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Synopsis of Biological Data for the Winter Flounder, *Pseudopleuronectes americanus* (Walbaum)

November 1978

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Synopsis No. 117

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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Juanita M. Kreps, Secretary
National Oceanic and Atmospheric Administration
Richard A. Frank, Administrator
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Synopsis of Biological Data for the Winter Flounder, *Pseudopleuronectes americanus* (Walbaum)

GRACE KLEIN-MacPHEE[1]

ABSTRACT

This monograph contains a synopsis of selected pertinent papers covering biological and technical data of the winter flounder, *Pseudopleuronectes americanus*, including life history, taxonomy, physiology, disease, ecology, population dynamics, commercial and sports fishery, behavior, environmental effects, and culture. One hundred and fifty-four published reports and 12 unpublished reports are covered. Twenty-one figures are included. Literature up to and including 1976 is covered.

1 IDENTITY

1.1 Nomenclature

After Jordan et al. 1930:227 and Norman 1934:345.

1.11 Valid scientific name

Pseudopleuronectes americanus (Walbaum).

1.12 Subjective synonymy

Pleuronectes. Schöepf 1788. Schrift. Ges. Nat. Freunde Berlin, VIII, p. 148.

Pleuronectes americanus Walbaum 1792. Artedi Ichth. (3), ed. 2, p. 113 (based on the flounder of Schöepf).

Pleuronectes planus Mitchill 1814. Rep. Fishes New York, p. 8.

Platessa plana. Storer 1893. Boston J. Nat. Hist., ii, p. 475; Rep. Ichth. Mass., p. 140.

Platessa pusilla De Kay 1842. Nat. Hist., New York (Fish), p. 296, pl. xivll; fig. 153 (New York).

Pseudopleuronectes planus. Bleeker 1862. Versl. Akad. Wet. Amsterdam, xiii, p. 428.

Pseudopleuronectes americanus. Gill 1864. Proc. Acad. Nat. Sci. Phila., xvi, p. 216.

Pseudopleuronectes dignabilis Kendall 1912. Bull. U.S. Bur. Fish., xxx, (1910), p. 392, pl. lvii (Georges Bank).

1.2 Taxonomy

1.21 Affinities

Suprageneric
Phylum—Chordata
  Subphylum—Vertebrata
   Class—Osteichthys
    Order—Pleuronectiformes (Heterosomata)
     Family—Pleuronectidae

Generic (data from Norman 1934)

Pseudopleuronectes. Bleeker 1862. Versl. Akad. Wet. Amsterdam, xiii, p. 428.
[*Pleuronectes planus* Mitchill]; Norman 1933, Ann. Mag. Nat. Hist. (10) xi, p. 220.
Limandella, Jordan and Starks 1906. Proc. U.S. Natl. Mus., xxxi, p. 204.
[*Pleuronectes yokohamae* Günther.]

Generic—Body ovate, compressed. Eyes on right side separated by narrow naked or scaled ridge, upper eye close to edge of head; postocular ridge, if present, rugose; snout and eyeballs not scaled. Olfactory laminae, parallel. without rachis. Mouth moderate sized, length of maxillary on blind side less than one-third that of head, jaws and dentition stronger on blind side, no more than six teeth on ocular side of either jaw, teeth compact incisorlike. close-set, sometimes forming continuous cutting edge. not enlarged anteriorly, uniserial in both jaws; vomer toothless. Gill rakers few, lower pharyngeals narrow. 120-180 mm in length, slender, not much approximated anteriorly, inner edges evenly curved, each with widely separated rows of conical teeth. Dorsal fin less than 85 rays beginning behind posterior nostril of blind side and above eye; all rays simple, some scaled on ocular side; tip of first interhaemal spine projecting in front of anal fin which has less than 65 rays. Pectoral fin of ocular side usually larger than one on blind side; middle rays branched. Caudal fin 13 or 14 branched rays; caudal peduncle short to moderate in length. Scales small, adherent, imbricate (at least anteriorly) ctenoid or cycloid; spinules, if present, short, few; no supplementary scales, lateral line curved above pectoral fin, supratemporal branch is present without posterior prolongations. Vent median or slightly on blind side between pelvics. Intestine narrow, elongate, with three or more coils; 3+1 pyloric appendages moderate or rather elongate. Three

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[1] U.S. Environmental Protection Agency, Environmental Research Laboratory, South Ferry Road, Narragansett, RI 02882.

species, one from Atlantic coast of North America; two from Japan.

Specific

Pseudopleuronectes americanus (Walbaum 1792) (Fig. 1).

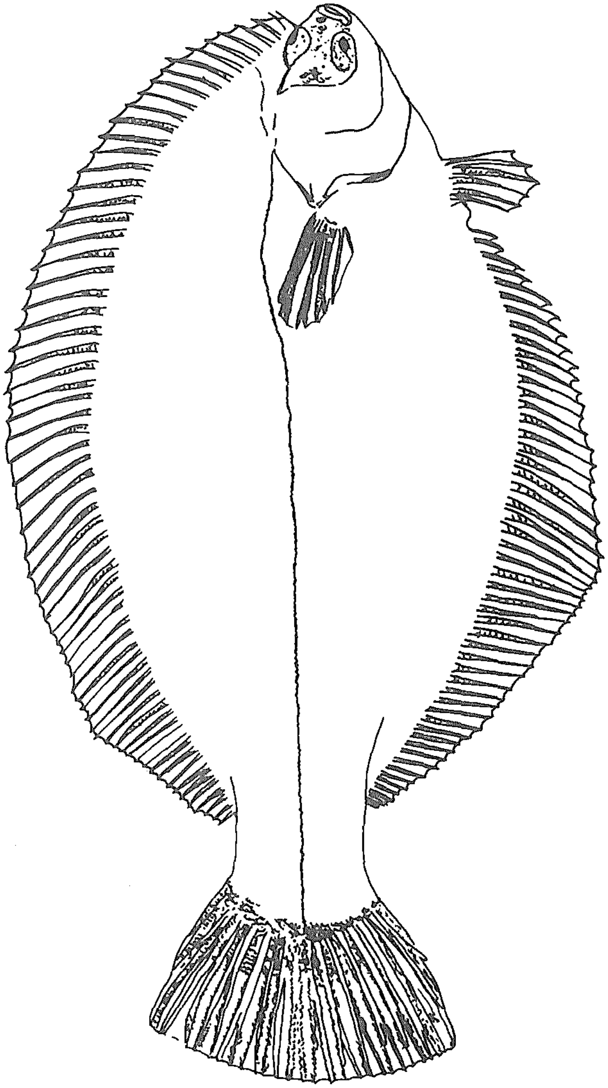

Figure 1.—Adult winter flounder.

Type—not traced.

Lateral line nearly straight, dorsal fin originates opposite forward edge of eye and is nearly equal in height throughout its length. Ventral fins alike on two sides of body, both separated. Synopsis of the species is taken from Norman (1934:342).

Synopsis of the Species

I. Eyes separated by a ridge, which is naked or scaled, width less than one-fourth diameter of eye; postocular ridge rugose.

A. Interorbital ridge nearly naked; tips of gill rakers sharply pointed; 68-75 scales in lateral line; dental formula[2]

$$\frac{0 + 14\text{-}23}{2\text{-}6 + 19\text{-}24} \qquad \text{1. } \textit{P. herzensteini.}$$

B. Interorbital ridge scaled; tips of gill rakers rounded or obtusely pointed; 75-90 scales in lateral line; dental formula

$$\frac{0\text{-}3 + 8\text{-}16}{0\text{-}4 + 12\text{-}20} \qquad \text{2. } \textit{P. yokohamae.}$$

II. Interorbital space flat, scaled, width one-third to one-half diameter of eye; postocular ridge not rugose; 78-89 scales in lateral line . . . . . 3. *P. americanus*.

1.22 Taxonomic status

Morpho—Species.

1.23 Subspecies

See section 1.31

1.24 Standard common names, vernacular names

Winter flounder, blackback, Georges Bank flounder, lemon sole, flounder, sole, flatfish, rough flounder, (Bigelow and Schroeder 1953). Plie rouge, carrelet (Leim and Scott 1966).

1.3 Morphology

1.31 External morphology

Gill rakers 7-8 (lower anterior arch); lateral-line scales 78-89; fin rays, dorsal 59-71($\bar{x}$ 73), anal 47-54($\bar{x}$ 46), pectoral 10-11 (5-7 branched); caudal 19 (13 branched); vertebrae 36 (10+26); pyloric caecae 3+1; dental formula $\frac{0\text{-}2 + 10\text{-}15}{0\text{-}2 + 10\text{-}17}$ (Norman 1934). See also Table 1.

1.32 Geographic variation

In 1912 W. C. Kendall described the Georges Bank flounder as a new species, *Pseudopleuronectes dignabilis*. He stated that the most conspicuous differential characteristics of this "species" are shorter head, larger number of vertical fin rays, color, and larger size (Kendall 1912). There is also a different spawning season (April-May).

Perlmutter (1947) compared counts of winter flounder north and south of Cape Cod and from Georges Bank. He felt that Georges Bank flounder had significantly different dorsal, pectoral, and anal fin ray counts showing there was little mixing of this stock with other winter flounder stocks.

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[2] Dental formula $\frac{\text{occular side + blind side (upper jaw)}}{\text{occular side + blind side (lower jaw)}}$

Table 1.—Comparison of fin ray counts of winter flounder by several investigators.

Dorsal rays	Anal rays	Pectoral rays	Reference and locality
			Kendall (1909)
68-78 $\bar{x}$ 70.6	50-54 $\bar{x}$ 52.3		*P. dignabilis* (Georges Bank)
61-67 $\bar{x}$ 64.7	46-50 $\bar{x}$ 48		*P. americanus*
			Perlmutter (1947)
63.97 ± 2.51	47.83 ± 1.82	9.84 ± 0.68	North of Cape Cod
64.05 ± 2.29	47.73 ± 1.88	10.08 ± 0.59	South of Cape Cod
68.93 ± 2.53	51.30 ± 1.96	10.58 ± 0.62	Georges Bank (*P. dignabilis*)
	$\bar{x}$	$\bar{x}$	Lux et al. (1970)
	64.94	48.89	Cape Cod Bay (North)
	66.87	50.42	East. Vineyard Sound (South)
Date			
			Georges Bank
1963	69.53	51.94	(*P. dignabilis*)
1964	69.58	52.14	
1966	70.28	52.61	

Lux et al. (1970) compared dorsal and anal fin ray counts on winter flounder from inshore waters off Massachusetts north and south of Cape Cod and from Georges Bank. An examination of water temperature at spawning time (March-April) for 1940-56 in records at the National Marine Fisheries Service at Woods Hole showed that, in March, water temperature ranged from 1.7° to 5.4°C. This is higher than at Woods Hole or Gloucester, Mass. The Georges Bank population may spawn at higher temperatures which might influence fin ray number. Norman (1934) believed *P. dignabilis* may represent a distinct race with a different spawning season as described by Kendall (1909) (Table 1).

Lobell (1939) believed racial groups were indicated in Long Island Sound since recoveries near the tagging localities occur simultaneously with recoveries from points relatively distant.

2 DISTRIBUTION

2.1 Total area

Atlantic coast of North America from the coast line to the offshore fishing banks (40-100 m) (Fig. 2). The winter flounder is common from the Strait of Belle Isle, North Shore of the Gulf of St. Lawrence to Chesapeake Bay. The extremes of distribution are the southern part of the Grand Banks, the northernmost record being Ungava Bay, Labrador (Kendall 1909); and the vicinity of Beaufort, N.C., the southernmost record from Georgia (Hildebrand and Schroeder 1928).

