relatively independent, localized stocks inhabiting the bays and estuaries along the coast." Additional evidence for this generalization is given by Saila (1961) who found that its movements were restricted to short distances. Discrete subpopulations in Narragansett Bay, Rhode Island, were inferred by the fact that displaced flounder often returned to the inlet where they were originally captured (Saila, 1959). Dickie and McCracken (1955) reported that no tagged flounder were recovered outside of St. Mary's Bay, Nova Scotia, during the summer, indicating the absence of major movements from this area at that season. McCracken (1954) also found that the population in Passamaquoddy Bay, New Brunswick, was relatively stable from May to September.

Two age-groups are to be considered in this paper: age-group 0 or young-of-the-year winter flounder, and age-group 1 or yearling fish between 1 and 2 years of age. Year-classes 1958 and 1959 refer to the year in which the fish were born; that is, the eggs laid in 1958 constitute the 1958 year-class. For convenience, the first of March is considered the birthday of each year-class.

*Methods.* A total of 612 collections for juveniles was made with a small beam trawl from July 1958 to February 1960. Collections were taken at Sts. 0.4, 1.4, 2.1, 2.8, 3.7, 5.1, 7.5, and 8.5—weekly during the spring and summer, biweekly during the fall, and monthly during the winter.



The beam trawl, 85 cm wide, had removable nets of different mesh size. A net with a 1 mm (square) mesh was used in the spring when the juveniles were smallest; at this time runners were attached to the trawl. After July, a 5-mm mesh bag was used without runners but with a tickler chain added. In late fall and winter a net with 13-mm mesh size was attached to the frame. In all cases the net was changed only if it precluded escapement of the smallest juveniles.

Measurement of the distance towed, enabling quantitative estimates of abundance, was calculated either from odometer readings or by towing the trawl between floats a known distance apart and by piloting with the aid of nearby landmarks, buoys, and ranges. The odometer, added to the trawl in the spring of 1959, was calibrated over measured courses on sand and mud bottoms; readings of replicate tows gave coefficients of variation of 2.5 and 4.6% respectively. The average distance towed was 15–30 m during the spring, when the finest mesh was used and when small juveniles were abundant, and about 60 m during the fall and winter, when the catches consisted of few large individuals.

Juveniles were sampled inshore as well from early spring to late fall, with a beach seine (12.2-m length, 6-mm mesh), at seine stations A–F; a total of 225 separate collections, each 15–30 m in length perpendicular to the shore, was made. Also, an otter trawl (5.2-m foot rope, 19-mm mesh with a 13-mm liner in the cod end) was used for collecting large juveniles. Tows with this trawl, totaling over 60, were taken regularly each month at Sts. 3.7 and 8.5 and irregularly at other trawl stations. These tows, made between buoys and landmarks, averaged several hundred meters in length.

All juveniles from the beam trawl collections, preserved in neutralized formalin, were measured and weighed. When catches with the otter trawl or beach seine were large, all fish were counted but only subsamples were preserved for length and weight measurements. Standard length (snout to hypural plate) of small age-group 0 flounder, 6–40 mm, was measured to the nearest 0.1 mm with the aid of a dissecting microscope and eyepiece micrometer. Wet weight was determined to the nearest milligram after removing excess water with filter paper. Large fish were measured to the nearest millimeter in length and to 0.1 g in weight. Since some of the large fish were not examined until a year after the date of collection, 94 fish were remeasured after a year's preservation. The average shrinkage in length was 3.7%, and correction for this was made wherever applicable. Only fresh specimens, however, were used in calculating the length-weight relationship.

*Preliminary Considerations.* Besides the results of other studies (see *Introduction*), the following comments are included on fishing intensity, gear selectivity, and sampling variability in partial support of the assumption that the catch/m<sup>2</sup> is an index of the juvenile density at the time and place of sampling.

1) The seasonal and spatial deployment of trawling effort was relatively constant throughout the sampling period and was independent of fish abundance. The actual area sampled at each station was only a small portion of the total area of the estuary. Collections were made at more-or-less random locations in the vicinity of each trawl station, thus reducing the possibility of depleting the number of juveniles. No effects of fishing effort were noted after repeated hauls at the same location.

2) Catches made by the beam and otter trawls in the same area were compared, and although catch/m<sup>2</sup> with the latter was often higher than that with the beam trawl, as one might expect, the mean difference was not significant ( $t = 1.33$ , 22 d.f.). Also, no consistent differences were apparent between either the mean size or the average catch/m<sup>2</sup> of large juveniles collected with these two trawls (Figs. 1, 3). Hence, the beam trawl apparently sampled the juveniles effectively, giving catches that were comparable to those of the otter trawl.

3) Because the difference in the catch/m<sup>2</sup> of beam trawl tows made at the same station during day and night was not significant ( $t = 1.56$ , 4 d.f.), there was no indication of increased visual avoidance of the trawls during the day.

4) The author noted, in both laboratory and field, that initially the disturbed flounder usually covered itself with sediment and remained motionless. Such behavior may be one reason why this flounder was so easily captured by trawling.

5) Replicate beam trawl collections allowed 20 individual comparisons of catch variation. The mean coefficient of variation,  $C$ , was 74% ( $C = 78\%$  for nonodometer trawl collections), which is similar to the variation of catches for individual species from replicate trawls reported by Barnes and Bagenal (1951).

6) Only 3 of 20 coefficients of dispersion or  $s^2/x$  (Blackman, 1942) calculated for these replicate tows were significantly greater than unity, suggesting that the sampling variability usually did not depart from randomness (Poisson). The spatial distribution of juveniles was observed frequently in laboratory aquaria, and no social interaction, such as gregariousness or territoriality, was indicated.

Due to variation in physical factors, such as salinity, sampling for flounder was conducted at the series of stations located from the mouth to the head of the estuary in order to provide data on horizontal variations in distribution. However, the distribution of juveniles was found to be fairly similar throughout the estuary during most of the year. The average catches for both upper and lower estuary were about the same, and the catches/m<sup>2</sup> at all stations on a sampling date usually varied less than an order of magnitude.

Large differences between the upper and lower estuary were evident only in the spring when metamorphosing and small 0-group fish were much more abundant in the lower estuary (particularly at St. 5.1) than in the upper estuary, where they were rare. In June, a four-fold decrease in catch/m<sup>2</sup> in the lower estuary corresponded to a two-fold increase in the average catch in the

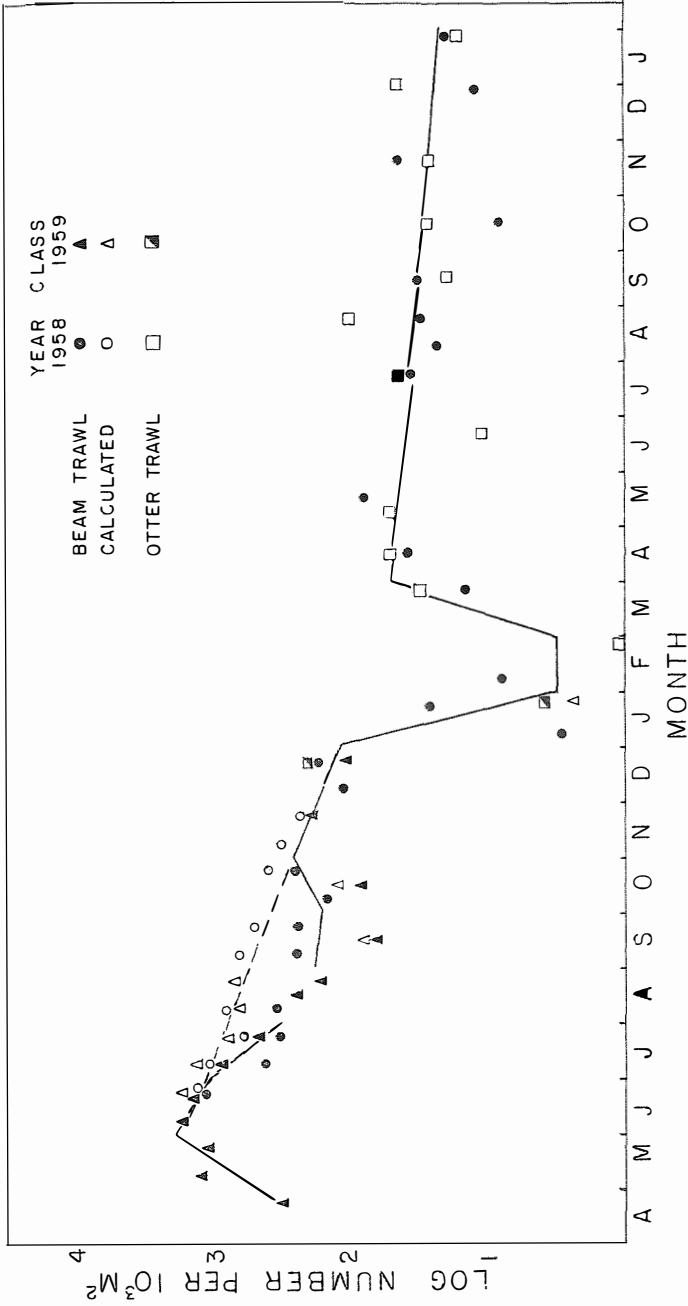


Figure 1. Catch Curve for Juvenile Flounder of Age-Groups 0 and 1 of the 1958 and 1959 Year-Classes in the Mystic River Estuary. Solid Curve: Fit to the Observed Frequencies. Dashed Line: Fit to the Calculated Frequencies (Open Circles and Triangles). Data on Shallow Water Catches incorporated.

TABLE I. NUMBER OF DORSAL AND ANAL FIN RAYS IN AGE-GROUP 0, 1958 YEAR-CLASS; FLOUNDERS FROM THE UPPER AND LOWER ESTUARY.

		Mean Number	Standard Deviation
Dorsal	Upper Estuary	66.27	2.500
	Lower Estuary	66.80	2.197
Anal	Upper Estuary	49.61	1.997
	Lower Estuary	50.41	1.793

upper estuary. During this same period there was also a marked increase in the catch of this age-group at the beach seine stations. These changes in distribution are thought to reflect an active dispersal of flounder within the estuary. It was noted that its size both in the upper estuary and in the shoal areas was larger than average, suggesting that the larger fish moved the farthest from the center of abundance.

Since the horizontal distribution of the juvenile within the estuary was similar, the catch/m<sup>2</sup> was averaged for the entire estuary to illustrate seasonal changes in abundance. Such temporal variations represent changes in population number only if a single homogeneous population within the estuary is sampled. Comments on several aspects of the flounder population in the estuary are given here since they give additional evidence for the localization and stability of populations.

The dorsal or anal fin-ray counts of 275 age-group 0 flounder are similar (Table I). The mean difference between meristic counts, when considered along with variance, indicated no separate subpopulations in the upper and lower estuary.

A marking study of juvenile flounder in the Mystic River provided some evidence for short-term stability of a portion of the population. An area about 30 × 60 m in the lower estuary (St. C) was systematically seined; the dorsal or anal fin of each flounder was conspicuously marked and the fish was immediately released. A total of 390 fish was marked during the first week. The number of captured, marked, and marked-recaptured (Table II) showed little

TABLE II. NUMBER OF AGE-GROUP 0 FLOUNDER MARKED AND RECAPTURED AT SEINE STATION C, JULY 26-AUGUST 12, 1959.