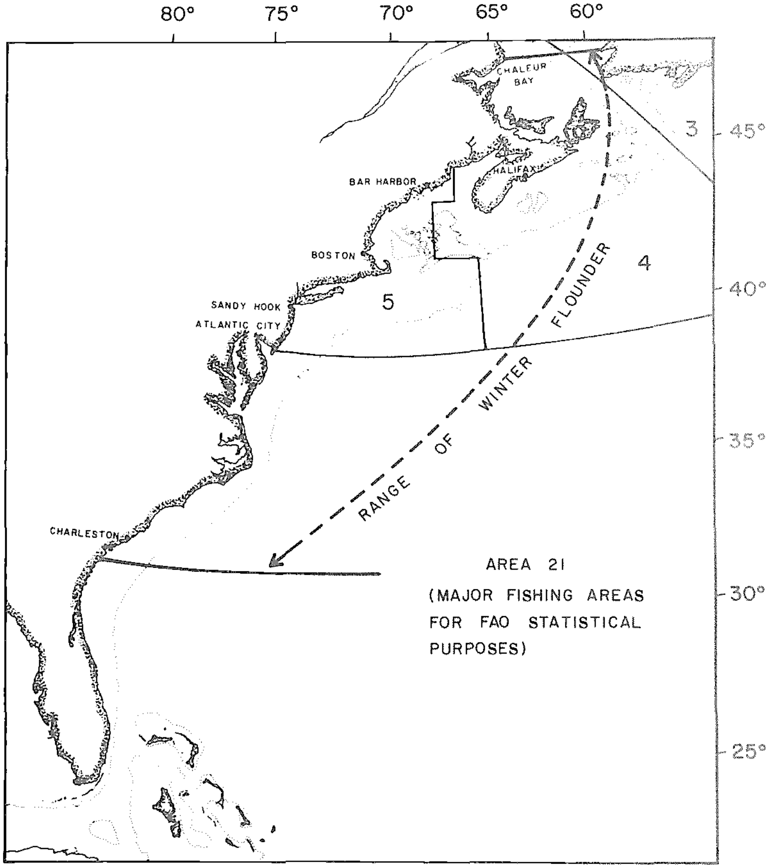

Figure 2.—Range of winter flounder.

2.2 Differential distribution

2.21 Eggs, larvae, juveniles

Marine Research, Inc.[3] mapped larval distribution in Narragansett Bay (Fig. 3). The most extensive work on differential distribution of eggs, larvae, and juveniles was done by Pearcy (1962a) in the Mystic River estuary, Conn. Spawning took place in the upper estuary. Young fish demonstrated both horizontal and vertical differences in distribution.

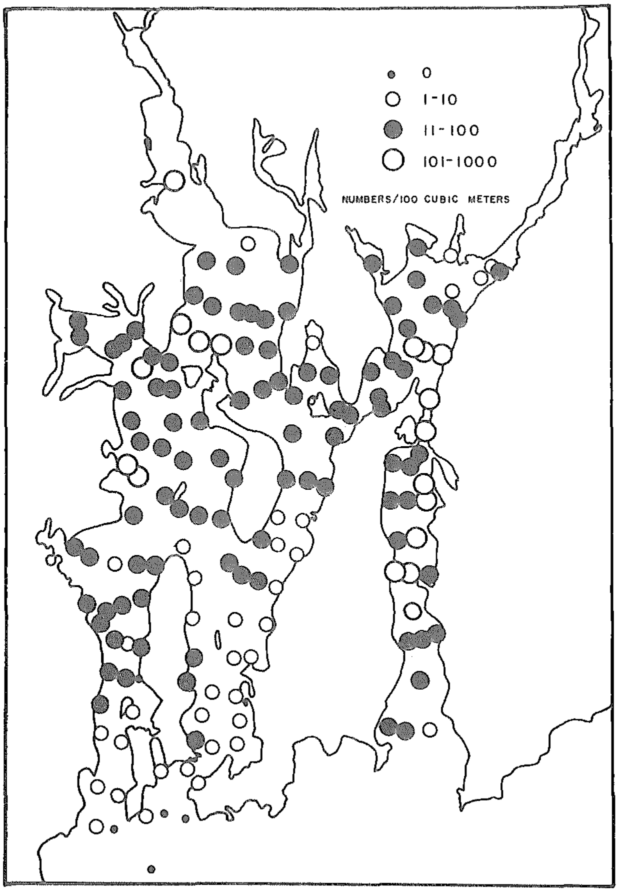

Figure 3.—Distribution of winter flounder larvae in Narragansett Bay (Marine Research Inc. 1974, see text footnote 3).

Horizontal distribution—During the early larval period (March to April prior to metamorphosis), the density of winter flounder larvae was 15 times greater in the upper Mystic River estuary than in the lower estuary. Later in spring, upper estuarine density declined. By May no larvae were caught in the upper estuary indicating that larvae moved down into the lower estuary. In the early season there was no difference in average length of larvae from the upper or lower estuary. During March and April the smallest sizes were found in the lower estuary and by mid-April the largest sizes were taken here.

Vertical distribution—Larvae had a passive sinking rate of 14 mm/s in seawater with a specific gravity of 1.022, so they were nonbuoyant and located near the bottom, partially benthic. The small larvae are poor swimmers which swim vertically in a 90° climb, stop, rotate 180°, and sink passively (Pearcy 1962a).

Perlmutter (1947) found the larvae spawn in shallow water in southern New England and New York. Larvae remain in shoal water near shores of bays and estuaries. As they grow older they tend to move into deeper water; entering the commercial and sport fisheries catch in the second and third years.

De Sylva et al. (1962)[4] reported that in the Delaware River estuary, Indian River Bay seemed to be an important nursery ground for young which first appeared in early June. Larvae were collected in late winter. Work done by Derickson and Price (1973) in the Indian River Bay area of the Delaware River and by McCracken (1963) on movements of immature flounders in Passamaquoddy Bay, Canada, supported the statement that, in general, in northern waters immature flounder occur inshore and move offshore during winter.

Lux et al. (1970) collected spent and spawning females off Georges Bank, Mass. The population spawns offshore and larvae and juveniles remain on the spawning area separated from nearby shore populations.

2.22 Adults—See section 3.53

2.3 Determination of distribution

Perlmutter (1947) stated that the predominant physical forces affecting movements of eggs and larvae in spawning habitats are wind and tide, but effects of these are reduced by eggs being demersal and adhesive, with early pelagic stages remaining in back waters of bays and inlets.

Pearcy (1962a) attributed the larval distribution inshore and close to the bottom to the fact that they are nonbuoyant. When not actually swimming they sink; and therefore, are not carried away by outward moving surface currents. The survival value of this is that it might reduce offshore dispersal, an important factor in loss rate for small larvae.

McCracken's (1963) laboratory studies of winter flounder reactions to light showed that small (60-90 mm TL (total length)) immature flounders are positively phototropic; medium (120-180 mm TL) flounders avoid light. He theorized that where flounder are found in shallow water during summer, the differential distribution between young immature and older immature may result from a different behavior pattern with size and maturity in relation to light.

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[3] Marine Research Inc. 1974. 19th Rome Point Investigations Narragansett Bay, Ichthyoplankton Survey Final Report to the Narragansett Electric Company.

[4] de Sylva, D. P., F. A. Kalber, Jr., and C. N. Shuster, Jr. 1962. Fishes and ecological conditions in the shore zone of the Delaware River Estuary with notes on other species collected in deeper waters. Univ. Del. Mar. Lab., Inf. Ser. Publ. No. 5, 164 p.

Experiments by Huntsman and Sparks (1924) and Battle (1926) on resistance to temperature stress showed that younger fish were more tolerant of high temperatures (29°-30°C) than older fish, which might also account for their being located in shallower waters in summer.

2.4 Hybridization

Nichols (1918) described a fish from the New York market believed to be a hybrid, *Pseudopleuronectes americanus* × *Limanda ferruginea*. Considering the Georges Bank flounder as a separate species, Morrow (1944) reported a record winter flounder (560 mm TL, 2,649 g) which appeared to be intermediate between *P. americanus* and *P. dignabilis*.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Winter flounder have separate sexes; there is little sexual dimorphism. Norman (1934) stated that scales on the blind side of males are ctenoid instead of cycloid, giving them a rough feeling. Perlmutter (1947) confirmed this generally, but mentioned that often large females have rough scaled blind sides.

3.12 Maturity

Winter flounder in the New York region mature at 2-3 yr when they are 200-250 mm TL long (Perlmutter 1947). Kennedy and Steele (1971) gave the age of maturity of flounder from Canada as age VI for males and VII for females. Fifty percent of the females and males were mature at 250 and 210 mm, respectively. Maturity may be related to size and not age; therefore, northern flounder may be older at maturity than southern ones.

3.13 Mating

No distinct pairing has been observed (Breder 1922). See 3.16.

3.14 Fertilization external (Breder 1922)

3.15 Gonads

In Long Pond, Newfoundland, male gonads began to enlarge earlier than female and males reached spawning stage before females. Ripening began in September, progressed slowly during winter months, and spawning took place March-June (Kennedy and Steele 1971).

Dunn and Tyler (1969) studied ovarian anatomy of winter flounder. They described the ovary as being an adaptation of the vertebrate compact ovary. It differs from most teleost ovaries in having a relatively short hilus and mesovarium. Ovaries are connected anteriorly to the peritoneum by a short mesovarium; arteries and veins pass through the hilus. Four oocyte types could be distinguished morphologically throughout the yearly cycle:

1) Small immature—10-80 μ diameter, irregular in shape, sometimes angled, darkly staining (basophilic) containing no yolk or fat droplets; nucleus with one or two large nucleoli.
2) Large immature—80-150 μ round, yolkless containing some fat droplets, granular looking cytoplasm. Nucleus with several darkly staining nucleoli around the periphery.
3) Maturing oocytes—150 μ massive deutoplasm fat and yolk deposits, small protoplasm, prominent theca. Visible yolk deposition occurs at 150 μ. At ovulation, diameter 40-850 μ.
4) Atretic or regressing oocytes—Shrinkage of zona radiata away from theca. Disorganized cellular structure including rupture of the nucleus and wrinkling of the theca, resorption of yolk and fat which leaves a mass of folded theca often containing dark staining amorphous material.

Three states of ovary development based on biological examination of follicular development were present for fish held in tanks:

1) Resting ovaries—Contain no oocytes with yolk deposits, have large intraovarian spaces, relatively thick walls. (Those on reduced rations often did not have thick walls).
2) Ripening ovaries—Contained maturing oocytes as well as atretic and immature ones.
3) Regressing ovaries—Portion of large immature oocyte had begun vitellogenesis normally but at the time of sampling were atretic. Ovaries less emaciated than resting types, immature oocytes more densely arranged. The frequency distribution of oocyte sizes in resting ovaries showed bimodal distribution.

Dunn and Tyler (1969) hypothesized a 2- or 3-yr cycle. Dunn (1970) found individual fish vary in their state of development at any given time, strengthening the 3-yr-cycle hypothesis. He studied fish 340-450 mm TL from September to December, and presented evidence for autumn growth of yolkless oocytes which would tend to split oocytes into two size groups. The proportion of small immature oocytes remained low so few oocytes were added to immature follicles. Increase in proportion of eggs in larger size classes (80-100 μ) with reduction in number of small eggs represented growth of a portion of the oocytes. Larger oocytes can be tentatively identified with those oocytes that in the following summer form the stock of large immature follicles which begin vitellogenesis to be spawned the next spring. Three year cycle—year 1, at least small immature oocytes become recognizable; year II they become larger immature oocytes; year III yolk is deposited and they are spawned.

Fecundity studies have been summarized in Table 2. Topp (1968) also measured ova density and found it ranged from 6,082 to 18,963 eggs/g of ovary with a mean of 10,595 eggs/g of ovary. Egg diameter ranged from 0.33 to 1.00 mm with a mean of 0.61 mm. There was no significant correlation between mean egg size and fish size; but egg size differed among age groups, age group three having the smallest eggs.

Table 2.—Fecundity values for winter flounder.

Number of eggs × 1,000	Age, weight or size (TL) of fish	Investigator
$\bar{x}$ 500 Maximum 1,500	1,531 g	Bigelow and Schroeder (1953)
435-3,329	3 yr (300-400 mm) to 5 yr (400-450 mm)	Topp (1968)
93-1,340 $\bar{x}$ 610	210 g, 250 mm to 1,052 g, 430 mm $\bar{x}$ 334 mm	Saila (1962a)
99-2,604 $\bar{x}$ 590	111 g, 220 mm to 1,300 g, 440 mm $\bar{x}$ 340 mm	Kennedy and Steele (1971)

3.16 Spawning—Once a year (Table 3)

Spawning times vary, beginning earlier in the southern part of the fish's range and progressively later as one proceeds northward.