Date	Total Marked	No. Recaptured	% Recaptured
July 26	75	6	8
27	21	1	5
27	7	1	17
28	49	6	12
30*	3	0	0
Aug. 10	66	7	11
12	86	10	12

\* Water temperatures of about 30°C recorded.

change in the percentage of recaptured fish during the two-week period; this suggests stability of juvenile numbers during the summer. It is of interest to see that inshore water temperatures were high (about 30°C) on July 30 when no flounder were captured. However, some of the marked individuals returned to this area and were recaptured at a later date.

A notable difference in abundance of the juvenile flounder between the estuary and the area just outside the mouth was noted; 27 trawl collections from deeper water near the mouth averaged only 2% of the estuarine catch during June–September. Such differences suggested a discontinuous distribution of the population.

These inferential data on stability distribution and movements of the flounder within the estuary, though admittedly incomplete, suggest a single population; and further, they support the assumption that average catch/m<sup>2</sup> is a representative index of population density within the estuary. Though seasonal movements were evident, the data indicate that the proportion of the juvenile population within the estuary is relatively constant from spring to winter; consequently, changes in population density during this period are thought to be largely the result of natural mortality.

*Seasonal Abundance.* Fig. 1 shows the logarithm of the average trawl catch/m<sup>2</sup> plotted for each month for juveniles in age-groups 0 and 1. This curve consists of a connected series of straight lines drawn by inspection through the average data for both year-classes of age-group 0, and fitted by the method of least squares for the data of age-group 1. Each line, therefore, is exponential and denotes a constant percentage change in average number for the period represented.

Although some of the declines in the catch curve illustrate trends of mortality, certain fluctuations are the result of either recruitment or local movements of the population. For example, the initial ascending portion of the curve for age-group 0 represents metamorphosing flounder and hence recruitment. Even though this recruitment from the larval population appears to be complete by June, when the highest densities occurred, some metamorphosing flounder were captured during June, so the initial post-recruit frequencies may underestimate the actual numbers at this time.

Following peak densities in June, average catches/m<sup>2</sup> declined irregularly during the summer and autumn and then descended to a winter minimum. The curve shows a peculiar dip in the summer and an increase in the fall for both the 1958 and 1959 year-classes. This concave portion is inversely related to catches of age-group 0 at the shallow water seine stations during the summer. The average seine catches (Fig. 2) are low early in the spring, high during the summer, and return to low catches in the fall. These seasonal trends are in agreement with results of seining studies of J. T. Allison (personal communication) at Sts. F and G in the Mystic River estuary (see fig. 1 in Pt. I)

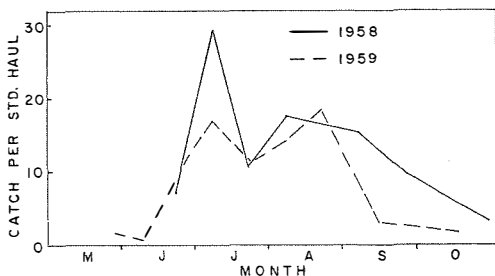


Figure 2. Average Catch of Age-Group 0 Flounder Per Standard Seine Haul, June–November 1958 and 1959.

and of Warfel and Merriman (1944) at Morris Cove, Conn., where high catches of juveniles were obtained in the warm seasons and low catches in the winter.

The catch curve exhibits a precipitous decline during January to low catches in January and February; this is especially evident during the cold winter of 1958–59. Although anecdotal information has suggested that these low catches were due to the flounder burying itself in the mud, behavior which has been suggested for the plaice (Wimpenny, 1953), catches with a scallop dredge, which digs deeper into the sediments than the trawls, were equally low at this time of the year.

Movement of this species out of shallow water in the fall or early winter, inferred by low catches (Warfel and Merriman, 1944; McCracken, 1954; Bigelow and Schroeder, 1953), offers an explanation for the low population densities in the winter. Recently Richards (in press, *a*) has offered direct evidence for such movement in reporting increased catches of young in Long Island Sound during the winter. Since it was noted that winter catches just outside the mouth of the Mystic River estuary were relatively high compared to those within the estuary, dispersal of the juveniles out of the estuary is believed to explain the low densities during this time.

As the flounder population returns to the estuary during the following spring, the number increases. The data for age-group 1 are variable, but in general they show a gradual decline in abundance from spring to winter. There is no indication, from either the catch curve or the summer seine catches, that this age-group moves into shallow waters in the summer. Another apparent difference between the distribution of the two age-groups (Fig. 1) is the relatively high abundance of the older fish in the estuary during the winter.

Results of a few supplementary experiments on the limiting effects of certain physical factors are also of interest. Both age-groups are euryhaline and eurythermal; they were found throughout the estuary at all seasons in water ranging

between 4–30‰ salinity and 0–over 25°C. Simple laboratory experiments suggested that the extremes of these factors may be close to lethal limits. The minimum salinity tolerance ( $LD_{50}$ ) varied between 1 and 5‰ after acclimation, even for small individuals of 7–10 mm. The minimum lethal temperature in the winter was usually between  $-1.0$  and  $-1.5^{\circ}\text{C}$ , when freezing of tissues was noted; freezing points of sera collected in the winter were likewise abnormally low for teleosts (Pearcy, 1961). The maximum temperature tolerated, about 30°C for fish collected in the summer, agrees with the findings of Battle (1926) and Huntsman and Sparks (1924) for this species; these authors reported a higher incipient lethal temperature for small flounder than for large, a difference which may influence depth preference and thus explain why large fish are more common in deeper water in the summer.

Response to light may also affect depth distribution. McCracken (1954) conducted several experiments which indicated that the small flounder was the least photonegative. Similar experiments by the author, which involved a choice between diffusely lighted and darkened halves of aquaria, showed no statistical evidence for a preference by age-group 0 during the spring or summer. Orientation was different for this age-group in the winter, however, and for age-group 1 during the summer, when they showed photonegative responses. Light intensity may then be another factor which is related to differences in vertical distribution or to the movement of young fish out of the shoals in the fall and winter.

*Growth.* A study of growth of the juvenile is important for two reasons: first, growth estimates are fundamental to a computation of production, and second, a description of growth provides information on ecological and physiological variations of this process in the estuary.

Periodic collections of juveniles throughout the year gave data on average sizes which were used to calculate growth. Over 5000, including all sizes of both age-groups, were measured. Age determination presented no special problems, as length alone was usually a reliable criterion of age for the first two age-groups. Otoliths were examined periodically, however, to verify size-age relationships.

Fig. 3 shows the average lengths calculated by pooling the data by weeks for each year-class and collection method. Since collections were made at weekly intervals for age-group 0 during the spring and summer when growth was most rapid, more averages are available for these small juveniles than for the remainder taken in biweekly or monthly collections. As is seen, there is general similarity in average sizes for both year-classes and for both types of trawl samples. These data are therefore considered together, and a smoothed average growth-in-length curve is drawn through the average lengths. Seasonal changes in growth are apparent. Stanzas for each age-group indicate fast growth in the spring and summer followed by slow growth in the winter. Note that, since

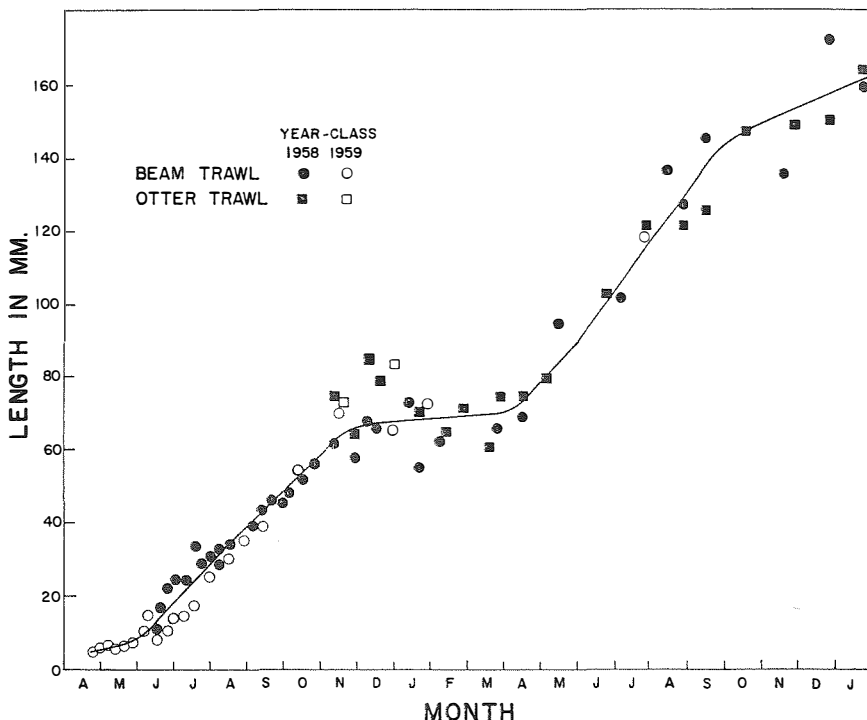


Figure 3. Growth Curve of Juvenile Winter Flounder As Estimated from the Average Length of Fish from Trawl Collections of the 1958 and 1959 Year-Classes in the Mystic River Estuary.

metamorphosis of the flounder was not completed until June, the first two months underestimate growth and are consequently excluded from further analysis.<sup>2</sup>

**GROWTH VARIATIONS.** The following remarks, though not essential for production estimates, give additional information on the variability of flounder growth in the estuary. As is seen in Fig. 3, there is appreciable variation in the average lengths within any month. This is due partly to the difficulties of calculating a representative average length, since prolonged spawning resulted in as much as four months difference in age for a year-class. Small sample sizes, consequently, contribute to variations in length, especially among older fish. Actual differences in individual growth rates are indicated by the increased range and variance of lengths with age. Juvenile growth may also differ between sexes (Berry, 1959).

<sup>2</sup> Many metamorphosing individuals captured in the beam trawl were only 6-7 mm, or shorter than maximal length of large larvae. This decrease in standard length is not surprising during metamorphosis, a period when the caudal fin differentiates and general body proportions change.