Tagging experiments at Woods Hole and Waquoit, Mass., performed by Nesbit (in Lobell 1939) showed that a significant number of fish returned to the same spawning grounds two or more successive years. He was not able to tell if these fish remained in the bay throughout the regular season, or moved out and returned to spawn.

Saila (1961) showed that winter flounder returned to the tagging locality with high frequency over the year of recovery data, after having left the area following the initial breeding season. (See section 3.51.)

Breder (1922) described spawning habits from observations made on fish held captive in large wooden tanks at Woods Hole. Spawning occurred at night, between 2200 and 0330, under artificial lights. Five fish, three males and two females, took part. Previous to spawning, they (especially females) exhibited a large amount of swimming activity.

Table 3.—Dates of winter flounder spawning at different geographic locations from north to south.

Dates	Peak	Area	Investigator
Mar.-June	—	Long Pond, Conception Bay, Newfoundland	Kennedy and Steele (1971)
Mar.-May	Apr.	Booth Bay Harbor, Maine	Hahn (Pers. commun. in Bigelow and Schroeder, 1953)
Feb.-May	—	Eel Pond, Woods Hole, Mass.	Sherwood and Edwards (1901)
Jan.-May	Feb.-Mar.	South of Cape Cod and Massachusetts Bay	Bigelow and Schroeder (1953)
Mid Feb.-Apr.	Mar.	Mystic River estuary, Conn.	Pearcy (1962a)
Dec.-May	Varies with water temp.	Southern New England—New York	Perlmutter (1947)
Nov.-Apr.	—	Indian River Bay, Del.	Fairbanks et al. (1971)

The fish swam rapidly in a circle about 1 ft in diameter, counterclockwise with vent outwards. As they swam, genital products were discharged. This took 10 s, then the fish swam to the bottom. During spawning, eggs were extruded from the female, flowed along the upper side of the anal fin and over the tail to spread out in all directions. Breder (1922) believed that females must release the eggs but males can hold the milt because, if frightened or alarmed, they do not take part in the activity. I can confirm this from personal observations.

See section 3.51 for information on spawning migration and section 7.2 for factors influencing maturation and spawning time.

3.17 Eggs

The eggs are demersal. Pearcy (1962b) showed that specific gravity with gum arabic and seawater was 1.085, and they sank in water of 30‰ salinity. He believed that morphological similarities among adults, and characteristics of the larvae of those pleuronectids with demersal eggs, suggest they evolved from species with buoyant eggs. The adaptive value of demersal eggs is that they would remain in inshore nursery grounds where conditions for development are favorable.

The eggs ranged from 0.71 to 0.86 mm in diameter with a mode of 0.81 mm. The spermatozoa are 0.030-0.035 mm long. Eggs are adhesive and clump together after fertilization, often becoming distorted and polyhedral in shape (Breder 1924).

See also section 3.21.

3.2 Preadult phase

3.21 Embryonic phase

Breder (1924) described the embryonic stages in eggs collected from ponds in the Woods Hole region during February when water temperature ranged from 1° to 2°C (Fig. 4).

1) Blastodisc—Large and pale amber, yolk colorless with a finely tuberculate surface.

2) First cleavage (temperature 21°C) 2½ h after fertilization.

3) 24 h after fertilization blastoderm has many cells.

4) 3rd day—Differentiation begins.

5) 6th day—Premature segmentation and cephalization begins. In many eggs a small sphere similar to the oil globules in pelagic eggs was observed (I believe this is Kuppfers vessicle); a few had several. Beyond this stage they disappeared. Embryo is pale amber and oil globule colorless.

6) 9 days—Embryo well differentiated, chrome yellow chromatophores are scattered over the body.

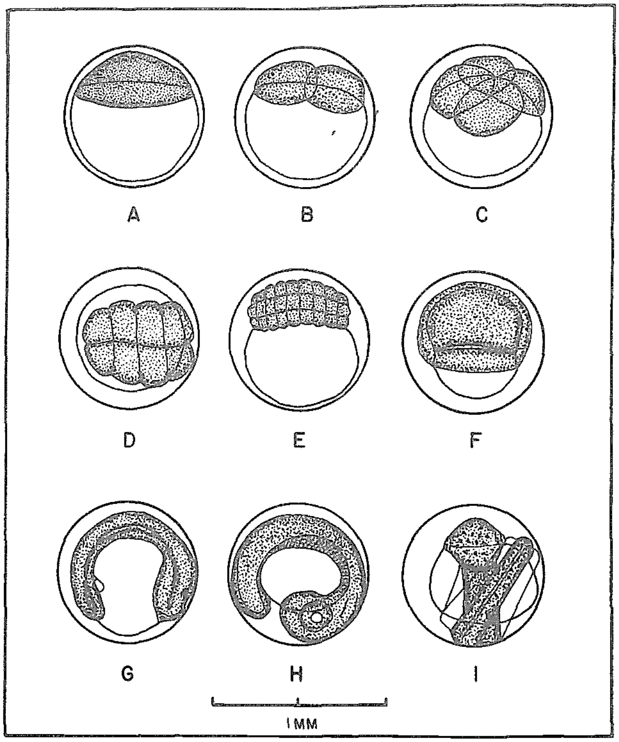

Figure 4.—Developmental stages of winter flounder. A. Unfertilized egg. B. Egg with blastoderm of two cells. C. Egg with blastoderm of four cells. D. Egg with blastoderm of eight cells. E. Egg with blastoderm of many cells. F. Embryo in early stage of differentiation. G. Embryo further differentiated. Note small sphere similar to an oil globule. H. Embryo in an advanced stage of differentiation. I. Egg about to hatch. (From Breder 1924.)

7) 15 days—Chromatophores have the same appearance but a concentration of them as a vertical band appeared in caudal region. The heart can be seen beating and the cephalic region looks finely tuberculate. After 15 days, hatching began. After hatching, eyes were sometimes unpigmented and sometimes had chrome yellow pigment. Pigment developed in all larvae within a few days. Later the pupils became tinged with green.

8) 19 days after hatch—Pupil black and iris with metallic green iridescence. Eyes directed forward and down. Mouth is large and functional; yolk absorbed, animal symmetrical. Pigment is darker, almost orange.

The temperature at which these eggs were incubated is not clear. The only temperature given (21°C) is lethal to winter flounder eggs. According to my experience, this timetable of events best corresponds to temperatures of 6°-8°C.

Sullivan (1915) observed hatching of eggs which had been stripped and fertilized in the laboratory. For a day or more before hatching, fish could move within the capsule. Movement occurred by a series of contractions from the posterior part which tended to push the fish forward and eventually ruptured the egg capsule at right angles to the long axis of the fish's body. The fish usually freed itself from the capsule within 10 min. Scott (1929) investigated effects of salinity and temperature on hatching of eggs. At 4°-5°C, 70% hatched at a maximum average time of 26 days as compared with 21 days at 0°C, and 18 days at 12°-17°C. At varying salinities (29.40 ± 2.2°/oo control) the highest percent hatching occurred at 7/8 and 1/8 parts salinity. The average percent hatching was lower for eggs in dilute seawater than control, and lower than the normal average. Percent hatch did not decrease linearly with decreasing salinity. He concluded that salinity has little effect on hatching but temperature is important. Rogers (1976) incubated winter flounder eggs under various conditions of temperature and salinity and found highest viable hatches occured at 3°C over a salinity range of 15-30°/oo. She constructed a diagram depicting the qualitative effects of temperature and salinity on development and hatching of winter flounder embryos (Fig. 5) Salinity appeared to influence time of embryo mortality. At 35-45°/oo at all temperatures mortality usually occurred at gastrulation and abnormal development of the embryo was observed. At 5-10°/oo embryos appeared to develop normally but died just prior to hatching; a fact which might be due to inability of the larvae to free themselves from their chorions. Analysis of variance showed salinity to be statistically more significant than temperature or the interaction of temperature and salinity. Oxygen effects were not considered.

Williams (1975) studied the survival and duration of development of winter flounder eggs at several constant temperatures from −1.8°C to 18°C with emphasis on development in the lower temperature range. Mean viable hatch was 33% for the lowest temperature tested (−1.8°C) and over 50% for 0°-10°C. Above 10°C survival was lower and many embryos were abnormal with narrow fin folds, short tails, or crooked vertebral columns. Upper lethal limit was 15°C. Williams thought that the immediate cause of embryonic death at high temperatures was microbial infection as mortality was often synchronous within a dish, and dishes with more than 100 eggs had higher mortality. Oxygen depletion might also have had an effect. The median duration of days to hatching as related to temperature was described by the regression equation fitted to points from 0° to 10°C (minimum mortality range) is $\ln x = 3.636 - 0.158\,t$ where x = number of days from fertilization to hatching, and t = temperature, $Q_{10} = 4.8$. Low temperature adaptation in the embryo did not depend on large additions of antifreeze to the ova prior to spawning as suggested by the freezing points of mature ovaries (−0.86°-0.98°C).

3.22 Larval phase

Sullivan (1915) described the larva from hatching to the end of the second month and divided larval history into four stages which he chose in order to show all diagnostic characteristics for identification (Fig. 6).

Stage 1.—Hatching (Fig. 6a) length 3.5 mm, depth 0.525 mm. A group of dark pigment spots on the posterior half of the body was the most important character for identification. Another pigment patch lay over the

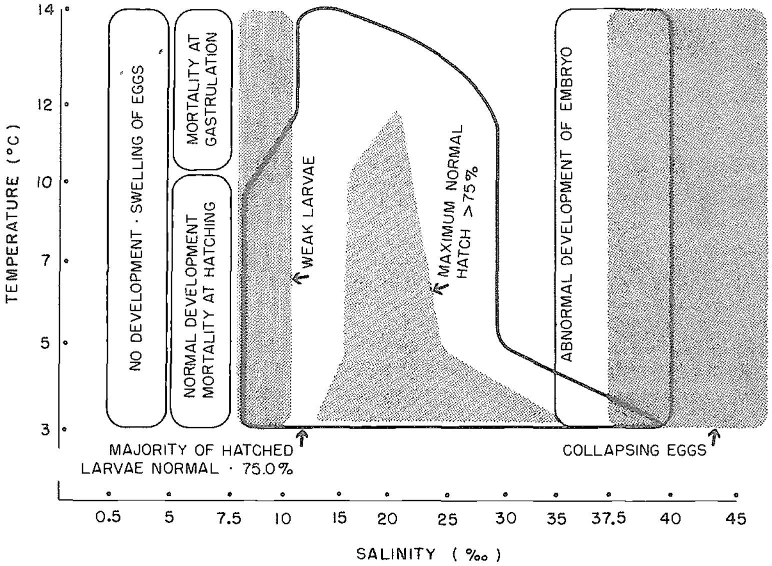

Figure 5.—Effect of salinity and temperature on hatching of winter flounder eggs (from Rogers 1976).

rectum posterior to the yolk. Notochord present as straight tube. Dorsal, anal, and caudal fins represented by unbroken finfold. Yolk absorption was gradual and varied with temperature. At 4°C, 12-14 days, at higher temperatures, 8 or 9 days.

Stage 2—Yolk absorption (Fig. 6b) 12 days (approximately) length 5 mm.

Between stage 2 and 3 several critical changes take place: 1) migration of eyes, 2) development of fin rays, and 3) differentiation of caudal fin accompanied by upward bending of notochord.

Stage 3—Metamorphosing larva (Fig. 6c) 5-7 wk old, 5.8 mm long. After sixth week pigment on left side tended to diminish in intensity.

Stage 4—Postlarva (Fig. 6d) about 8 wk old, 6.5 mm long, average depth 2.75 mm.

In later stages there was loss of pigment on the left side and increase on the right. In 8 mm long fish the right side was devoid of pigment except for about 20 spots scattered near the snout. These were gone by the time the fish were 20 mm long.

The medusae *Sarsia tubulosa* prey upon larvae (Pearcy 1962a). Their distribution and time of relative abundance coincided with winter flounder larvae. Pearcy postulated a differential predation rate, assuming that small larvae have less ability to escape the medusa, which helps explain high mortality rates for small larvae. A density dependent numerical response seemed improbable in spite of the fact that the numbers of *Sarsia*

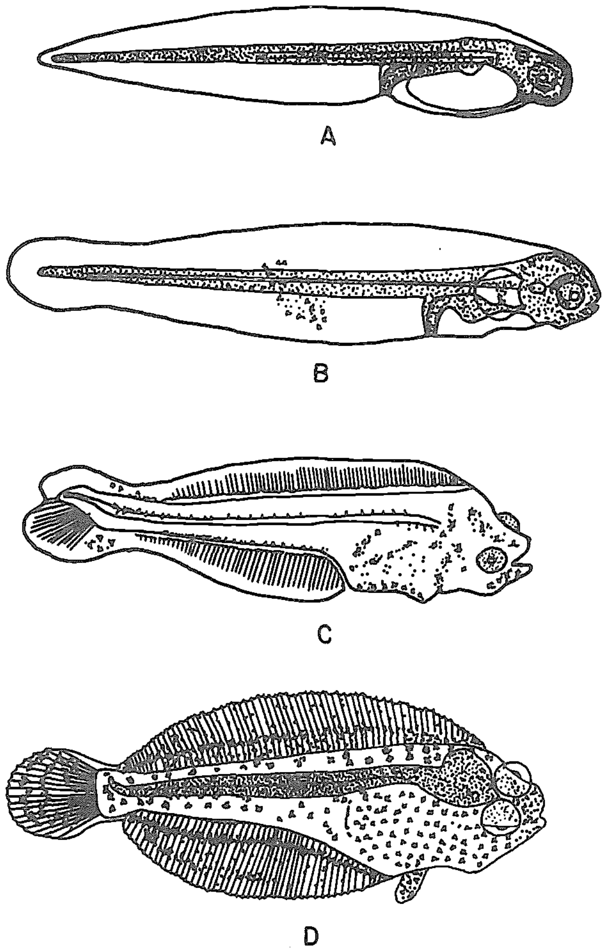

Figure 6.—Larval development in winter flounder. A. *Pseudopleuronectes americanus* at hatching (3.5 × 0.523 mm). B. *P. americanus* at 12 days (3.0 × 0.724 mm). C. *P. americanus* at 6 weeks (3.8 × 1.33 mm). D. *P. americanus* at 8 weeks (6.5 × 2.75 mm). (From Sullivan 1915.)

rose and fell with that of the flounder population because the medusae do not bud. He also felt a functional response was improbable because medusae have limited sensory and locomotory abilities.

Sullivan (1915) described behavior of newly emerged larvae. The larvae exhibit intermittent swimming alternating with resting on the bottom. If fish were kept in continuous motion for 30 min, they showed no sign of fatigue; therefore, intermittent swimming appeared to be a behavioral characteristic of the newly hatched larvae.

In fish under 10 days old, no preference was shown as to which side they rested on; after 10-12 days they favored the left side. Fish 2 wk old rested on the left side 75% of the time.

Food—See section 3.42.

3.23 Adolescent phase

Young-of-the-year remained in waters along shores of bays and estuaries where they were spawned (Perlmutter 1947). Poole (1966b) collected young-of-the-year flounder in Shinnecock and Peconic Bays, Long Island. He found that saltwater coves were preferred habitats of this age group in both bays.

Several important commercial and sport fishes prey upon winter flounder juveniles. A list of predators is presented in Table 4. There are no real competitors of juvenile winter flounder reported (see The Population in the Community and the Ecosystem). A list of collections of eggs, larvae, and juveniles with data, collectors, and geographical area is presented in Table 5.

Table 4.—Predators of juvenile winter flounder.

Predator	Citation
Summer flounder, *Paralichthys dentatus*	Pearcy (1962a)
Striped bass, *Morone saxatilis*	Derickson and Price (1973)
Bluefish, *Pomatomus saltatrix*	Derickson and Price (1973)
Toadfish, *Opsanus tau*	Pearcy (1962a)
Cormorant, *Phalocrocorax auritus auritus*	Pearcy (1962a)
Harbor seals, *Phoca vitulina* and *Phoca groenlandica*	Fisher and MacKenzie (1955[1])

[1] Fisher, H. D., and B. A. MacKenzie. 1955. Food habits of seals in the Maritimes. Fish. Res. Board Can. Prog. Rep. (Atl.) 61:5-9.

See also sections 3.4, 3.5, 3.53.

3.3 Adult phase

3.31 Longevity

Saila et al. (1965) prepared age-length tables from fish caught in Charlestown Pond and Narragansett Bay, R.I. The oldest fish were estimated age XII. The average total length of these age XII fish was calculated as 379 mm for males and 441 mm for females. Calculations were made from otoliths and Walford plots for fish older than 3 yr. The largest recorded winter flounder (Bigelow and Schroeder 1953) was 570 mm TL and was probably considerably older than 12 yr.

Table 5.—Dates of field collections of winter flounder eggs, larvae, and juveniles (from north to south).

Field collections	Eggs	Larvae	Juveniles
Scott (1929); St. Andrews N. Brunswick Mud Flats	20 May-6 June		
Haedrich and Haedrich (1974); Mystic River, Mass.			June-Nov.
Fairbanks et al. (1971); Cape Cod Canal, Mass.	Feb.-May	Mar.-June	
Breder (1924); Woods Hole Region Ponds, Mass.	Feb.		
Herman (1963); Narragansett Bay, R.I.		Feb.-June (3.24-7.20 mm)	
Marine Research Inc. (1974)[1]	Jan.-May	Feb.-July	
Pearcy (1962a); Upper Mystic estuary, Conn.	Feb. (?) 0.75-0.96	Mar.-June (2.5-7.6 mm)	July-Feb. (6-40 mm)
Wheatland (1956); Long Island Sound		Mar.-June (2.80-8.5 mm)	
Richards (1963); Long Island Sound			Year-round
Poole (1966b); Shinnecock and Peconic Bay, Long Island			June-Oct.
de Sylva et al. (1962)[2]; Delaware River estuary			Mar.-Nov.
Richards and Castagna (1970); Eastern Shore Virginia midway in channel and tidal creeks			May-June (27-80 mm)

[1] Marine Research Inc. 1974. 19th Rome Point Investigations, Narragansett Bay Ichthyoplankton Survey Final Report to the Narragansett Electric Company.

[2] de Sylva et al. 1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary with notes on other species collected in deeper waters. Univ. Del. Mar. Lab., Inf. Ser. Publ. No. 5, 164 p.

3.32 Hardiness

Winter flounder are very hardy. They are commonly found in waters between 4 and 30‰ salinity at 0°-25°C (Pearcy 1962a).

Sometimes fish kills occur under extreme conditions. Nichols (1918) reported a large kill in St. Moriches Bay, Long Island, when the temperature rose to about 30°C. Bigelow and Schroeder (1953) mentioned that fish may be killed by anchor ice in winter if they are trapped in shallow water by a sudden freeze.

3.33 Competitors—See section 4.6

3.34 Predators

Dickie and McCracken (1955) listed monkfish (*Lophius piscatorius*), dogfish (*Squalus acanthias*), and sea raven (*Hemitripterus americanus*) as predators of winter flounder in Canadian waters. Tyler[5] listed sea raven and two species of birds—blue heron and osprey—but did not say whether these prey on juveniles or adults.

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[5] Tyler, A. V. 1971. Monthly changes in stomach contents of demersal fishes in Passamaquoddy Bay, N.B. Fish. Res. Board Can., Tech. Rep. 288, 114 p.

3.35 Parasites, diseases, injuries, and abnormalities

Parasites—The principal work on parasites of winter flounder was done by Linton (1901, 1914, 1921, 1924, 1933, 1934, 1941), Heller,[6] and Ronald (1957, 1958a, 1958b, 1959, 1960, 1963) (Table 6).

Diseases—Levin et al. (1972) reported methods for isolating and identifying the bacteria *Vibrio anguillarium*, how to identify vibriolike organisms as either *V. anguillarium* or *V. variable*, and how to diag-

Table 6.—**Parasites of winter flounder.**

Parasite	Site of Infestation	Geographic Region	Reference
Protozoa			
Glugea microspora stephani	intestine wall	Woods Hole Region	Stunkard and Lux (1965)
Trichodinid	gills	Martha's Vineyard	
Platyhelminthes		Bay of Fundy	Lom and Laird (1969)
Trematoda			
Derogenes varicus	stomach and intestine	Canada	Ronald (1960)
Distomum appendiculatum	stomach and intestine	Woods Hole	Linton (1901)
D. grandiparum	stomach and intestine	Woods Hole	Linton (1901)
D. globeparum (?)	stomach and intestine	Woods Hole	Linton (1901)
D. vitellosum	stomach and intestine	Woods Hole	Linton (1901)
D. aerolatum	stomach and intestine	Woods Hole	Linton (1901)
Stephanostomum baccatum	superficial musculature	Canada, Passamaquoddy Bay	Wolfgang (1954a)
Stephanostomum hystria	dermal surfaces		Stafford (1904)
Steringophorous furciger	stomach and intestine	Canada	Ronald (1960)
Podocotyle atomon	intestine	Canada	Cooper (1915)
Cryptocotyle lingua	skin	Long Island Sound	Smith (1935)
Hemiuris sp.	intestine	Canada	Ronald (1960)
Cestoda			
Bothrimonus intermedius	intestine		Cooper (1918)
Diplocotyle olrikii	intestine	Passamaquoddy Bay	Ronald (1958b)
Bothriocephalus clavipes	intestine	Passamaquoddy Bay	Ronald (1958b)
Bothriocephalus scorpii			Leidy (1855)
Tetrarhynchus bisculcatus	stomach wall	Woods Hole	Linton (1901)
Tetrarhynchus sp.	peritoneum	Woods Hole	Linton (1901)
Aschelminthes			
Nematoda	stomach		
Ascaris	muscle intestine	Woods Hole	Linton (1901)
Ascaris acutus	muscle intestine	Long Island	Leidy (1904)
Contracaecum aduncum	intestine, body cavity	Canada	Heller (1949)[1]
C. gadi	intestine, body walls	Canada	Ronald (1963)
Grillotia erinaceus		Woods Hole	Linton (1924)
Lacistorhynchus tenuis		Woods Hole	Linton (1924)
Scolex pleuronectis		Woods Hole	Linton (1924)
Terranova sp.	axial musculature, body cavity exterior or pyloric caecae and intestine	Canada	Ronald (1963)
Stomachinae larvae	musculature, body cavity, surface external organs		Ronald (1963)
Acanthocephala			
Echinorhynchus laurentianus	digestive tract	Gulf of St. Lawrence	Ronald (1957)
E. acus	intestine	Gulf of St. Lawrence	Linton (1901)
E. gadi			Linton (1933)
E. sacealis			Stiles and Hassall (1894)
Corynosoma sp.		Magdalin Island	Montreuil (1955)
Cucullanus heterochrous	intestine	Canada	Ronald (1963)
Branchiura			
Argulus megalops	skin body surface	Canada	Ronald (1958a)
A. funduli		Canada	Bere (1930)
A. m. spinosus	skin body surface	Canada	Ronald (1958a)
A. laticaudata	not given		Rathbun (1885)
Acanthochondria cornuta	not given	Bay of Fundy	Stock (1915)
A. depressus	not given	Woods Hole	Wilson (1932)
Copepoda			
Caligus rapax	not given	Woods Hole	Wilson (1905)
Lepeophtheirus hidekoi	not given	Woods Hole	Ho (1962)
Isopoda			
Gnathia elongata	not given	Bay of Fundy	Wallace (1919)

[1] Heller, A. F. 1949. Parasites of cod and other marine fish from the Baie de Chaleur region. Fish. Res. Board Can. Tech. Rep. No. 261, 23 p.

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[6] Heller, A. F. 1949. Parasites of cod and other marine fish from the Baie de Chaleur region. Fish. Res. Board Can., Tech. Rep. 261, 23 p.

nose the disease vibriosis. *Vibrio anguillarium* was isolated from skin and muscle lesions of winter flounder from Narragansett Bay. External manifestations of disease include dermal lesions usually accompanied by fin necrosis. These lesions included petichiae and ecchymoses in their acute stage and frank ulceration in the more chronic manifestation. Necrosis of the fin began at the periphery and extended inwards including long rays. Microscopic lesions of the kidney also occurred. Characteristics of diagnostic importance to pathologists are dermal hemorrhage and ulceration, focal skeletal muscle necrosis, renal erythroblastic hyperplasia, and anemia. Organisms isolated from the lesions identified as aeromonads, plesiomonods, or vibrios by being Gram-negative, asporogenous, polar flagellate, oxidase-positive fermentative, anaerogenic rods.