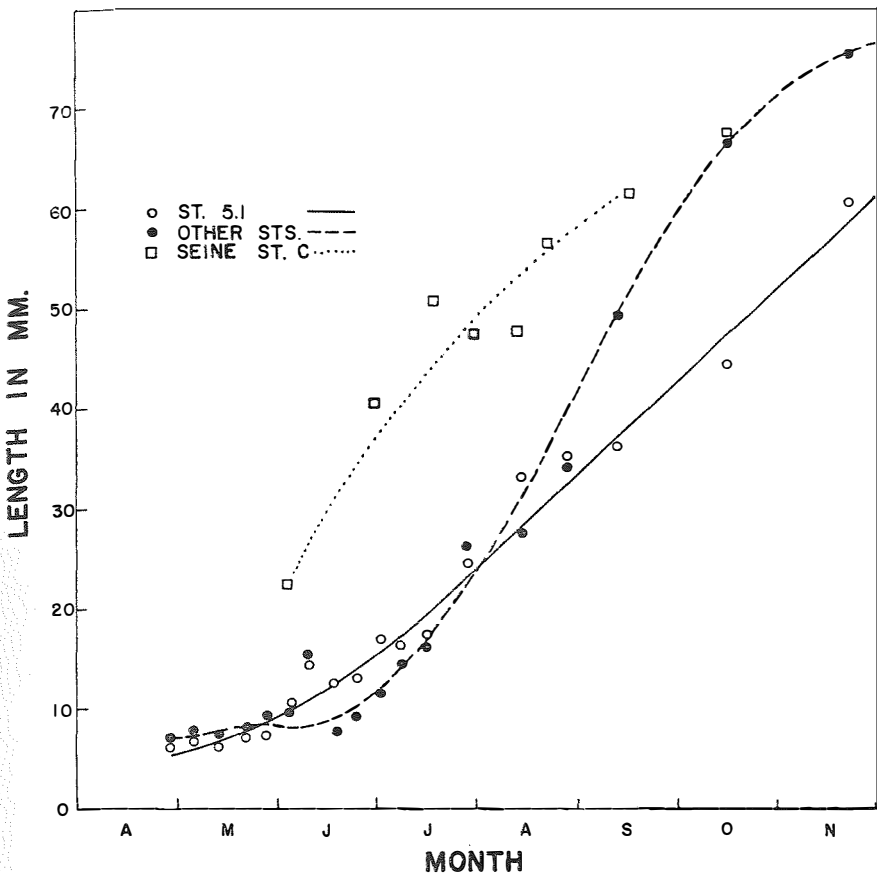


Figure 4. Growth of Age-Group 0 Flounder As Estimated from Average Fish Lengths from Three Locations, April to November 1959.

The average lengths of age-group 0 are plotted (Fig. 4) to illustrate possible differences in growth among fish of the same year-class from several locations. The 0-group, collected by seining, were significantly larger than the fish collected by trawling throughout most of the summer, a difference that was apparent by visual comparison of fish of both year-classes. This difference, which could not be explained by gear selectivity, is thought to be due to larger fish moving farther into the shoals in June. Such a size difference between shallow-water and deep-water fish may explain why the lengths given in other studies (Perlmutter, 1939; Warfel and Merriman, 1944; Bigelow and Schroeder, 1953; and Berry, 1959) are generally larger for a given month than those in Fig. 1.

Comparison of the average sizes of flounder taken at St. 5.1 with those at the remaining trawl stations illustrates a negative correlation between growth and flounder density. Metamorphosing individuals were very abundant at St. 5.1, and the density of the 0-group there averaged about five times higher than at the other stations during the summer. Fig. 4 shows that the average growth increments at this station are only about one-half those of the other stations after July or August, suggesting retardation of growth at high densities. Perhaps at sizes smaller than 20–30 mm, intraspecific competition for available food was not limiting growth.

The otolith of the winter flounder, which has been used for age determination by Berry (1959) and E. F. Thompson (personal communication), consists of an opaque center surrounded by alternating concentric hyaline and opaque rings; deposition of the opaque material is thought to correspond to periods of fast ("spring") growth, the hyaline portions to relatively slow ("summer") growth. The following seasonal pattern of otolith growth was inferred from examination of 422 otoliths from juveniles. All otoliths for 0-group fish were completely opaque until about mid-June; by the end of July all otoliths had a recognizable hyaline margin. The first opaque ring was deposited between October and March and hyaline growth followed in the spring for age-group 1.

An interesting variation in the above pattern concerns the formation of the first opaque ring. For the 1958 year-class, 8% of the fish examined had narrow but entire opaque bands prior to January 1959, 50% had this ring by March, and 100% by April. The 1959 year-class of age-group 0, however, was surprisingly different; 56% had completed opaque rings by January 1960, indicating early resumption of "spring" growth during this mild winter. In addition to this year-class variation, some differences in otolith ring formation were related to the size of individuals within a year-class. During November and December of 1959, 75% of those under 80 mm had opaque rings whereas only 34% of those over 80 mm had a completed opaque ring. Accelerated growth could not be detected from successive average lengths for periods that corresponded to opaque ring formation late in the year, and growth during midwinter was probably low regardless of the type of otolith margin present. None-the-less, the deposition of opaque otolith material in the fall, also reported by Berry (1959), is of particular interest since it has not been found in other age-groups and suggests changes in growth physiology with age.

In addition to revealing information on year class and size variation, otoliths may also be helpful in providing information on the relationship between size of otolith and subsequent growth of an individual. For 37 0-group fish collected from late summer, correlation coefficients were calculated between fish length at capture and (1) maximum length of the otolith, and (2) maximum length of its opaque center. The difference between the two  $r$ 's, 0.956 and 0.598 respectively, was significant ( $t = 4.97$ ). Assuming a constant relationship between otolith length and fish length as well as formation of the hyaline margin

at about the same calendar time, these results suggest that growth of the otolith after deposition of the opaque center was variable. In view of these results and of the variations in otolith growth with fish size and year classes, it is concluded that exact age within the 0 age-group cannot be determined by otolith characteristics.

The equation of otolith length ( $Y$ ) and standard length ( $X$ ) for the above 37 fish was  $Y = 0.39 + 0.0293 X$  (both lengths in mm). The otoliths from 18 small juveniles (6.3–12.0 mm) were more lobate and circular than those from older fish, giving the equation  $Y = -0.240 + 0.058 X$ , which indicates a steeper slope than the first equation and formation of the otolith when larvae were about 5 mm in length. (No ossified otoliths were found in fresh specimens until the left eye was in the median position, or when the fish was about 7.0 mm) The equation given by Berry (1959) for large flounders indicates an even larger intercept and lower slope. Together these equations suggest a parabolic relationship between flounder length and otolith length, with relatively slow otolith growth in large fish.

**GROWTH IN WEIGHT.** The average length of flounder in millimeters at the beginning of each month was converted to weight in grams by means of the length-weight relationship,

$$W = .000017 L^{3.0}, \quad (1)$$

which was based on measurements of over 1000 juveniles. The logarithm of the initial monthly weight is plotted in Fig. 5. Although this method depicts growth as exponential between months, it is clear from the curve that growth can be estimated in this manner only over short intervals. The growth-in-weight

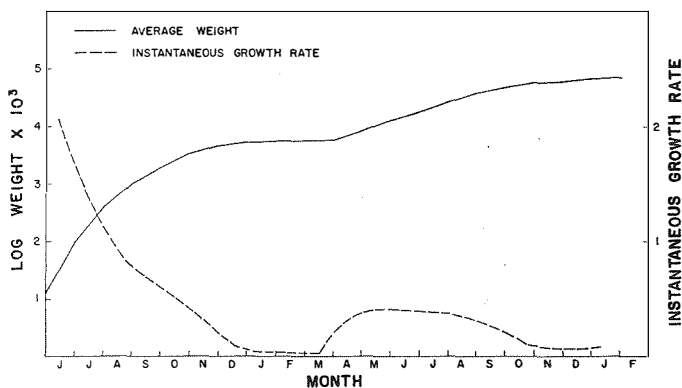


Figure 5. Average Monthly Weights of Individual Juvenile Flounder of the 1958 and 1959 Year-Classes Collected by Trawling and Their Instantaneous Rates of Growth.

curve consists of stanzas for each age-group, with rapid growth before November followed by slow growth during the winter and early spring.

The instantaneous rates of growth,  $k = dw/dt$ , are calculated from the relative growth  $b$ , where

$$b = \frac{W_{o_{i+1}} - W_{o_i}}{W_{o_i}}. \quad (2)$$

$W_o$  is the average individual weight at the beginning of month  $i$ . Therefore,  $e^k = b + 1$ . The basic variations of instantaneous growth are also shown in Fig. 5. Age-group 0 displays very rapid growth in June, after which there is a continuous decline to minimal growth in the winter. The range of instantaneous growth coefficients for age-group 1 is only about one-sixth that of age-group 0. Growth rates increase during the second spring to a maximum in June–July and then decline in the fall to a winter low.

*Net Production.* Net production is the total quantity of biomass formed during a stated period regardless of whether or not all of it survives to the end of that period (Ivlev, 1945; Clarke, 1946). In this paper the methods of Ricker (1946) and Ricker and Foerster (1948) are used; net production is calculated as the product of average population biomass and the rate of increase in weight during a specified interval. Since both flounder density and growth vary seasonally, production is calculated for each month separately, with monthly increments added together to give annual production.

Since monthly estimates are available for both flounder density (Fig. 1) and growth-in-weight (Fig. 5), production can be computed as a product of instantaneous growth ( $k$ ) and average population biomass ( $\bar{W}$ ). Because instantaneous rates are additive, monthly values for  $\bar{W}$  can be derived from the equation

$$\bar{W} = W_0 \frac{e^{k-d} - 1}{k-d}, \quad (3)$$

where  $\bar{W}$  equals the average population weight or biomass at the trawl stations,  $W_0$  the initial population weight for each month,  $k$  instantaneous growth in weight, and  $d$  the instantaneous change in population number, where  $\text{antilog}(\log N_{o_{i-1}} - \log N_{o_i}) = e^{-d}$ .

Table III shows these monthly computations for the juvenile winter flounder (for additional explanations see Ricker and Foerster, 1948). Note that initial population weights as calculated in this table are similar to values which are simply a product of mean individual weights and observed flounder numbers, thereby substantiating the calculated rates. The monthly values for both production and biomass in grams wet weight per 1000 square meters are graphically presented in Fig. 6.

TABLE III. COMPUTATION OF NET PRODUCTION OF JUVENILE WINTER FLOUNDER ON A MONTHLY BASIS FROM INSTANTANEOUS GROWTH RATES AND AVERAGE POPULATION BIOMASS.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
Month	Av. Indiv. Wgt. ( $\bar{W}$ )	Growth Rate Rel. ( $b$ )	Growth Rate Instant. ( $k$ )	Log Pop. No./1000 $m^2$	Inst. Rate for Pop. No. ( $d$ )	Net Instant. ( $k-d$ )	Change In Wgt. ( $e^{k-d} - 1$ or $1 - e^{-k-d}$ )	In Bio-mass	Initial Pop. Calc. ( $W_0$ )	Wgt. Obs. ( $W_1$ )	Av. Pop. Wgt. ( $\bar{W}$ )	Produc. ( $\bar{W}$ ) (4)
May	0.037	2.351	1.214	2.65	-1.382	2.596	12.410	20.35	1.64	1.64	7.84	9.5
June	0.124	6.992	2.078	3.25	.575	1.503	3.4952	76.86	21.99	22.05	51.2	106
July	0.091	2.971	1.379	3.00	1.151	.228	.2561	25.32	98.85	99.10	111.3	153
Aug.	0.3935	1.5235	0.926	2.50	.575	1.575	.4205	52.23	124.2	124.3	149.1	138
Sept.	0.9930	.9895	.688	2.25	1.115	.573	.7911	139.5	176.4	176.5	243.7	168
Oct.	1.976	.6962	.528	2.20	.437	.965	1.6248	513.3	315.9	313.1	527.2	278
Nov.	3.351	.3936	.332	2.39	.368	-.036	-.0353	-29.3	829.2	822.7	806.6	268
Dec.	4.670	.0942	.090	2.23	.368	-.278	-.2427	194.1	799.9	793.0	692.2	62
Jan.	5.110	.0450	.044	2.07	3.615	-3.571	-.9719	588.8	605.8	600.4	163.4	72
Feb.	5.340	.0450	.044	0.50	0	.044	.0450	0.76	17.0	16.88	17.3	0.8
March	5.580	.0450	.044	0.50	-2.694	2.738	14.456	256.7	17.7	17.64	93.1	4.1
April	5.830	.384	.325	1.675*	.084	.241	.2725	74.8	274.5	275.7	311.8	101
May	8.070	.510	.412	1.637*	.084	.328	.3822	133.5	349.3	349.8	407.5	168
June	12.19	.480	.392	1.599*	.084	.308	.3607	174.1	482.8	484.2	570.0	223
July	18.04	.471	.386	1.561*	.084	.302	.3526	231.6	656.9	656.5	766.5	296
Aug.	26.53	.407	.341	1.523*	.084	.257	.2930	260.3	888.5	884.7	1009	344
Sept.	37.35	.303	.265	1.485*	.084	.181	.1984	227.9	1149	1141	1250	331
Oct.	48.67	.155	.144	1.447*	.084	.060	.0618	85.1	1377	1362	1403	202
Nov.	56.23	.093	.089	1.409*	.084	.005	.005	7.3	1462	1442	1443	128
Dec.	61.48	.0823	.079	1.371*	.084	-.005	-.005	-7.3	1469	1445	1438	114
Jan.	66.54	.0865	.089	1.333*	.084	.005	.005	7.3	1462	1436	1465	130
Feb.	72.30	-	-	1.295*	.084	.005	.005	(7.1)	1469	1426	(1429)†	(127)
March	-	-	-	(1.257)*	.084	.005	.005	(7.2)	-	(1433)	(1436)†	(128)
April	-	-	-	(1.219)*	.084	.005	.005	(7.2)	-	(1440)	(1443)†	(128)
											17,234	3679

\* Calculated from regression equation. ( ) Calculated from previous rates only. † Simple average from column (11).

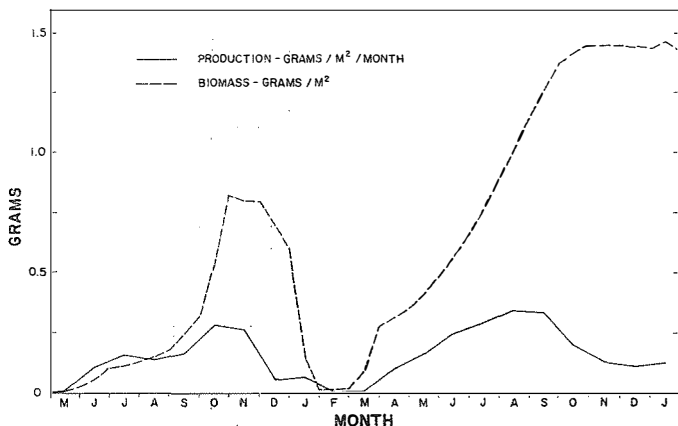


Figure 6. Average Monthly Biomass and Net Production of Age-Group 0 and 1 Flounder in the Mystic River Estuary.

There are distinct seasonal variations in biomass or standing crop of juveniles related to both flounder density and growth (Figs. 1, 5). The biomass of age-group 0 increases during the spring and summer and then rises rapidly to a peak in October, which may be partially due to flounder movement into deep water at this time. Biomass falls to extremely low values in the winter and then ascends the following spring when age-group 1 returns to the estuary. Biomass during this second year reaches values which are almost twice those of age-group 0.

The curve for net production (Fig. 6) shows a similar seasonal pattern for both age-groups. Highest production occurs in the fall for age-group 0 and during the summer for age-group 1, *i. e.*, 0.28 and 0.34 g/m<sup>2</sup>/mo. respectively. The products of  $k$  and  $\bar{W}$  are approximately the same for both age-groups despite large changes in density and growth with age. Peak production is found late in the year in both cases, while biomass is high, and prior to a marked deceleration of growth.

The mean biomass for both age-groups at the trawl stations is 1.44 g/m<sup>2</sup>. The total annual production for each age-group, obtained by summing the monthly production increments in Table III, equals 1.36 g/m<sup>2</sup> for age-group 0 and 2.32 g/m<sup>2</sup> for age-group 1. The combined net production for both juvenile age-groups collected at the trawl stations is over twice the average biomass, 3.68 g/m<sup>2</sup>/year or about 33 lbs/acre/year. Correcting for the amount of water (Vinogradov, 1953), net production of *P. americanus* is 0.66 g dry wt./m<sup>2</sup>/year or, using the energy contents of a related species (Hatanaka, *et al.*, 1956), 4.05 k cal/m<sup>2</sup>/year.

*Juvenile Survival.* Survival, or conversely, mortality, can be estimated by comparing the average density of the juvenile flounder during successive peri-

ods when the percent of the population within the estuary is constant, namely from spring to winter.

The curve for age-group 0, however, is noticeably influenced by lateral movements of fish into shallow water during the summer, a difficulty which is circumvented by calculating the survival rate for this period with two partially dependent methods. The first simply excludes the data for the summer and uses the spring and fall averages before and after this movement is detectable. By the second method, the density of fish in shallow water is estimated and added to the density at the trawl stations. Replicate seine and trawl samples in shallow water during the summer give the regression (through the origin),  $\text{trawl catch/m}^2 = .0125 \text{ standard seine haul catch}$ . Since about two-thirds of the estuary is above 1.5 m at mean low water, about the lower limits of beach seining, the adjusted trawl catches were estimated by,

$$\text{Adjusted catch/m}^2 = \log [\text{trawl catch/m}^2 + 2 (.0125 \text{ seine catch})]. \quad (4)$$

In effect this equation concentrates all flounders into the deeper one-third of the estuary, which is presumed to be adequately represented by samples taken at the trawl stations. These adjusted frequencies (open symbols, Fig. 1) result in a more regular decline throughout the summer than the unadjusted averages.

In both cases mortality was computed from the slopes (as calculated by the method of least squares) of the biweekly averages for both year classes (Table IV). Both estimates indicate that the average monthly survival rate is about 69% for age-group 0 (95% C.I., 62.5–76.6%). The slope of curve for age-group 1 gives a mean monthly survival rate of 92% (95% C.I., 83.2–100%). Thus mortality is about four times greater for the young flounder. Note that an extension of the slope of the age-group 0 survival curve intercepts the base of the curve for the next age-group, indicating that mortality over the winter is about the same as that for the preceding seasons.<sup>3</sup>

*Predation.* Although supporting evidence is meager, due in part to lack of investigation, predation is thought to be a major cause of juvenile flounder mortality. The fish fauna of the Mystic River estuary consists mainly of small species (Pearcy and Richards, in press), but two large predacious species were present throughout the estuary: the toadfish (*Opsanus tau*), which may feed on winter flounder (Bigelow and Schroeder, 1953), and the summer flounder (*Paralichthys dentatus*); large summer flounder were common in the estuary from June to October, and stomach contents of over 20 of these fish were examined; though most stomachs were empty, several included fish remains, three containing identifiable 0-group winter flounder. Of the piscivorous birds,

<sup>3</sup> Dickie and McCracken (1955), on the other hand, believed that the winter mortality of commercial-sized winter flounder was close to total annual mortality for the population of St. Mary's Bay.

TABLE IV. ESTIMATION OF MEAN MONTHLY MORTALITY OF AGE-GROUP 0 (A) AND AGE-GROUP 1 (B) FROM CATCH STATISTICS (FIG. 1) BY THE METHOD OF LEAST SQUARES. THE SLOPE IS CALCULATED FOR AGE-GROUP 0 FROM ADJUSTED FREQUENCIES WHICH INCORPORATE SEINE DATA AND UNADJUSTED FREQUENCIES (SEE TEXT).

(A) 0 Group					(B) 1 Group		
Biweekly Code	Adjusted		Log. Number		Monthly Code	Log. Number	
	1959	1958	1959	1958		Beam T.	Otter T.
1 ...	3.21	3.11	3.21		1.5 ...	1.580	1.699
2 ...	3.21	3.06	3.13	3.05	2.2 ...	-	1.699
3 ...	3.07	2.77	-	-	2.6 ...	1.903	-
4 ...	2.86	2.90	-	-	3.8 ...	-	1.041
5 ...	2.81	-	-	-	4.9 ...	1.568	1.623
6 ...	2.85	-	-	-	5.9 ...	1.484	2.013
7 ...	-	2.81	-	-	6.4 ...	1.491	-
7.5 ...	1.89	-	-	-	6.6 ...	-	1.301
8 ...	-	2.70	-	-	7.5 ...	0.903	1.462
9 ...	-	2.55	-	-	8.7 ...	1.634	1.447
9.5 ...	2.09	-	-	-	10.0 ...	1.079	1.672
10 ...	-	2.59	-	-	10.8 ...	1.279	1.255
11 ...	-	2.50	-	-			
12 ...	2.33	2.36	2.33	2.36	slope (b)	= - .038	
13 ...	-	2.05	-	2.05	$s_b$	= .02	
14 ...	2.02	2.24	2.02	2.24	95% C.I.	= - .038 ± .042	
14 ...	2.30	-	2.30	-			
slope (b)	-.087	-.076		-.079			
$s_b$		.0105		.0212			
95% C.I.		-.080 ± .022		-.079 ± 0.05			

cormorants were abundant in the late summer and fall, and mergansers were often numerous in the upper estuary in the winter. The cormorant, *Phalacrocorax auritus auritus*, was actually observed feeding on young flounder; it is perhaps pertinent to note that Steven (1933) found that flatfish formed nearly 40% of the diet of a related species in England.

*Larval and Juvenile Survival.* Since metamorphosing larvae were not completely vulnerable to the sampling methods used, and since determination of their age was difficult, vital statistics on this period are lacking. Mortality during this transition from larva to juvenile can be approximated, however, by comparing the mean density of larvae just before metamorphosis with the mean density of juveniles after recruitment is completed. This calculation is made (below) by using the average density 2.40/m<sup>2</sup> for larvae taken on April 29, 1959, when the first metamorphosing larvae were observed, and 1.633/m<sup>2</sup>



for fish taken 37 days later when the bulk of the population was fully recruited as juveniles. Assuming both categories equally vulnerable to capture, the change in density can be used to calculate survival,  $s$ , where

$$\log s = (\log 1.633 - \log 2.40)/37 = -0.0043, \quad (5)$$

giving a survival rate of 99.1% per day or 74% per month. This estimate is a little higher than the survival given for postlarvae and falls just within the 95% confidence limits of the age-group 0 estimate. Consequently, there is no indication of accelerated mortality during the period of metamorphosis for this flatfish.