Stunkard and Lux (1965) described a common microsporidian infection of the digestive tract of winter flounder. The disease was first reported by Linton (1901) in the Woods Hole region, and it may be identical with infections of European flounders caused by the parasite *Nosema stephani* (later transferred to the genus *Glugea* and referred to as *G. stephani* or *G. hertwigi*). Stunkard and Lux (1965) inspected over 1,000 winter flounder of different sizes taken from various locations in New England. Their results showed 3.5% of 751 flounder (length 120-270 mm TL) collected from Woods Hole Harbor; 16.7% of 126 flounder (length 210-500 mm TL) from Nantucket Shoals; 15.8% of 19 flounder (length 310-450 mm TL) from off Plymouth, Mass.; and 54.1% of small flounder (length 41-110 mm TL) from Lake Tashmoo, Marthas Vineyard, were infected with this parasite. There was no effect of seasonal or sexual differences. The Georges Bank population (38 fish, 110-650 mm TL), isolated from the rest, showed no incidence of the disease. Infections were classified as heavy (infiltration massive, gut largely destroyed) or light (1-20 cysts in wall of intestine). Almost all heavily infected fish were less than 80 mm long. Evidence indicates fish heavily infected during their first year of life do not survive.

The site of infection was primarily the wall of the intestine and pyloric areas. Other structures adjacent to or in contact with the gut such as the bile duct, liver, mesenterial lymph nodes, and ovary, may be involved. In light infections cysts were usually found on the external wall of the intestine; in heavy ones, the gut wall was largely supplanted by layers of cysts and the intestines had a chalk-white pebbled appearance with a rigid thickened wall. The cysts were spherical to oval and measures 0.6-1.0 mm in diameter. The walls were composed of laminated layers that had the structural appearance and staining reactions of host connective tissue. There were also masses or strands of spores scattered throughout the tissue of the gut wall often associated with distinct blood vessels. Below the connective capsule of the cyst was often a narrow layer of material containing large oval, apparently pycnotic nucleii with fragmented chromatin and distinct nucleoli. This suggested that cysts formed around a number of host cells whose cytoplasm had been consumed. Spores were oval to ovate measuring 4 × 2.5 . The basal wider end of the spore contained a large vesicle, the apical end a smaller one, the central part a band of chromatic material, and a single strand extending to the apical end.

Attempts to obtain experimental infection of fishes by feeding them microsporidian cysts from gut walls of infected flounder embedded in pieces of clam were unsuccessful, so the life cycle is not known. Since fish become infected when only 50 mm in length when their diet consists of small invertebrates, a second intermediate host may be required in the parasite life cycle although no intermediate host animals have yet been found for microsporidia.

Another parasitic infection with metacercarial cyst of the trematode *Stephanostomum baccatum* has been studied by Wolfgang (1954a, b) in winter flounder from eastern Canada. He found that infection in inshore waters was greater near open water than on shoal grounds. Larger fish had heavier infections than small ones, the growth of the flounder was not impeded by heavy cyst infections, and no marked seasonal variation of the infection could be demonstrated.

The life cycle of the parasite in eastern Canadian waters is as follows: mollusks, *Buccinum undatum* and *Neptunea decemcostatum*, primary intermediate hosts; six common pleuronectid species second intermediate hosts; *Hemitripterus americanus* and *Hippoglossus* common definitive hosts. Experimental proof of relationships between *S. baccatum* adults in sea raven and the larvae in winter flounder was established. Experimental infections of winter flounder with *S. baccatum* cercariae dissected from infected snails was observed. The cercariae do not swim towards the flounder but wait until touched by the fish. They burrowed into a suitable site and encysted in muscle or connective tissue by secreting a hyaline cyst about themselves.

Young-of-the-year flounders, seined in midsummer onshore and taken in surface tows near shore, were never infected. The smallest metamorphosed flounders (35 mm TL) were infected lightly at the end of August. Small fish (below 90 mm) taken during summer (age 0) date the earliest time at which a flounder may be infected.

Because of the close nature of the association between hosts and the problems involved in eliminating any one of the hosts, control of the parasite is impractical. It does not slow the growth rate of flounder and does not harm man nor develop in him.

Fish (1934) described a fungus disease of epidemic proportions in sea herring, *Clupea harengus*, and winter flounder throughout the Gulf of Maine. The causative agent was a species of fungus belonging to the genus *Ichthyosporidium* and the species was tentatively identified as *hoferi*, first described in winter flounder by Ellis (1928). The organism is believed to be a normal parasite in herring, reaching epidemic proportions only when certain unknown factors are operative. The epidemic, once initiated, increases in severity, reaches a peak, and subsides. Flounder may be an accidental host since infected flounder have been taken only in regions where large numbers of dead sea herring were available as food. Fish

(1934) believed the flounder acquired the infection by consumption of infected herring which acquire it by ingesting parasites liberated from fish in the same school; however, since winter flounder rarely eat fish and their mouths are too small to eat herring, this does not seem probable. It is more likely that scavenger organisms fed on the herring, after which flounder ate the scavengers, thus acquiring the parasites. The infection is believed to be established by way of the alimentary canal and spread throughout the host by the blood stream or lymphatics.

There is no reason to believe this parasite capable of infecting warm blooded animals.

The complete life cycle of the organism is not known. The most common stage encountered in host tissues is the resting stage which appears as a spherical cell, composed of a heavy double wall enclosing the protoplast. Organisms ranged from 5 to 164.5μ within which there appeared to be no difference in internal structure other than density of the cytoplasm and number of nucleii. From this stage (regardless of cell size), hyphal division may take place. The mycelium bores through surrounding tissue and breaks up into a large number of daughter cells. The hyphal wall disintegrates and spores are liberated.

Pathology—In flounder, internal lesions may occur in heart, liver, spleen, kidneys, intestinal tract, brain, and spinal chord. Macroscopic lesions appeared as white spherical firm masses or cysts. The viscera may be riddled with these from microscopic to bean-size cysts. In advanced lesions, firm cysts tended to disintegrate more pronouncedly in herring than in flounder. Microscopically, lesions were similar in all organs and hosts. An infiltration of mononuclear cells followed ingress of a single parasite. Tissue surrounding the parasite is replaced by an epithelioid type of tissue apparently derived from wandering monocytes. This was replaced eventually by connective tissue believed to represent the host's chief defense mechanism to prevent spread of the parasite. As infection progresses, the parasites increased until the area once contained in the "tubercle" becomes a heterogeneous mass of parasites, infiltrating monocytes and epithelioid tissue, connective tissue, and necrotic debris.

Mahoney et al. (1973) described a fin rot disease which reached epizootic proportions in 1967 in the New York Bight and has continued to occur annually. Winter flounder were among the 22 principal species affected. The external signs of disease were fin necrosis often accompanied by skin hemorrhages, skin ulcers, and blindness. Bacteria of three genera, *Aeromonas*, *Vibrio*, and *Pseudomonas* were implicated as infective agents of disease. Water pollution was thought to have a role in the disease as unsanitary conditions in aquaria are associated with similar epizootics, and the primary epizootic center is lower New York Harbor which is grossly polluted with sewage and industrial wastes.

Infective bacteria are believed to be water borne. Disease incidence tended to parallel the seasonal regime of temperature increasing from low levels in spring, reaching highest levels from July to September, and decreasing again in fall.

Ziskowski and Murchelano (1975) reported the incidence of fin erosion in winter flounder from four areas: 1) New York Bight Apex, heavily polluted by dumping of sewage, sludge, and acid wastes; 2) ocean outside of the Bight, unpolluted; 3) Sandy Hook-Raritan Bays, domestic and industrial pollution impacted area; 4) Great Bay, N.J., relatively unpolluted. Results showed there was a significantly greater incidence of disease in the Bight Apex (371 or 14.1% of the fish affected) than outside the apex (36 or 1.9%).

Smith (1935) described a hyperplastic epidermal disease in winter flounder which resembles a papillomatous disease called "carp pox" that affects cyprinids in European waters. The disease occurred in two specimens of winter flounder from Long Island Sound and was characterized by grayish white, irregular slightly elevated patches on the pigmented surface of the body. The histological characteristics of disease are a hyperplasia of epithelial cells without keratinization. The chorium is slightly edematous and thickened but without inflammatory cells. In many places irregular, elongated, fibrous bands extend from the chorium into the epithelium. There is a rich capillary blood supply in diseased areas and in some areas large nucous cells and cells with eosinophilic granules appear. Both of these fish were also infested with the parasite *Cryptocotyle lingua*, a trematode occurring as larvae encysted in the fishes' skin. Transplantation of diseased tissue into four normal flounders was not successful. The disease is probably benign as invasion of underlying structures and metastases were not present. There was no direct evidence that encysted larvae acted as a causative agent.

Abnormalities—An abnormal variety of black bellied fish was reported by the Rhode Island Fish Commission for 1900 (Sherwood and Edwards 1901). Thirty-three percent of the flounder were ambicolored in 1898, 4% in 1900, and none by 1901. No reasons were given for this occurrence. Abnormalities reported for winter flounder are presented in Table 7.

3.4 Nutrition and growth

3.41 Feeding

Winter flounder are sight feeders. The importance of vision in juvenile feeding was studied by Pearcy (1962a). Fish fed in a dark room did not eat until zooplankton died and sank to the bottom. Field observations confirmed that feeding occurs during the day. Stomachs emptied faster than indicated in laboratory experiments.

Olla et al. (1969) also confirmed that winter flounder are sight feeders and active at day. At night they lie flat, heads resting on the bottom and eye turrets retracted, in a quiescent state. They assumed this state within 30 min after evening civil twilight and remained so until the beginning of morning civil sunrise. Relative volume of

Table 7.—Abnormalities in winter flounder.

Abnormality	Remarks	Source
Albinism (partial)	Dorsal wound	Breder (1938)
	Dorsal wound	Eisler (1963)
	Abnormal squamation, loss of dorsal pterygiophores	Dawson (1962, 1967)
Reversal	—	Gudger (1935)
	—	Gudger (1945)
	—	Medcof (1946)
	—	Bishop (1946)
	—	MacPhee (1974)[1]
Tailless	No hypural plate, only 26 vertebrae, probably result of accident	Pearcy (1962c)
Ambicoloration (incomplete)	No other abnormalities	Gudger (1934)
(complete)	—	Gudger (1934)
	Left eye just over dorsal crest, hooked dorsal fin, abnormal branching of lateral line	Gudger (1934), Eisler (1963)
Unpigmented spots on eyed side	4-13% of 1959 year class from Georges Bank affected	Lux (1973)

[1]Unpublished data.

gut contents showed day feeding. Samples taken between 0800 and 1300 contained food, samples at 0415 were empty indicating fish had not fed. Probable clearance time for the stomach is 7 to 11 h.

Tyler (see footnote 5) reported on yearly feeding cycles of winter flounder in Passamaquoddy Bay. He found they had progressively more food in their stomachs after the first spring feeding in April when water temperature was between 3° and 4°C. The peak in quantity came at the end of May. Increased bottom temperatures during summer were accompanied by a decrease in stomach content volume. The lowest quantity was reached in November when some winter flounder ceased feeding. Water temperature at the onset of winter fasting had dropped to 5°-6°C from a peak of 10.1°C in September.

Frame (1972) studied feeding habits and food of age I flounder in the Weweantic estuary, Mass. His findings were similar to Olla et al. (1969). He also found that the quantity of food consumed daily was variable. On cloudy days in summer, feeding may begin well after sunrise, so fish consume less. In winter, age I fish consumed less food, and their stomachs remained empty longer.

3.42 Food

Sullivan (1915) stated that until yolk absorption, larvae did not eat. Larvae up to 3 wk ate only diatoms, a little later they ate small crustaceans.

Pearcy (1962a) gave a detailed account of larval and young juvenile feeding habits. He also cited S. W. Richards' unpublished data that dinoflagellates were the most frequent food eaten by larvae from Long Island Sound. Young flounder from the Mystic River estuary, Conn., fed largely on invertebrates (Table 8). Empty stomachs were found in 72% postlarvae, 25% metamorphosing larvae, and 0.6% juveniles. Juveniles are euryphagus. Seventy-seven organisms from seven phyla were identified. There was a high degree of selectivity at certain times of the year. Comparisons of food of flounder inhabiting shores vs. deep water showed that the major groups of animals were the same but genera differed.