With estimates of survival for both larval and juvenile stages of the winter flounder, survival for both of these phases can be examined together. Table V summarizes the statistics as an ecological life table, where  $x$  is the age in months,  $l_x$  the number surviving at the beginning of an age interval,  $d_x$  the number dying within the interval, and  $q_x$  the mortality rate (Pearl, 1940). The statistics for the two age categories of larvae are based on daily mortality rates within the estuary of 0.18 and 0.02 (see Pt. II), rates which are probably conservative since this assumes that the mortality of larvae which drifted out of the estuary is the same as the mortality of those within the estuary. The juvenile mortality rates, as derived from the slopes of the catch curve (Fig. 1), averaged 0.31 and 0.084 per month for age-group 0 and 1 respectively.

Table V shows that the mortality rate, which is on a percentage basis as  $100 q_x$ , is about the same for both the larval and the juvenile stages. Both periods were accompanied by mortality rates of over 95%. This is important since it shows that juvenile mortality, though extended over a longer period, is also high. The number of survivors,  $l_x$ , and age are plotted arithmetically in Fig. 7 to give a positively skewed survival curve, the type of curve that Pearl and Miner (1935) presumed for pelagic fish with high fecundity. It dramatically illustrates the age incidence of mortality—over 97% of the total deaths occur during the first larval phase (between 0.7 and 1.5 months). After

TABLE V. PROVISIONAL LIFE TABLE FOR LARVAL AND JUVENILE STAGES OF WINTER FLOUNDER.

	$x$ (Age in months)	$l_x$	$d_x$	100 $q_x$
Larvae	0.7-1.5	100,000	97,459	97.46
	1.5-2.4	2,541	1,099	43.25
Juveniles	2.4-12.4	1,442	1,398	96.95
	12.4-22.4	44	26	59.09
	22.4-	18		
				99.982 %

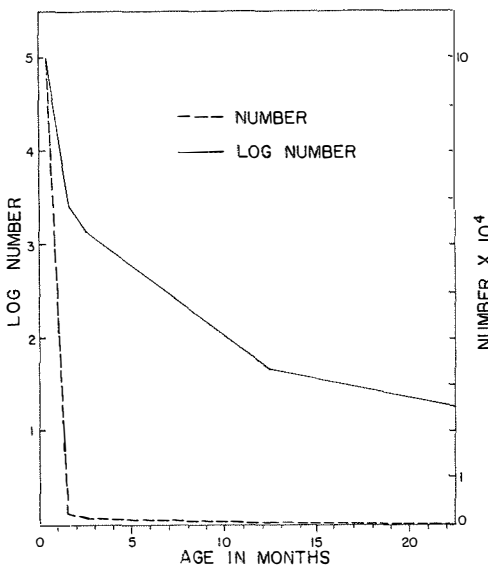


Figure 7. Survival Curve for Larval and Juvenile Winter Flounder.

this initial decrement, the arithmetic plot shows relatively small changes in the remaining number of cohorts.

The logarithm of  $l_x$  (solid line, Fig. 7) is more instructive for the examination of mortality rates; it reveals significant changes in mortality among all age categories. Mortality rates decrease between each phase, indicating an increased expectation of survival with age. (An even further increase in survival rate with age is suggested by the natural mortality estimate of 30% per year for adult winter flounder of a different population given by Dickie and McCracken, 1955). Although this curve was constructed by using rates that were assumed constant for each category, there is no indication that mortality rates in general were constant during either the larval or the juvenile stage of the life history. The data taken together, in fact, suggest a continuous and gradual decrease in mortality with age. It is important to note that, even if this curve is smoothed, survival does not show a constant rate of change; the greatest deceleration occurs early in larval life.

Since eggs of the winter flounder are demersal and were not sampled quantitatively, egg mortality cannot be accurately estimated. Saila (unpublished) estimated that the average fecundity of the winter flounder is 630,000 eggs per female. Scott (1929) reported that 33-73% of its eggs hatched in the laboratory; but this estimate may be too high for eggs in nature. The neonate frequency of 100,000 (Table V) may therefore be a rough approximation of the number of eggs that hatch per female. Accordingly, the number of juve-

nile progeny 22.4 months later is 18. Assuming a 1:1 sex ratio, female maturity at three years of age, and a continuation of age-group 1 mortality until spawning, the above estimate suggests a more than adequate steady-state survival for the perpetuation of the population, especially since a female may spawn more than once during its life. Besides our lack of knowledge about egg mortality, several other factors influence this estimate and should be considered. Larval mortality in offshore waters is thought to be higher than that in the estuary. If the value for total larval loss from the estuary, 99.4%, including larvae that drift from the estuary, is used to represent larval mortality, then seven survivors will be left at the end of 22.4 months. Fishing mortality and natural mortality before maturity are also unknown, but they would reduce the number of juveniles that reach maturity even further. The total larval and juvenile mortalities estimated in these two ways for the 0.7-22.4 month period are 99.982% and 99.993% respectively.

*Discussion.* Using different methods, Richards (in press, *b*) estimated that the net production and biomass for juvenile winter flounder of Long Island Sound were 0.03 g/m<sup>2</sup>/year and 0.05 g/m<sup>2</sup> respectively (*cf.* 3.7 g/m<sup>2</sup>/year and 1.44 g/m<sup>2</sup> in the estuary). In other words, flounder production in the estuary was over 70 times that in the nearby Sound, thus indicating the importance of small estuaries as nursery grounds for this species. The low standing crop in Long Island Sound is one reason for the low production there, and in addition, the seasonal distribution of flounder also affected this estimate, since the highest numbers of 0-group fish were taken in the Sound during the winter when growth was slowest.

The net production of these two age-groups of a single species compares favorably with other estimates for the production of communities of marine fishes. Based on commercial landings, Clarke (1946) calculated that the net production of fish on Georges Bank was 7-33 lbs/acre, about the same or lower than that of flounder in the estuary. Harvey (1950) estimated that the daily production of demersal fishes in the English Channel was 0.001 g dry weight/m<sup>2</sup>, about one-half that of the juvenile flounder for a standing crop that is about four times larger than that of the flounder. The production-to-biomass ratio for the juvenile flounder is therefore high due to rapid growth of many young individuals in the estuary.

In view of the high fecundity of many marine teleosts and the relatively smaller numbers of adults, it is known that survival during early life must be very low. It has been suggested furthermore that the size of a year-class is determined early in life (Hjort, 1926). For these reasons the variations in survival during the early life history of fishes are of singular interest. Although there has been considerable speculation about the shape of the survival curve for young fishes, unfortunately, little observational information is available. No other survival curve is known for both larval and juvenile stages.

Several survival curves do exist, however, for larvae of marine fishes. They are alike in having high mortality rates for the period as a whole. In most, namely the Pacific sardine (Ahlstrom, 1954), the jack mackerel (Farris, 1960), the Japanese sardine and the Japanese anchovy (Nakai and Hattori [1955], cited by Farris [1960]), there are differential rates in which the highest mortality is found early in larval life. Although Sette (1943) mentioned that post-larval mortality rates for the Atlantic mackerel were more moderate than for earlier stages, in general the changes in mortality rates were not as striking as those in the other curves. The differences in the form of these survival curves are not surprising in view of the variations in the species genotype, diverse physical, chemical, and biological environments, as well as differences due to sampling or computation of statistics. Moreover, many of the environmental influences are problematical and may vary from year to year, such as is evidenced for different year-classes of the Pacific sardine and the jack mackerel.

Though both density-dependent and density-independent mortality coefficients of a population are superimposed on each other in varying ways and degrees to determine the rates of survival, it seems reasonable, on the basis of the stability of many populations, that density-dependent mortality is an underlying influence acting at one or more stages in the early life history to determine the number of young of a species living to adulthood (Ricker, 1954; Beverton and Holt, 1957; others). It is of interest to note that the shape of the survival curve for the young winter flounder, a species in which dominant year-classes are not obvious, is similar to the hypothetical curve constructed by Beverton and Holt (1957: 51), based on density-dependent mortality during this period, density being inversely related to age; with the exception of one period of high intrinsic mortality (which "might be taken to represent metamorphosis in flatfish . . ."), their curve represents decreasing mortality coefficients with age also giving a concave curve. Since intraspecific competition for available food may directly or indirectly result in density-dependent mortality, it is tempting to speculate that this concave type of mortality curve is more probable where populations of high absolute densities are localized in small areas. Since there was some evidence for density-dependent growth in the juvenile winter flounder, and since predatory fish such as the summer flounder are limited to small-size prey, it is conceivable that density-dependent mortality of the juveniles could be effected by a higher predatory rate on small or slow-growing fish (Ricker and Foerster, 1948). A similar mechanism may apply to the larvae (Pt. II).

Discussion of differential rates on mortality focuses attention on the "critical period" in the early life history of fish. Hjort (1926) stated that the size of a year class was determined at a very early age, and he indicated that the "very earliest larval and young fry stages are most important and the stages in which the most critical period is to be sought." He pointed out two possible events that might determine the survival of a year-class: (1) lack of proper food im-

mediately after yolk sac absorption, and (2) offshore drift of young larvae. Hence, he referred to two phenomena: a direct causal mechanism during a specific stage and an indirect cause during a general period. There is little evidence for the first cause, a "critical period" following yolk sac absorption, in nature (Marr, 1955; Farris, 1960), but the importance of currents and offshore dispersal of young has been indicated by several authors (Walford, 1938; Sette, 1943; Wiborg, 1957; for others, see Bishai, 1960).

More recently the critical period has been defined as "catastrophic mortalities restricted to a brief period" (Marr, 1955: 169) or "that very brief portion of a fish's life when it has a reduced chance of survival which . . . governs the size of the ensuing year-class" (Farris, 1960: 299). Such definitions are descriptive and may be applied to certain survival curves where there are abrupt changes in mortality rates with age, as shown by Farris for larval jack mackerel. Yet it should be realized that the "critical period", by these definitions, is a relative concept and depends not so much on the absolute rates of mortality as upon the differences of slope within the curve. Two examples may clarify this point. No specific period of accelerated mortality is clearly evident within the survival curve for the Atlantic mackerel even though numbers decrease by about five log units (Sette, 1943). However, if data were available for the juvenile mackerel of this year-class, they would probably indicate that the entire larval period could be termed "critical" by comparison. The survival curves for Japanese anchovy larvae (Nakai and Hattori, cited by Farris, 1960) and for the winter flounder provide the second example. They show relatively high rates of mortality early in life, thereby fulfilling certain "critical period" criteria, but both of these curves are concave, with mortality gradually decreasing with age. There are no abrupt changes in slope. As a result, any distinction between "critical" and "non-critical" periods is clearly arbitrary.

Judging from the available data, it appears that Hjort was correct in suspecting that the highest mortality rates occur during early larval life. There is little evidence, however, in support of his supposition that the size of a year-class is determined during any single larval phase. It seems more plausible that mortality, which is a combination of density-dependent and density-independent variables, is important throughout the entire early life history. If compensatory mortality occurs, then examination of a single phase will give little information on the resulting size of the reproductive population. That data are required for the whole early life history is indicated by the survival curve for the winter flounder, where juvenile mortality is high and where it also undergoes significant changes with age. This suggests that the "critical period" concept is equivocal and over-simplified. It is of limited value since it tells little about the causes, distribution, or rates of mortality.