Table 8.—Food of winter flounder postlarvae to age I (Pearcy 1962a).

Postlarvae	Metamorphosing	Juveniles	Age I
3.4 mm			
Copepods	Copepods (Harpacticoid)	Copepods	Polychaetes
Phytoplankton (pennate and filamentous)	Nauplii	*Eurytemora* *Diaptomus* *Paracalanus*	*Neanthes* *Cirratulus*
	Polychaetes	Amphipods	Amphipods *Harmothoe*
Protozoanlike organism	Nemerteans	*Ampelisca* *Corophium* Polychaetes	
Invertebrate eggs	Ostracods	Maldanids *Clymnella* *Neanthes* *Cirratulus*	*Ampelisca* *Corophium*
4-5 mm			
Nauplii			
6-8 mm			
Polychaetes			
Larval and small			

The time required for juveniles fed in the laboratory to evacuate stomachs was determined by preserving individuals at different times (Table 9). The rate of feeding of juveniles 22-55 mm during four intervals (water temperature 20°-22°C) was approximately 2.0-3.4% body weight/day. The results are questionable because of rapid growth of individuals during the summer in the wild, and daily feeding rate shown for other juveniles (Pearcy 1962a).

Table 9.—Stomach evacuation time of juvenile winter flounder (Pearcy 1962a).

Length of fish (mm)	Water temp. (°C)	Number of hours	
		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

Tyler[7] described the digestive tract of winter flounder as follows: narrow buccal cavity and pharynx; incisorlike teeth on premaxillary and dentary; stomach without fundus; four large pyloric caecae distal to pyloric valve; intestines coiled in coelome (viewed from blind side), two complete clockwise coils followed by one complete counterclockwise, situated between first two coils; intestinal-rectal valve present. Relative length of parts of the alimentary tract (expressed as percent of total tract

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[7] Tyler, A. V. 1973. Alimentary tract morphology of selected North Atlantic fishes in relation to food habits. Fish. Res. Board Can., Tech. Rep. 361, 23 p.

length) are: 6.3, lips to first gill cleft; 4.9, first gill cleft to stomach; 10.1, stomach length; 69.8, pyloric valve to intestinal-rectal valve; 8.9, rectum length.

Winter flounder cease to feed in winter, fasting from November to April (Tyler 1972b). Olla et al. (1969) observed feeding behavior of winter flounder in their natural habitat by means of scuba. While actively feeding, the flounder lies with head raised off the bottom and 12-17 rays of the dorsal fin braced vertically into the substrate. The left pelvic fin and several anal fin rays were used to support the head. In water currents of 20 cm/s the fish maintained its position by tucking the distal edges of the dorsal and anal fins into the bottom substrate. The eye turrets were extended and the eyes moved independently of one another. After sighting prey, the fish remained stationary pointed towards the prey, then lunged forward and downward covering about 10-15 cm to seize the prey. Mud, sand, and debris were expelled through the right branchial aperture. The fish then resumed the feeding position. If no food was sighted, the fish would swim to another location less than 1 m away and again resume feeding position.

Adults—Throughout their range, winter flounder eat polychaete worms, amphipod and isopod crustaceans, pelecypods, and plant material. They are omnivorous and seem to be opportunistic, eating whatever is available (Pearcy 1962a; Richards 1963; Mulkana 1966; MacPhee 1969; Frame 1972).

Richards (1963) stated they ate a greater variety of food than any other demersal fish. Seasonal changes in the type of prey consumed were due partly to availability of prey, and number and age of the predators. She also found that correlations between food diversity and total number of flounders were sometimes close, the highest numbers of flounders and number and varieties of amphipods, polychaetes, and molluscs occurring in spring and fall.

Pearcy (1962a), Richards (1963), and Mulkana (1966) mentioned that with progressive increase in size, young winter flounder tend to prefer larger prey organisms.

Frame (1972) compared species diversity in the stomach contents of age I winter flounder with contents of Petersen dredge hauls collected in the same area of the Weweantic estuary, Mass., from January to October. He used a modified percent overlap technique in an attempt to compare food utilization with prey diversity and availability. He found a low overlap value between dredge hauls and stomach contents in spring when the young flounder prefer planktonic copepods. By June the fish assumed a more benthic habit, and overlap values were higher. The value increased in July and October suggesting flounder adapt to a benthic existence by the midpoint of their first year. He proposed this dietary shift may be due to the animals' physiological requirements rather than age alone. An example of this is that in spring, young flounder live at low salinities and temperatures which produce lower metabolic rates and consequently the fish uses less calories for metabolic maintenance; therefore, they survive on plankton. With increased temperatures and salinities later in the season, the metabolic rate increases requiring more calories. (See also section 3.44).

Tyler (1972b) studied food resource division among northern marine fish predators in Passamaquoddy Bay. He showed that although over 100 prey species were included in stomachs of predators, each took only three or four principal species of prey which made up 70-99% of the mass of food for each predator. Winter flounder ate three principal species of polychaetes *Nephtys*, *Lumbrinereis*, and *Praxillella*. (See also section 4.6.)

MacPhee (1969) showed that the most important category of food in the winter flounder's diet depends upon the type of bottom which the fish inhabits. The diet of flounder living on a predominantly rocky bottom is more variable than flounder living on a soft bottom. Frame (1972) agreed that winter flounder adapt their diet to environmental conditions. Fourteen phyla and 260 species have been found in winter flounder stomachs by a series of investigators (Table 10).

3.43 Growth rate

Pearcy (1962a) gave comprehensive data on growth rates of age group 0 flounder (Fig. 7). He pointed out there is a great deal of variation in average lengths within many months, which is partly due to difficulties in calculating a representative average length since prolonged spawning resulted in as much as 4 mo difference in age for a year class. Seasonal changes in growth were apparent. Growth is fast in spring and summer, slow in winter. Because metamorphosis of flounder was not completed until June, the first 2 mo underestimated growth and were excluded from analysis. This decrease in standard length often occurs during metamorphosis when caudal fin differentiation and body proportions change. Measurements of maximum length of otoliths of year class 0 and maximum length of the opaque center compared with fish length at capture show that growth of the

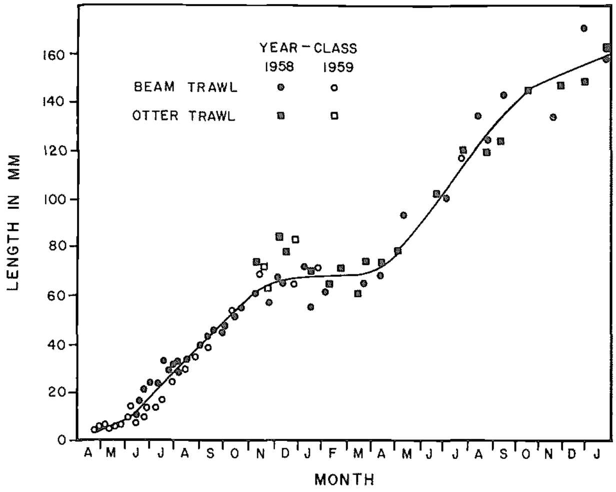

Figure 7.—Growth curve of juvenile winter flounder (from Pearcy 1962a).

Table 10.—Food organisms found in stomachs of winter flounder from different geographic areas. A. Long Island Sound (Richards 1963). B. Point Judith and Narrow River estuary, R.I. (Mulkana 1966). C. Mystic River, Conn. (Pearcy 1962a). D. Several—Cape Cod. Mass., to York, Maine (MacPhee 1969). E. Weweantic estuary, Mass. (Frame 1972). F. Conception Bay, Nova Scotia (Kennedy and Steele 1971). G. Bay of Fundy, Passamaquoddy Bay, N.B. (Wells et al. 1973).

Organism	Area
Chlorophyta	
Chaetomorpha linum	D
Cladophora serica	G[1]
Enteromorpha intestinalis	G[1]
Monostroma oxysperma	D
Spongomorpha arcta	D
Ulva lactuca	D
Chrysophyta	
Diatoms	A,D
Phaeophyta	
Ascophyllum nodosum	D
Ectocarpus siliculosis	G[1]
Leathesia difformis	D
Pylaiella littoralis	G[1]
Rhodophyta	
Acrosiphonia arcta	G[1]
Ahnfeltia plicata	D
Asparagopsis hamifera	D
Callithamnion byssoides	D
Ceramium rubrum	D
Chondrus crispus	D
Corallina officinalis	D
Dumontia incrassata	D
Euthora cristata	D
Polysiphonia lanosa	D
Rhodymenia palmata	D
Porifera	
Grantia sp.	A,D
Coelenterata	
Diphasia fallax	B,D,G
Obelia enseralis	G
Nemertinea	
Cephalothorax linearis	B,D
Cerebratulus luridus	A
Nematoda	G
Annelida	
Oligochaeta	
Clitella arenarius (?)	A,B,D
Enchytraeus albidus	A,D
Polychaeta	
Ammotrypane acuta	G
Ampharete acutifrons	A[2]
Amphicora fabricii	A
Amphitrite johnstoni	G
Antinöe sarsi	F,G
Arabella iricolor	B-E,G
Arenicola marina	F
Aricidea fragilis	D,G
Autolytus cornutus	B,D,G
Capitella capitata	B,D
Cirratulus cirratus	D
Cistenides grandis	A,C
C. gouldi	A,G
Clymnella torquata	D
Dodecaceria concharum	D
Drilonereis elizabethae	D
D. longa	A
Eteone arctica	F
E. longa	D,G
E. trilineata	F
Eudora truncata	G
Eulalia viridis	D,F,G
Eumida sanguinea	B,D
Eunoa nodosa	D
Eupomatus dianthus	A,C,E
Eusullis tubifex	F
Fabricia sabella	D[3]
Flabelligera affinis	A[2]
Glycera americana	A,E,G
G. dibranchiata	A
Goniada gracilis	A
Harmothoe extenuata	D
H. imbricata	A,C,D,G[3,4]
Lepidonotus squamatus	A
L. variabilis	D
Lumbrinereis	A,B,G
L. fragilis	A,G[3,4]
L. tenuis	E
Maldanopsis elongata	E
Marphysa belli	D
Megalona papillicornis	A
Neanthes caudata	A,B,E
N. succinea	A-E[2,5]
N. virens	A,B[6]
Nephtys caeca	A
N. incisa	A,B,G[2,6]
N. picta	D
Nereis ciliata	A
N. furcata	D
N. megalops	D
N. pelagica	A,D,F[4]
N. tenuis	D
N. virens	D,G,F[1,4]
Nicolea zostericola	D[3]
Ninoe nigripes	G
Ophelia radiata	F
Pectinaria gouldi	E,F
Peloscolex benedeni	G[1]
Phyllodoce fragilis	A,D
P. groenlandica	D
P. maculata	D[3]
Polycirrus exemus	A
Polydora ligni	D
Potamilla neglecta	A,D
Praxillella gracilis	A,G
P. praetermissa	A,G
Prionospio malmgreni	B[6]
Pygiospio elegans	A,B,G
Scalabregma inflatum	A
Scolopus armiger	A,D,F
Spirorbis borealis	D,G
Sthenelais gracilis	A
Stylaroides arenosa	D
Syllis gracilis	A,F,G[2]
Terrebelloides stroemi	G
Tharyx acuta	A,G
Sipunculoidea	
Phaslosoma procerum	D
Mollusca	
Amphineura	
Ischnochiton ruber	F,G
Lepidochiton marmorea	D,F
Gastropoda	
Acmea testudinalis	A,D,G[3,4]
Anoba aculeas	D
Bitteum alternatum	E
Buccinium undatus	D
Cerastoderma pinnulatum	F
Crepidula fornicata	D
Crucibulum striatum	E

Table 10.—Continued.