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Вильям Г. Перси

Экология предустьевой популяции зимней камбалы  
*Pseudopleuronectes americanus* (Walbaum).

III. Распространение, обилие, рост и выращивание молоди;  
выживание молоди и личинок.

Краткий Обзор

Молодь камбалы возрастных групп 0 и 1 собирали тралом в эстуарии реки Мистика. Средняя густота населения очень большая; густота группы 0 весной достигала выше чем  $1/m^3$ . Рост молоди быстрый во время теплого сезона, Месячные подсчитывания густоты и роста употреблялись для оценки продуктивности. Продуктивность обеих возрастных групп была максимальной поздним летом и осенью, а минимальной зимой, когда и густота и рост были очень незначительны. Годовая продукция молоди очень велика,  $3.7 g/m^2$ ; средняя биомасса  $1.44 g/m^2$ .

Средняя месячная смертность, вычисленная на основании кривой полученной с уловов в периоды достаточного обилия молоди, равнялась 31% у возрастной группы 0 и 8% у группы 1. Данные взаимной смертности у личинок и молоди представлены кривой выживания. Наименьший процент выживания у личинок раннего возраста. Он увеличивается постепенно в продолжении личиночной жизни. Общая смертность личинок и молоди во всех их стадиях равнялась приблизительно от 99.98% до 99.99%.

Понятие о „критическом периоде“ подвержено обсуждению. Оно обладает ограниченной полезностью в описании смертности, особенно в период ранней жизни зимней камбалы.



*Ecology of an Estuarine Population of  
Winter Flounder, Pseudopleuronectes americanus  
(Walbaum).*

*IV. Food Habits of Larvae and Juveniles*<sup>1</sup>

By

William G. Pearcy

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ABSTRACT

Empty stomachs in larval winter flounder ranged from 72% for small postlarvae to 25% for metamorphosing larvae. In contrast, only 6% of the juveniles had empty stomachs. Nauplii, polychaetes, and invertebrate eggs appeared frequently in larval stomachs, as did many small protozoan-like animals that could not be positively identified. The predominant food for metamorphosing larvae and for juveniles up to 10 mm in length was harpacticoid copepods, and for age-group 0 juveniles until August, calanoid copepods. After this time amphipods and polychaetes were most important. Polychaetes became increasingly important by volume with age. *Ampelisca* and *Neanthes* were the two most important prey of juveniles.

The juveniles were euryphagus; 77 food organisms from seven phyla were identified. A high degree of food selectivity was indicated at certain times of the year; for example, when large numbers of calanoid copepods were found in year-old flounder.

Winter flounder fed primarily by day. It is estimated that stomachs of age-group 0 during the summer normally emptied during the night, or in about eight hours.

*Introduction.* The importance of the estuary in the ecology of young *Pseudopleuronectes americanus* has been indicated in the two previous papers herewith. The estuary is densely populated by larval and juvenile flounder, their growth is rapid, and the estimate of juvenile productivity is high. These population parameters depend upon adequate nutrition of the young and suggest that the standing crops and productivity of food organisms in the lower trophic levels must also be high.

Although the feeding habits of the winter flounder in adjacent areas have been studied (Linton, 1921; Smith, 1950; Richards, in press), there has been no analysis of its food habits in an area which is intensely utilized as an estuarine nursery. Neither are there reports of the ontogeny of its feeding habits through

<sup>1</sup> Contribution No. 19 from the Marine Research Laboratory, University of Connecticut.

both the larval and juvenile stages. This paper describes the food habits of flounder from the Mystic River estuary and compares these findings with those from other areas to see if any unique differences exist. Richards (1959), for instance, noting a high percentage of empty stomachs in winter flounder larvae of Long Island Sound, suggested that they may not feed as efficiently as other species on the zooplankton present and that they may have a more suitable source of food inshore. It has been one of the purposes of this study to determine if the frequency of empty stomachs of larvae in the estuary is significantly lower than in the adjoining Sound.

*Methods.* Larvae and juveniles used in the food habits study were collected within the estuary, mainly at Sts. 3.7 and 5.1, by methods previously described. The larvae were collected during April and May of 1959, and most of the juveniles were collected at trawl stations, though some were collected by seining. Juveniles represented age-group 0 and age-group 1 of both the 1958 and 1959 year-classes. All the material was preserved in the field with 10% formalin in seawater.

Following measurement of the fish (standard length), the alimentary tract of the individual larva or the stomach of the juvenile was removed with the aid of a dissecting microscope. Each larval gut was transferred to a clean glass slide and dissected with needles; the particulate contents were examined under a compound microscope. In general, only the dissecting microscope was used for the dissection or examination of the stomachs of juveniles. A total of 315 larvae and 359 juveniles was examined.

The degree of fullness of flounder stomachs was categorized as empty, full, or to the nearest quarter fullness. Food organisms were separated into four major categories: polychaetes, copepods, amphipods, and miscellaneous. Whenever possible, or feasible, specific identification of an individual organism was made. The number of animals in each category, or in taxonomic subdivisions of a category, was counted from individual stomachs. The relative abundance of each category was estimated by inspection for juveniles under 30 mm and for larvae. The abundance of each category was determined by displacement volume for collections consisting of juveniles over 30 mm. The excess fluids in these items were removed with filter paper, and the food organisms were added to calibrated centrifuge tubes or graduates which contained a known amount of fluid. The total displacement volume of each food category was recorded after all the stomachs from a collection were analyzed, this giving an estimate of the average diet.

Since major emphasis is placed on variations of food habits with flounder size and season of year, the results of several collections within a month were combined. Although this procedure introduced differences associated with station location, time of day, perhaps size, etc., it was noted that the diet or the fullness of stomachs varied appreciably within single collections. A detailed

analysis is therefore difficult, and the results herein illustrate the generalized food habits of the flounder in the estuary.

*Results: Larvae.* The results of the analyses are shown relative to larval size in Table I. Only larvae without yolk-sacs, or postlarvae, were examined. A high percentage of empty stomachs (anterior portion of the gut) was found, ranging from 72% for small larvae to 25% for metamorphosing larvae. The data indicate that the proportion with empty stomachs decreased appreciably with larval size.

Nauplii, polychaetes, invertebrate eggs, and phytoplankton were the major items identified from the stomach contents of small 3–6 mm larvae. Nauplii, eaten by nearly all sizes, were most common in the stomachs of those 4–5 mm long when the frequency of occurrence was 28%. The remains of larval polychaetes were common, consisting mostly of epidermis and setae; polychaetes, due to their comparatively large size, were probably more important from the standpoint of volume than is indicated in Table I. Small invertebrate eggs appeared frequently in the small larvae. Phytoplankton, such as pennate and filamentous diatoms, were noted occasionally in the smallest larvae (3–4 mm), but usually they were found when other organisms were present in the stomachs, and they may have been the food of other ingested animals.

TABLE I. A. NUMBER OF FLOUNDER LARVAE OF VARIOUS SIZES WITH EMPTY AND PARTIALLY FULL STOMACHS, AND THE PERCENTAGE WITH EMPTY STOMACHS.  
B. FREQUENCY OF OCCURRENCE OF DIFFERENT PREY IN THE DIET OF LARVAL FLOUNDER. FIGURES ARE GIVEN AS A PERCENTAGE OF ALL LARVAE IN THE SIZE CATEGORY THAT HAD FOOD IN THEIR STOMACHS.

	Larval Length (mm)					Metamorphosing
	3-4	4-5	5-6	6-7	7-8	
A. No. with:						
empty stomachs . . . . .	58	28	11	8	12	47
food in stomachs . . . . .	22	15	19	11	14	140
Percent With Empty Stomachs . . . . .	72	65	37	42	46	25
B. Nauplii . . . . .	2	28	18	7	—	4
Harpacticoids . . . . .	—	—	—	—	7	46
Calanoids . . . . .	—	—	—	—	7	10
Polychaetes . . . . .	9	—	12	26	28	7
Invertebrate Eggs . . . . .	17	11	6	—	—	—
Nemertean . . . . .	—	—	—	—	—	7
Phytoplankton . . . . .	17	—	—	—	—	—
Unidentified animal material . . . . .	55	61	64	60	50	30

The major identified food of postlarvae 6–8 mm long was small polychaetes, sometimes as many as eight individuals being found in a single stomach. Many of these polychaetes had a long pair of cirri like those of the family Spionidae. Crustacea, including nauplii as well as both harpacticoids and calanoid copepods, were preyed upon by larger larvae 7–8 mm in length.

Copepods were the most important food of the metamorphosing flounder larvae. Harpacticoids were especially common, being found in 46% of the stomachs containing food. The fact that adult copepods were not preyed upon until late in larval life is probably due to the inability of larvae to capture and ingest these relatively large sized animals before this time. Their depth distribution may have affected food selection also, as the larger larvae were more abundant near the bottom, where harpacticoids are also presumed to be concentrated. Nauplii and polychaetes were eaten also by the metamorphosing larvae, and nemerteans and a few ostracods were preyed upon by this stage for the first time.

Some portion of the gut contents of over one-half of the premetamorphosing larvae could not be positively identified and was listed as unidentified animal remains (Table I). This category includes several types of organisms. Many were 100–300  $\mu$  long, some with arenaceous tests (possibly *Tintinnopsis*); others had external features that resembled either hypotrichs or rotifers. It is unfortunate that a more detailed analysis of this fraction was not possible since it was an important part of the larval diet.

*Results: Juveniles.* Unlike the larvae, only 21 out of 359 juveniles had empty stomachs, the majority of these being found in fish taken during the winter months. The fullness of individual stomachs was variable either for a collection or for a season, but in general stomachs were 25–75% full during all seasons, excepting the winter, when most were about 25% full or less.

The relative importance of the major food categories of juveniles in the estuary is shown in Table II. In June, small juveniles (less than 10 mm) preyed almost exclusively on copepods, especially harpacticoids, which made up over 80% of the diet. On the other hand, larger juveniles (10–25 mm) ate more amphipods and polychaetes and fewer copepods during this month.

During July there were also distinct differences. The diet of fish less than 25 mm was again almost exclusively copepods, but at this time calanoids, whereas the stomach content of the larger flounders of this age-group was composed of nearly equal volumes of copepods, amphipods, and polychaetes.

In August, and succeeding months, no marked differences in the feeding habits were noted among the different sizes of fish in a collection. Polychaetes composed the greatest bulk of the diet in August, followed by copepods, which were numerically the most important, and then amphipods. From September

TABLE II. STOMACH CONTENTS OF JUVENILE WINTER FLOUNDER THROUGHOUT AGE-GROUP 0 AND I, INCLUDING THE PERCENTAGE OF TOTAL VOLUME COMPOSED OF COPEPODS, AMPHIPODS, POLYCHAETES, AND MISCELLANEOUS ORGANISMS.

Month	Size (mm)	No. Exam.	No. With Empty Stom.	Percent of Total Volume as			
				Copepods	Amphipods	Polychaetes	Misc.
Age-group 0							
June .....	6-10	31	1	83	5	6	6
June .....	11-24	38	0	38	30	19	13
July .....	10-25	18	0	88	10	1	1
July .....	26-42	16	0	30	25	33	12
Aug. ....	20-47	35	0	25	7	65	3
Sept. ....	34-85	14	0	1	62	35	2
Oct. ....	40-75	17	0	1	90	6	3
Nov. ....	40-70	24	0	3	82	6	9
Dec. ....	50-80	29	4	16	23	53	8
Jan. ....	45-85	18	8	7	59	17	17
Feb. ....	42-88	15	1	0	63	26	11
Age-group I							
Mar. ....	60-90	21	2	73	1	11	15
Apr. ....	75-100	16	1	< 1	45	51	3
May .....	55-102	7	0	< 1	34	25	41
Aug.-Sept.	90-128	21	1	< 1	16	71	13
Oct.-Dec...	103-145	7	0	0	11	65	24
Jan.-Mar...	117-165	10	3	0	4	87	9

to March amphipods were usually the basic food organisms for this age-group, with polychaetes and copepods of secondary importance.

The high relative abundance of copepods during March is surprising, since relatively large flounder, 60-90 mm long, which are normally considered benthos predators, selected small calanoid copepods as food. Many full stomachs contained only copepods at this time.

After March, when the juveniles were over a year old, polychaetes and amphipods were the major prey animals, and polychaetes became increasingly important, constituting over 60% of the food volume from summer to winter.

The animals identified from the stomachs of juveniles, listed in Table III, permit a brief discussion of the important ones from the various taxonomic groups. Copepods, as noted, were the most important food for small juveniles; at first harpacticoids were predominant, and calanoids became more important for larger fish. The most common calanoid copepod found in juveniles during June was *Eurytemora*, which was observed to be very abundant in the spring in the upper estuary, especially in plankton tows made near the bottom. During

TABLE III. LIST OF THE FOOD ORGANISMS IDENTIFIED FROM STOMACHS OF JUVENILE WINTER FLOUNDER.

COELENTERATA	ARTHROPODA (cont.)	ARTHROPODA (cont.)
hydroids	CRUSTACEA	CRUSTACEA
NEMERTEA	Ostracoda	Isopoda
<i>Cerebratulus</i> spp.	<i>Cylindroleberis mariae</i>	<i>Cyathura carinata</i>
ANNELIDA	<i>Pontocypris edwardsi</i>	<i>Edotea montosa</i>
<i>Anaitides</i> sp.	<i>Pseudocytheretta edwardsi</i>	<i>Edotea triloba</i>
<i>Arabella</i> sp.	<i>Sarsiella americana</i>	<i>Erichsonella attenuata</i>
Capitellidae	<i>Sarsiella zostericola</i>	<i>Faera marina</i>
<i>Cirratulus grandis</i>	Mysidacea	<i>Leptochelia savignyi</i>
<i>Clymenella</i> sp.	<i>Neomysis americana</i>	Decapoda
<i>Ctenodrilus</i> sp.	Cumacea	<i>Crago septemspinosus</i>
<i>Drilonereis</i> sp.	<i>Cyclaspis varians</i>	<i>Palaemonetes vulgaris</i>
<i>Eupomatus dianthus</i>	<i>Oxyurostylis smithi</i>	zoëa
<i>Glycera americana</i>	Amphipoda	INSECTA
<i>Glycera</i> sp.	<i>Aeginella longicornis</i>	Tendipedidae (larvae)
<i>Harmothoë imbricata</i>	<i>Ampelisca</i> spp.	PYCNOGONIDA
<i>Lumbrineris tenuis</i>	<i>Batea catharinensis</i> *	<i>Nymphon</i> sp.
Maldanidae	<i>Byblis serrata</i>	ARACHNIDA
<i>Maldanopsis elongata</i>	<i>Calliopius laeviusculus</i> *	Halacaridae
<i>Neanthes succinea</i>	<i>Caprella geometrica</i>	MOLLUSCA
<i>Neanthes caudata</i>	<i>Caprella linearis</i>	<i>Gemma gemma</i>
<i>Polydora ligni</i>	<i>Corophium cylindricum</i>	<i>Haminea solitaria</i>
Spionidae	<i>Corophium</i> sp.	<i>Lyonsia hyalina</i>
Terebellidae	<i>Cymadusa filosa</i> *	<i>Mya arenaria</i>
ARTHROPODA	<i>Gammarus annulatus</i>	<i>Nassa</i> sp.
CRUSTACEA	<i>Gammarus locusta</i>	<i>Solemya velum</i>
Cladocera	<i>Idunella</i> n. sp.†	ECHINODERMATA
<i>Podon leuckarti</i>	<i>Jassa falcata</i> *	Ophiuroidea
Copepoda	<i>Lembos smithi</i>	CHORDATA
<i>Eurytemora</i> spp.	<i>Leptocheirus pinquius</i> *	<i>Molgula</i> sp.
<i>Paracalanus</i> sp.	<i>Listriella</i> n. sp.†	<i>Apeltes quadracus</i> (eggs)
<i>Pseudodiaptomus coronatus</i>	<i>Lysianopsis alba</i>	
Harpacticoida	<i>Metopa pusilla</i> *	
	<i>Microdeutopus gryllotalpa</i>	
	<i>Phoxocephalus holbölli</i> *	
	<i>Unciola irrorata</i> *	
	<i>Unciola</i> sp.	

\* Identified by Pierre Brunel, Station de Biologie Marine, Gaspé, Quebec, Canada.

† According to Pierre Brunel these species may represent the first record of the family Lilljeborgiidae on the east coast of North America.

July, however, the high relative abundance of copepods in the flounder's food (88%) was mainly due to *Pseudodiaptomus*, a genus not noted in the spring. *Paracalanus* was eaten during the summer and *Eurytemora* was preyed upon heavily by the next age-group in March. These variations are interesting in

light of the seasonal distribution of some copepods reported by Frolander (1955) for nearby Narragansett Bay, Rhode Island. He found that *Eurytemora* was abundant from April to July and that *Pseudodiaptomus* was abundant during July but was absent during the spring. Such differences in the seasonal availability of these copepods no doubt influenced the occurrence of the different genera in the diet of the flounder.

Amphipods, important as food throughout the juvenile life of the flounder, were most important by volume relative to other food categories when flounder were between 40 and 90 mm. Amphipods were usually the dominant animals by numbers except when copepods were common. *Ampelisca*, eaten more often than any other amphipod, outnumbered all other types of amphipods in the food from June to December for age-group 0. There are indications that the variety of amphipods eaten increased during the first winter. At this time *Corophium*, *Microdeutopus*, and *Phoxocephalus* of the amphipod group were most common, not *Ampelisca*; and *Batea*, *Byblis*, *Gammarus*, *Metopa*, *Lysianopsis*, *Jassa*, and *Calliopius* were also present. Though many types of amphipods were eaten by age-group 1, *Ampelisca* and *Corophium* numerically exceeded all others during May and June, with *Ampelisca* the most common amphipod in the diet during the fall.

*Caprella geometrica* and *C. linearis* were identified from food contents, but they were rarely found and were not important.

Polychaetes were generally more difficult to identify than the amphipods or other crustacea, as they were often fragmented and partially digested. For this reason the variety of polychaetes listed in Table III is relatively low. Although they occurred less frequently in the diet than crustacean food, their relative volume was often high due to the large bulk of a few specimens.

During June and July of the first year the polychaetes, which appeared in over half of the stomachs examined, consisted mainly of malidanids, though small *Neanthes* and *Drilonereis* were also present. In the fall and winter, when polychaetes occurred in less than half of the stomachs, *Clymenella*, *Neanthes*, *Lumbrineris*, *Cirratulus*, *Eteone*, and malidanids were found. *Clymenella* was the most important volumetrically from October to January; it constituted a large proportion of the volume of polychaetes (53%) reported for December (Table II).

The larger volume of polychaetes consumed during the second year was due to the larger size of the prey rather than to greater numbers. Often times a single *Neanthes succinea* made up most of the food volume. Terebellids also composed a significant part of the diet, especially during the summer. Maldanids, glycerids, lumbrinerids, *Cirratulus*, *Drilonereis*, and *Harmothoë* were also found in age-group 1 flounder.

Nemertean, ostracods, isopods, decapod crustacea, and mollusks were the most important constituents of the "miscellaneous" category (Table II). The variations of these organisms in the juvenile's diet depended largely on the

flounder's size or the season of the year. Nemerteans were the most important members of this category by either numbers or volume for the small juveniles before August of the first year; sometimes they formed up to 75% of the volume in an individual stomach. Even though they appeared in the diet of older juveniles during all seasons, they were of minor importance after the first summer.

Ostracods, also eaten by both juveniles age-groups, were common in the diet only during the first spring of juvenile life. *Sarsiella*, *Pseudocytheretta*, *Cylindroleberis* and *Pontocypris* were identified from their food.

Isopods were of relatively minor importance. The maximum (on two occasions) was only 2% of the total volume of all food categories. Nor were they invariably present in the diet of the flounder that had completed metamorphosis, as reported by Sullivan (1915). Both age-groups ate *Erichsonella*, *Edotea*, *Cyathura*, and *Jaera*, the first of these being the most common.

*Neomysis americana*, which first appeared during August in age-group 0, was present in the diet every month thereafter. Sometimes during the fall it formed the major portion of the volume in the miscellaneous category. *Crango septemspinosus* was also preyed upon after the first summer; though it was not frequently a part of the diet, it constituted a large part of the volume when present.

Mollusks were rarely eaten by age-group 0, but they were important during the second year when they composed up to 18% of the total diet for several months in the spring and fall. *Lyonsia*, *Solemya*, and *Haminea* were also found in the food.

Other organisms listed in Table III were of minor significance. Cumacids, namely *Cyclaspis varians* and *Oxyurostylis smithi*, were frequently found in the food contents but their volume was negligible. Hydroids, found several times during the winter and spring, sometimes accounted for a large percentage of the miscellaneous category, such as the 41% found for May of the second year. Filamentous algae were found in stomachs of juveniles several times during the late fall or winter.

The stomach contents of age-group 0 inhabiting shore waters during the summer were examined to compare their feeding habits with those of flounder in deep water. The shoal water fish preyed mainly on polychaetes and amphipods. However, the fish in a seine collection made in July had been feeding almost exclusively on calanoid copepods and ostracods. Thus the major groups of animals in their diet were similar to those of fish in deeper water. The genera of prey differed somewhat. *Neanthes* was the predominant polychaete eaten in both shallow and deep water, but *Corophium* and *Microdeutopus* were the most common amphipods in the shoal water fish, largely replacing *Ampelisca*. Isopods, such as *Edotea* and *Leptocheilia*, were also more frequent in the stomachs of the shoal-water flounder.



TABLE IV. TIME REQUIRED FOR JUVENILES FED IN THE LABORATORY TO EVACUATE THEIR STOMACHS, AS DETERMINED BY PRESERVING INDIVIDUALS AT DIFFERENT TIMES.