Organism	Area
Hydrobia minuta	G[4]
Lacuna pallidula	G
Littorina littorea	D,G[3, 4]
L. palliata	D
L. saxitilis	D
Lunatia heros	E,G
Margarites groenlandica	D
M. helicinus	G
Melampus bidentatus	D
Mitrella lunata	E
Nassarius trivitatta	A,D
Natica pusilla	A,E
Neptunea decemcostatum	G
Puncturella noachina	G
Retusa canaliculata	E[7]
Sella adamsi	A,E
Skenea planorbis	D
Thais lapillas	G
Turbonilla interrupta	E
Pelecypoda	
Anomia aculeata	D
A. simplex	D
Bivalve siphons	E[3]
Cerastoderma pinnulatum	F
Clinoeardium ciliatum	F
Crenella faba	F
Cyrtopleura costata	E
Ensis directis	A,F[2]
Gemma gemma	B,C
Haminea solitaria	C
Hiatella arctica	F
Laevicardium mortoni	F[2]
Lyonsia hyalina	A,C
Macoma baltica	D,E,G[4]
M. tenta	E
Mercenaria mercenaria	E
Mesodesma arctata	D
Modiolus modiolus	D
Mulinia lateralis	A,E[2]
Mya arenaria	C,D,F,G[3, 4]
Mytilus edulis	D,B[3, 4]
Nucula proxima	B,D[7]
N. tenuis	A,D,E
Nymphen grassipes	A
Saxicava arctica	D
Serripes groenlandicus	F
Siliqua costata	D
Solemya borealis	D
S. velum	C,F
Tellina agilis	B,E[7]
Yoldia sapotilla	D
Y. limatula	E
Arthropoda	
Crustacea	
Amphipoda	
Aeginella longicornis	A-D
Ampelisca spinipes	D
A. macrocephala	A-D[2]
Amphithoe longimana	D
A. rubricata	D,G[1]
Anonyx nugax	D
Batea catherinsis	C
Byblis serrata	C,D
Calliopius laeviusculus	C,D[3]
Caprella geometrica	C
C. linearis	A,D
Carinogammarus mucronatus	B-D
Casco biglowi	G
Corophium (volutator?)	A,D,G[2, 3]
C. cylindricum	C
C. bonelli	F[4]
Cymedusa filosa	B,C
Dexamine spinosa	F,G[4]
Erichthonius brasiliensis	A
E. difformis	D
Gammarus annulatus	B-D
G. lawrencianus	F,G[1]
G. oceanicus	A,D,F,G[1, 4]
G. marinus	D
Grubia compta	D
Ischyrocerus anguipes	D,F[4]
Jassa falcata	D,G
J. marmorata	D[3]
Lembos smithi	B-D[6]
Leptochirus pinguis	A,C,D,F,G[1, 2]
Lysianopsis alba	C,D
Melita dentata	D,G
Mesometopa neglecta	F
Metopa pusilla	C[5]
Metopila carinata	F
Microdeutopus gryllotalpa	B,C[5]
Monoculodes edwardsi	A,F
Orchomenella minuta	F[4]
Photis reinhardi	A
Phoxocephalus holbolli	A,C,D,G[3, 5]
Podoceropis nitida	A[2]
Pontogeneia inermis	D,F
Stenothoe cypris	A
S. minuta	A
Sympleustes glaber	F
Typhosa pinguis	D
Unicola irrorata	A-D,G
U. leucopis	F
Cirripedia	
Balanus balanoides	A,C,F,G
Cladocera	
Evadne nordmanni	C
Podon leuckarti	C
Copepoda	
Acartia sp.	A,B
Eurytemora sp.	C[5]
Paracalanus sp.	C
Pseudodiaptomus coronutus	A,C
Temora longicornis	A,B,E,F
Cumacea	
Cyclaspis varians	A-C
Diastylis polita	D
D. quadruspinosa	A
Oxyrostylis smithi	A-C
Isopoda	
Chiridotea caeca	B,G
Clathura polita cyathura	A
Edotea triloba	C[5]
E. montosa	A-C,G[6]
Erichsonella attenuata	D
Idotea baltica	D[3]
I. metallica	D
I. phosphorea	D
I. viridis	B
Jaera albifrons	G
J. marina	D
Leptochelia savignyi	B-D[6]
Ostracoda	
Cylindroleberis mariae	B,C[6]
Pontocypris edwardsi	B,C
Pseudocytheretta edwardsi	C

Table 10.—Continued.

Organism	Area
Sarsiella americana	B,C[6]
Sarsiella zostericola	A,C
Decapoda	
Cancer irroratus	F
Crangon septimspinosus	A-C[7]
Neomysis americana	A,C[2,5]
Neopanope texana sayi	B
Pagurus longicarpus	A,D-F
Palaemonites vulgaris	C
Polyonyx machrocheles	B
Sabinea sarsii	A
Upogebia affinis	A
Insecta	
Insect larvae	A,D-F
Invertebrate eggs	B,D
Echinodermata	
Asteroidea	
Asterias forbesi	D,F
A. vulgaris	D
Echinoidea	
Arbacia punctulata	D
Strongylocentratus drohbachiensis	D,F,G
Holothuroidea	
Cucumaria frondosa	D,G
Ophiuroidea	
Amphipholis squamata	C-E
Ophiophalis aculeata	D
Chordata	
Molgula manhattensis	C,D
Didemnum candidum	G
Pisces	
Fish remains	F
Fish eggs	D,F[4]

[1] Wells et al. (1973) by percent weight.
[2] Richards (1963) by occurrence and percent volume.
[3] MacPhee (1969) numbers and occurrence.
[4] Kennedy and Steele (1971) numbers plus volume.
[5] Pearcy (1962a) by volume.
[6] Mulkana (1966) by mean number/stomach and percent frequency occurrence.
[7] Frame (1972) numbers and occurrence.

otolith after deposition of the opaque center was variable, and therefore exact age within the 0 group cannot be determined by otolith characteristics. No calcified otoliths were found in fresh specimens until the left eye was in the median position (7.0 mm or greater).

Growth in weight was calculated by Pearcy (1962a) from average length of flounder in millimeters at the beginning of each month converted to weight in grams by the formula: $W = 0.000017L^3$ (Fig. 8).

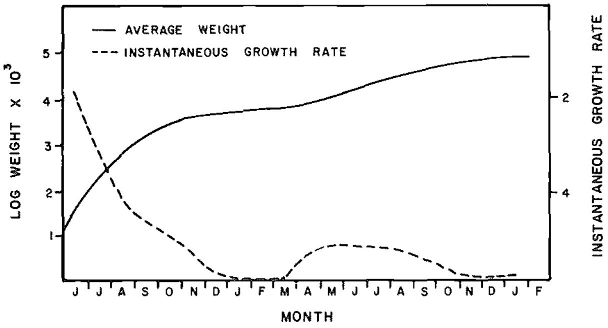

Figure 8.—Average monthly weight gain in the Mystic River estuary in winter flounder (from Pearcy 1962a).

The instantaneous rates of growth ($k = dw/dt$) were calculated from relative growth by means of the formulas:

$$b = (Wo_{i+1} - Wo_i) / Wo_i$$

where: Wo = average individual weight at beginning of month i

b = relative growth and $e^k = b + 1$.

Laurence (1975) studied growth of laboratory reared winter flounder larvae from hatching through metamorphosis at 2°, 5°, and 8°C. The fish were reared in all black 38-liter aquaria at a stocking density of approximately 13/liter. The aquaria were semiclosed and aerated. Salinity varied between 28 and $30^{\circ}/_{\circ\circ}$. Larvae were fed wild zooplankton (principally copepod nauplii at concentrations of 2,000/liter). Growth was measured weekly. Specific daily growth was calculated from the formula

$$SG = 100 \frac{\log_e WT - \log_e wt}{T}$$

where SG = specific growth
WT = dry weight at the end of the time interval
wt = dry weight at the beginning of the time interval
T = time in days.

Temperature strongly influenced growth of larvae and juveniles, growth being directly related to temperature. Regression analysis of the semilog arithmetic transformation of growth on time gave the following linear equations:

$$8^\circ\text{C: } \text{Log } Y = 0.755 + 0.358X \quad r = 0.99$$
$$5^\circ\text{C: } \text{Log } Y = 0.840 + 0.213X \quad r = 0.97$$
$$2^\circ\text{C: } \text{Log } Y = 0.840 + 0.110X \quad r = 0.85.$$

Growth rate was significantly greater at 8°C than at 5°C, and greater at 5°C than at 2°C, but not significantly so. Larvae held at 2°C died before completing metamorphosis. Time to metamorphosis was 49 days at 8°C and 80 days at 5°C. Daily specific growth was greater at higher temperatures and was highly variable from week to week. Mean specific growth rates were 10.1%/day at 8°C, 5.8%/day at 5°C, and 2.6%/day at 2°C.

Adults—Several authors have calculated growth rates of adults (Fig. 9). Kennedy and Steele (1971) calculated the age of Long Pond, Newfoundland, flounder from otoliths. They found no difference between growth curves of males and females until age IX when the females were much larger. This could be due to low numbers of females involved, or failure to age the fish correctly. The regression equations for the fish were:

Females: $\text{Log } W = 3.1441 \log L - 2.0702$
Males: $\text{Log } W = 2.9833 \log L - 1.9041$

with L in centimeters and W in grams.

Berry et al. (1965) determined age from otoliths and scales of winter flounder in Rhode Island. They found that scale markings were unreliable for making age determinations, and that otoliths provide fully reliable estimates only to age III, which agrees with Landers (1941). Their growth equations, based on the Walford plot, are:

Females: $l_{t+1} = 395.7(0.34) + 0.66 l_t$
Males: $l_{t+1} = 323.1(0.42) + 0.58 l_t$

where l_t = length in millimeters at time t.

They concluded a typical growth curve for winter flounder could not be developed because the species consisted of discrete stocks which were subject to variable rates of exploitation and environmental conditions; and that females grew faster than males.

Poole (1966b) studied growth rates of fish collected in several south shore bays of Long Island. He used otoliths and agreed with Berry's (1959) description of opaque band formation where the first opaque band useful for judging age appears in October and continues its growth to July when the fish is several months beyond age group I. Poole found that females grew faster than males and that the growth rate was different in certain bays.

Lux (1973) calculated age and growth of winter flounder on Georges Bank by means of scale analysis. Direct proportion growth calculations were made using the equation:

$$L_n = C + S_n/S[L - C]$$

where L_n = fish length (TL) at time of formation of nth annulus
C = fish TL at scale formation
S_n = anterior scale radius to nth annulus
S = anterior scale radius at capture
L = fish TL at capture.

He found growth was more rapid on Georges Bank than on inshore areas, fish from eastern Georges Bank growing slightly faster than those from the western part. Females grew faster than males after age II. Growth equations were:

$$lt = l\infty(1 - \exp[-K(t - t_0)])$$

where lt = length in centimeters
$l\infty$ = theoretical maximum length
K = rate of change in length increment
t_0 = age at which growth in length theoretically begins

Male: $lt = 550(1 - \exp[0.37(t + 0.05)])$
Female: $lt = 630(1 - \exp[0.31(t - 0.05)])$

where lt = length at age t.

Howe and Coates (1975) described growth of winter flounder off the Massachusetts coast. They plotted "Walford lines":

$y = a + bx$
$L_t = (x)$—length in millimeters at time t

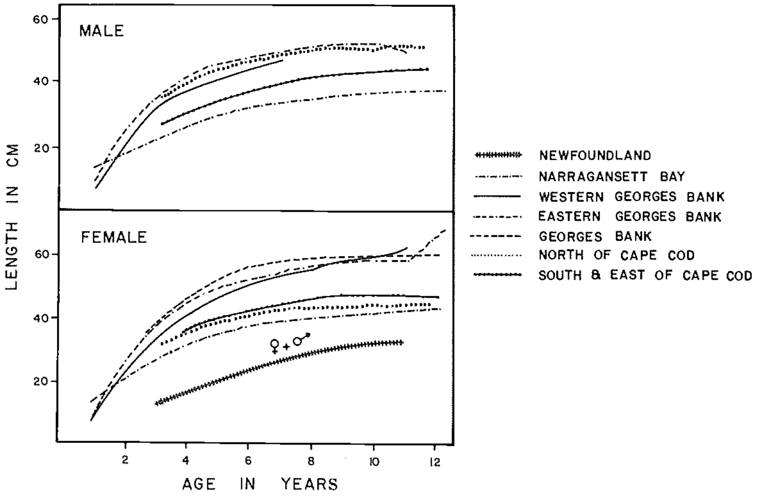

Figure 9.—Growth curves of adult winter flounders (from Saila et al. 1965; Poole 1966a; Kennedy and Steele 1971; Lux 1973; and Howe and Coates 1975).