Length (mm)	Water Temp. (°C)	No. of Hrs. for Stomachs to be	
		Half Empty	Empty
9-14	13-15	9	19
10-15	14-16	7-10	13.5-18
29-50	20.5-22	6-8	11-14

*Feeding Experiments.* During the spring and summer of 1959 three experiments were conducted on young-of-the-year fish to estimate their rates of digestion. Flounder were held without food for 48 hours in aquaria connected with a circulating seawater system. Then excessive amounts of either copepods or *Artemia nauplii* were added to the aquaria. After 30-50 minutes of feeding, the flounder and plankton were separated by rinsing the plankton and fish in a coarse mesh net that retained only the fish. Chopped *Mytilus* was fed to another group of larger juveniles until they were satiated. In all experiments some fish of a group were preserved before the others were fed; all of these controls had empty stomachs. Following this, several fish were preserved at intervals of 3-4 hours up to 20 hours after the food was introduced. The results are summarized in Table IV. The stomachs were emptied after 11-19 hours, indicating a rather slow rate of digestion. However, several factors, which may have retarded digestion, introduced unnatural conditions into these experiments. The prior starvation may have influenced the rate of passage of food through the gut (Blaxter and Holliday, 1958), since the flounders gorged themselves after having had no food for 48 hours. Also the fish may have been disturbed by handling.

Collections in the field showed that juvenile flounder fed primarily during the day and that their stomachs were emptied in a shorter time than indicated above. Out of 37 fish collected by seining at St. F (fig. 1, Pt. I), from 2030-2130 on July 15, 1959, 27 stomachs were full. But of 22 fish collected at 0430 during the same week, 19 had empty stomachs. And all but two of 25 fish, collected by trawling just prior to sunrise during the summer, had empty stomachs, whereas fish collected in the late afternoon usually had stomachs that were over half full. These observations, showing a high percentage of full stomachs at dusk and empty stomachs at dawn, indicate that the flounder feeds largely during the day and that the stomachs are normally emptied during the night, or after 7-9 hours.

A few experiments in the laboratory suggest that feeding is mainly by vision (although a diurnal cycle of feeding may also be involved, Hoar, 1942). Fish that were not fed for 48 hours were placed in two aquaria—one in diffuse

daylight, the other in a dark room. Food was added to both. Those in the lighted aquarium fed immediately; those in the dark room did not feed unless zooplankton died and were concentrated on the bottom of the aquarium.

The method of Bajkov (1935) was used in an attempt to approximate the total amount of food eaten per day by juveniles. During September, a total of 58 age-group 0 flounder were collected at four hour intervals from St. 5.1, from 0930-1920. Half of the fish from each collection were preserved immediately in the field; the other half were taken to the laboratory and placed in aquaria supplied with circulating seawater and from which light was excluded with an opaque cloth. When digestion had proceeded for four hours, these fish were also preserved and a new collection was made. The difference in stomach content weight between the field and laboratory collections preserved at the same time gives an estimate of the amount of food eaten during the four-hour interim. This assumes that the fullness of the stomachs of the group preserved immediately is representative of the population, and that the difference in the quantity of food in the stomachs of the two groups is the amount consumed in four hours. The above procedure for collections made periodically throughout the day, therefore, provides an estimate of the daily feeding rate. The weight of the stomach contents was determined as the difference between the weight of stomachs with food and the weight of empty stomachs.

Table V gives the average percentage of the body weight constituted by the stomach contents for four intervals. Though the ratios are variable, together they suggest that the rate of feeding during this period was about 2.0-3.4% of the body weight per day. However, in view of the rapid growth of estuarine flounder during the summer and the limited and variable nature of the data, this estimate of the daily feeding rate appears to be of questionable

TABLE V. RESULTS OF A FEEDING EXPERIMENT GIVING THE PERCENTAGE OF MEAN BODY WEIGHT CONSUMED BY JUVENILE FLOUNDER (22-55 mm) DURING FOUR INTERVALS ON SEPTEMBER 12, 1959 (WATER TEMP. 20-22°C).

Time of Day	No. Fish	Mean % of Body Wgt. as Food	Std. Dev. (s)	Per cent of Body Wgt. Consumed in Interval
Empty Stomachs	6	1.06	.016	.18
0930	10	1.24	.065	
0930	10	1.90	.571	(-.67)
1300	5	1.23	.044	
1300	8	1.62	.054	1.62
1630	10	3.25	1.072	
1630	8	2.74	1.371	0.96
1920	6	3.70	1.508	

reliability. Moreover, it is low compared to the daily feeding rate cited for other juveniles during the growing season by Ricker (1946) and Hatanaka, *et al.* (1956).

*Discussion.* Although the feeding habits of the larval winter flounder have not been well defined by this study, it is apparent that crustacea and polychaetes, along with protozoan-like animals, formed the bulk of the diet of postlarval flounder in the estuary. Copepods were not fed upon intensively until the larvae were undergoing metamorphosis, and at this time also there was a lower frequency of empty stomachs than in any other part of the larval period. Copepods were also the most important food of small juveniles. Thus there was no marked change in the major type of food consumed immediately after metamorphosis. Amphipods and polychaetes comprised most of the food volume of larger juveniles. Amphipods were the most important prey for age-group 0; polychaetes for age-group 1.

The juveniles of both age-groups ate a wide variety of food organisms including infauna, epifauna, and plankton. Seventy-seven different prey were identified, representing seven phyla; eight orders of the class Crustacea were represented. Generally, the larger fish had the most diverse diet. Many prey species were eaten by both age-groups, including such important animals as *Ampelisca* and *Neanthes*. Hence, different age-groups, though preying on different sizes of the same species, often competed for available food animals.

Although the winter flounder is euryphagous and preys on a diverse assemblage of invertebrates, its feeding is influenced by size and by the availability of food species. It is a small-mouthed pleuronectid and, as a result, its food is usually limited to small items. This was apparent from the flounder's diet. The size difference between predator and prey was usually large. The fact that the year-old flounder fed almost exclusively on calanoid copepods during March illustrates not only its ability to eat small prey but also its ability to be highly selective and to concentrate its feeding on an opportune food supply. Other changes in feeding habits may be related to the physical limitations of ingesting large food. For example, large postlarvae and recently metamorphosed juveniles fed mainly on harpacticoid copepods, while slightly larger juveniles fed mainly on calanoid copepods. This difference may have been due to the inability of the smaller fish to eat the relatively large calanoids, such as *Eurytemora*. The apparent increase in the diversity of prey for large juveniles may also be due to the ability of larger fish to prey upon a greater variety of invertebrates of different sizes. Exceptions to the generalization that the winter flounder is restricted to eating relatively small prey animals are found in the soft-bodied polychaetes; full stomachs frequently contained only one large *Neanthes*.

Comparing the feeding habits of the estuarine winter flounder with those from other areas, we find that a high frequency of empty larval stomachs is

not uncommon. Richards (1959, and unpublished) found that 70% of the small larvae (2.0–3.9 mm) and 40% of all larvae from Long Island Sound had empty stomachs. Judging by the percentage of empty stomachs of larvae from both areas, there is no evidence for a higher availability of larval food in the shoal, estuarine waters. These studies, however, tell us only if food was in the stomach; they provide no information on nutrition or rates of digestion, which may still differ significantly among the larval populations. In the estuary, small protozoan-like animals and polychaetes were important as larval food (before metamorphosis). In the Sound, nauplii constituted the bulk of the stomach contents of small larvae, and copepods of large larvae. It may be that crustacea, with their chitinous exoskeletons, are digested at a slower rate and hence are more frequent in larval stomachs than the non-crustacean prey of the estuarine larvae. The fact that estuarine waters in the spring were warmer than offshore waters may contribute to an accelerated digestion rate for larvae in the estuary. The depth of water from which collections were taken may also be important, since the vertical distribution of the larvae and of their food was not uniform. Such differences make valid comparisons between different populations of the same species difficult. Comparisons between species are confounded by additional factors such as differences in swimming ability and size of mouth and gullet.

A high frequency of empty stomachs has been cited for other species of fish larvae (Lebour, 1921). Shelbourne (1953) found that 44% of the plaice larvae (*Pleuronectes platessa*), another species of flatfish, had empty stomachs. The reason for the low incidence of food, which will not be considered in detail here, has been explained by postulating rapid rates of digestion for larvae (Lebour, 1921) and by nutrition from "dissolved" organic matter (Morris, 1955).

Plant material occurred more frequently in the diet of larvae from other areas than in those from the estuary. Dinoflagellates were the most numerous organisms in the stomachs of larvae from Long Island Sound (Richards, unpublished), and Sullivan (1915) mentioned that only diatoms were eaten by winter flounder up to three weeks of age. These algae were uncommon or not found in larvae from the estuary.

The types of invertebrates preyed upon by the juvenile in the estuary were similar to those of other regions. Linton (1921) found that juvenile winter flounder from the Woods Hole, Massachusetts, region ate about 51% copepods until 25 mm in length; amphipods and polychaetes predominated for larger fish, with an increase in the annelid-to-crustacea ratio with fish size. Richards (in press) reported that the first two age-groups of winter flounder from a sand-shell bottom in Long Island Sound ate many different types of food and that polychaetes and amphipods were the most important. It is interesting that many of the same species were common in the diet of the juvenile flounder from the Sound and the estuary. There were also some important differences

in the dominant species of prey between these areas. In the diet of the flounder from Long Island Sound, *Neanthes succinea* and *Ampharete acutifrons* were the two most important polychaetes, and *Ampelisca* and *Leptocheirus pinquus* were the two most important amphipods. In the estuary, *Neanthes* and *Ampelisca* were the two most important prey, but *Ampharete* and *Leptocheirus* were absent or of minor value.

Concerning the feeding of adult winter flounder, Smith (1950) found that the dominant food organisms in Block Island Sound were the amphipods *Leptocheirus pinquus* and *Unciola irrorata*. Although several species of polychaetes were present in the diet, they were relatively unimportant.

After spawning, adult winter flounder remained in the Mystic River estuary during the spring before migrating into the deeper waters of the Sounds. While in the estuary, the adults fed heavily upon invertebrates, such as the polychaete *Neanthes*, perhaps competing for food at this time with the juveniles.

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### Вильям Г. Перси

#### Экология предустьевой популяции зимней камбалы *Pseudopleuronectes americanus* (Walbaum).

#### IV. Обычай питания у личинок и молоди

##### Краткий Обзор

Число личинок зимней камбалы с пустым желудком колеблется от 72 у маленьких постларвальных стадий до 25% личинок в стадии метаморфоза. В противоположность этому только у 6% молоди найдены пустые желудки. Науплиусы, полихеты и яйца беспозвоночных часто попадают в желудке личинок, а кроме того встречаются и много маленьких животных, которых нелегко определить, но свиду напоминающих простейших. Преобладающая пища личинок в стадии метаморфоза и молоди длиной до 10 мм. состоит из гарпактироидных копепод, а молоди группы 0 из каланоидных копепод. до Августа, а после этого амфиоды и полихеты становились более важными. С растущим возрастом значение полихетов росло благодаря их величине. *Ampelisca* и *Neanthes* были наиболее важной добычей. для молоди.

Мальки эврифаги: 77 пищевых организмов принадлежавших семи различным типам были определены. Большая разборчивость в пище была наблюдена в некоторые времена года. Так на пример большое число каланоидных веслоногих было найдено в камбалах однолетнего возраста.

Зимняя камбала питается преимущественно днем. Подсчитано что желудки молоди возрастной группы 0 нормально становятся пустыми в течении ночи, то есть приблизительно через восемь часов.