$L\infty$ = a—theoretical maximum length
y = growth/month in millimeters
b = rate of change in growth.

There were significant growth differences between geographic areas. The growth rates of females (F) south of Cape Cod were greater than those north of Cape Cod but less than those from Georges Bank. Males (M) grew faster on Georges Bank than south of Cape Cod. Females grew more rapidly than males south of Cape Cod but not on Georges Bank. The growth equations calculated for the fish are as follows:

Area	*Sex*	*Ford-Walford Growth Equation*
North of Cape Cod	F	$L_{t+1} = 455.38\,(1 - 0.69) + 0.69L_t$
East and south of Cape Cod	M	$L_{t+1} = 476.76\,(1 - 0.78) + 0.78L_t$
	F	$L_{t+1} = 487.38\,(1 - 0.71) + 0.71L_t$
Georges Bank	M	$L_{t+1} = 534.40\,(1 - 0.69) + 0.69L_t$
	F	$L_{t+1} = 622.38\,(1 - 0.64) + 0.64L_t$

where L = length in millimeters
t = time in years.

3.44 Metabolism

Laurence (1975) studied metabolism of laboratory-reared larvae and juveniles. He used Warburg respirometers to measure oxygen consumption for 2-h periods. Absolute values of larval oxygen consumption increased until metamorphosis, at which time they declined. After metamorphosis, oxygen consumption again increased. Temperature directly affected oxygen consumption with higher consumption at higher temperatures. Metabolic rate on a unit weight basis decreased with increasing size from hatching through metamorphosis. Absolute values of routine metabolism expressed in liters of oxygen consumed, regressed on body weight were best described by a third degree polynomial.

$$\begin{aligned}
2°\text{C}: O_2 &= 0.451 + 6.0 \times 10^{-3}W - 1.1 \times 10^{-6}W^2 \\
&\quad + 1.5 \times 10^{-10}W^3 \\
5°\text{C}: O_2 &= 0.601 + 3.3 \times 10^{-3}W - 1.7 \times 10^{-6}W^2 \\
&\quad + 2.5 \times 10^{-10}W \\
8°\text{C}: O_2 &= 0.379 + 6.8 \times 10^{-3}W - 4.3 \times 10^{-6}W^2 \\
&\quad + 7.6 \times 10^{-10}W^3
\end{aligned}$$

The metabolic rate of fish with respect to weight is usually described by the linearly related log transformation $\log_{10}$oxygen consumption = $a + b \log_{10}$weight in which the slope value is approximately 0.80.

Although larval winter flounder conformed to this type of relationship, metamorphosed juveniles did not. Therefore, continuous metabolism of this fish must be described by a different analysis than standard log-log transformation. This change in metabolic patterns probably reflects changes in body shape and activity patterns occurring at metamorphosis, and perhaps reflects physiological changes in the respiratory system. Salinity effects were not examined.

Frame (1973a) studied oxygen uptake rates of young winter flounder from the Weweantic River estuary, Mass., to determine the effects of estuarine conditions (salinity and temperature differences) on respiration and metabolic rates. He found that the quantity of O_2 uptake (ml O_2/h per g) as a function of increased temperature did not differ significantly between salinities of 10-20‰ but is 40-50% higher at 30‰. Metabolic rates per gram did not differ between fish sizes used (10.0-13.5 cm TL and 14.0-17.5 cm TL) or between sexes. Two factors, temperature and weight, were necessary for calculation of a fish's energy expenditure under routine metabolic conditions (Fig. 10). The expression for the equations in Figure 10 is:

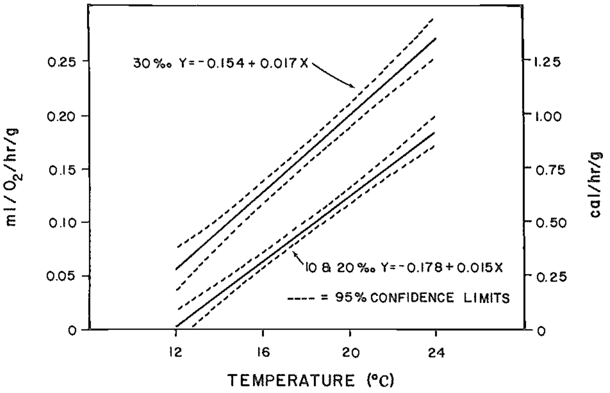

Figure 10.—Oxygen consumption (Y) of winter flounder at different temperatures and salinities and effect of weight (X) (from Frame 1973a).

$$\frac{Y = \text{oxygen (ml } O_2\text{/h per g)}}{X = \text{temperature (°C)}}.$$

This is based on the assumption that 1.0 ml O_2 is equivalent to 5.0 calories. Adjustment of the metabolic level by immature fish indicates the euryhaline nature of this species and suggests a physiological reason why young flounder are found in estuaries.

Voyer and Morrison (1972) studied respiration of winter flounder at different temperatures and oxygen concentrations. They found the average rate of oxygen consumed by flounder at 10°C was 35 and 55 mg (O_2/kg body weight per hour at 3.5 and 8.6 mg dissolved oxygen (DO)/liter, respectively. ($\bar{x}$ fish weights 18.0-24.39 g for high O_2 and 13.0-22.64 g for low O_2.) At 20°C the average rate of O_2 uptake was 70 at 8.2 mg DO/1 and 97 at 6.3 mg DO/1. Oxygen consumption rates were significantly greater at 20°C than 10°C. In two of three experiments, rates of oxygen uptake were lower among groups of flounder maintained at reduced dissolved oxygen concentrations for 15-25 h. No dissolved oxygen-temperature interactions were apparent.

Huntsman and Sparks (1924) studied the effect of size on respiratory rate which they measured by counting opercular movements per minute (Table 11). As the size of the fish increased, the respiratory rate decreased; the maximum movements showed the most regular decrease with increase in size.

Table 11.—Effect of size on respiratory rate (opercular movements/minute) of winter flounder (from Huntsman and Sparks 1924).

Size (mm)	Initial	Maximum	Final
100	141	191	130
150	100	135	103
200	76	109	51
250	86	93	61
300	73	81	53

Horton et al.[8] determined oxygen consumption to be 42.15 mg O_2/kg body weight per hour at a mean temperature of 13.4°C and salinity 30°/₀₀ for mean body weight of 852 g.

Frame (1973b) measured food intake and conversion efficiency for age I winter flounder under different temperatures and salinities. He defined conversion efficiency as increase in the weight of a fish divided by the weight of food ingested for a given period of time. Only fish held at 12°C and 16°C in 20°/₀₀ salinity had a normal growth rate. Conversion effiency ranged from 13.9 to 19.0%. The regression equation relating daily growth in average body weight (Y) to daily ration/average body weight (X) was $Y = 1.651 + 1.832X$. Temperature rather than salinity appears to have caused stress conditions although metabolic factors such as lipid synthesis and protein loss may have masked the effect of salinity. Frame proposed flounder survival may be controlled by their ability to move gradually into favorable temperature-salinity environments. Unseasonal temperature-salinity regimes imposed on age I flounder may be fatal.

Endocrine system and hormones—Phillips and Mulrow (1959) found that winter flounder corpuscles of Stannius, previously thought to be analagous to the adrenal cortex, were not concerned with the production of adrenocorticosteroids. They did not, however, suggest what the function of the corpuscles of Stannius might be.

Grafflin (1935) studied kidney concentration of urea and urine flow in winter flounder. The highest urine plasma ratios fall in the lower range of urine flow (urea plasma milligrams percent in plasma $\bar{x}$ 12.0, range 8.5-18.4; in urine $\bar{x}$ 16.0, range 10.9-25.9; renal urine/plasma ratios x 1.3, range 1.0-1.8; urine flow cm^3/kg per 24 h x 23.0, range 8.3-45.6). Considerable variation occurred in chloride concentration (0-87 millimoles/liter) and the actual rate of urine flow. Grafflin concluded there was no direct relationship between rate of urine flow and urinary chloride concentration.

Grafflin and Gould (1936) found that approximately one-half the normal total nitrogen of winter flounder urine could not be accounted for by ordinary nitrogenous constituents. Percent of total nitrogen (N) (43.4 mg N/100 cm^3 urine) of urine = urea 21.2%, ammonia N 1.8%, uric acid 1.2%, total creatinine N 15%, amino acid N 4.2%, and undetermined 51.1%. Trimethylamine oxide was absent or present in very small concentrations in the urine.

Maack and Kinter (1969) reported the first quantitative evidence for transport of intact filtered proteins across the kidney tubules. Morphological observations obtained by Bulger and Frump[9] suggest that intact protein is first transported across the brush border into the cell, from there to the intercellular spaces, and finally across the basement membrane to the peritubular space. Maack and Kinter (1969) speculated that transtubular transport of intact protein was the primary mechanism for handling normal protein loads, catabolism only occurring when an overload of protein is presented to the renal tubules.

Kleinzeller and McAvoy (1973) conducted studies on the transport systems for sugars at the peritubular face of the renal tubular cells to obtain information on the reabsorptive process using various sugars as inhibitors. A three carrier mediated pathway of sugar transport at the antiluminal cell face of the flounder renal tubule seemed to be operating: the pathway of the nonmetabolizable *a* methyl D-galactoside (not shared by D-glucose); the pathway shared by D-galactose and D-glucose; the pathway shared by the D-galactose and 2-deoxy-D-galactose.

Ammonia is the primary nitrogenous excretory product in teleosts. For the most part, ammonia is produced from precursers in the liver, transported by the blood to the gills, and excreted by diffusion (Janicki and Lingis 1970). Liver homogenates from winter flounder produce ammonia from L-aspartate and L-glutamate at the rate of 2.7 ± 0.8 μmoles NH_3/g tissue wet weight per hour at 25°C for the former and 10.0 ± 0.9 μ moles NH_3/g tissue wet weight per hour at 25°C for the latter. Mitochondrial and cytoplasmic fractions combined, produced ammonia from L-aspartate but single nuclear mitochondrial and cytoplasmic fractions did not. Results are consistent with a general scheme in which the amino group of L-aspartate undergoes transamination with *a* ketoglutarate to form L-glutamate by action of L-aspartate aminotransferase, and ammonia is liberated from L-glutamic acid by L-glutamic acid dehydrogenase. However, it is not clear which transaminase is involved.

Goldstein and Forster (1965) studied urea production in winter flounder. Although teleosts are considered ammoniotelic, teleost blood contains significant quantities of urea (the origin of which is unknown since the complete cycle for synthesizing urea is not present in living teleost fishes). Activity of the uricolytic pathway

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[8] Horton, D. B., D. W. Bridges, and J. J. Cech, Jr. 1973. The development of biomedical procedures for establishing water quality criteria of marine fish. First Annu. Rep. to Environ. Prot. Agency, Contract R-80031, 48 p.

[9] Bulger and Frump. Pers. commun., mentioned in Maack and Kinter 1969.

(uric acid-urea) was assayed in slices from winter flounder livers. The rate of conversion of uric acid to urea was 23 μ moles urea/g per hour. Allantoin and allantoic acid were also converted to urea at the same rate. Uric acid could be converted to urea by a three step process: urate →allantoin→allantoicicate→urea. Purines are, therefore, a source of urea in fishes.

Hormones—Donahue (1941) tested extracts of winter flounder ovaries for their estrogenic properties and found that the extracts contained estrogen but in quantities less than one standard rat unit. This might be useful for comparison to mammals but it is not clear how this relates to fish.

3.45 Physiology

Pesch (1970) studied the electrophoretic profiles of plasma protein (thought to be reliable indicators of physiological well being). Variations are related to changes in the body's metabolic requirements, defense against invasion and injury, maintenance of body pH, osmotic pressure, and regulation of cellular activity and function.

Plasma protein concentration in flounder was 3-4 g/100 ml of plasma, the slow and medium group being most prominent. In both sexes the concentration of individual fractions differed according to stage of gonad maturation. Total concentration was greater in mature than in immature fish. In females, the slow fraction was responsible for the increase and was due to addition of vitellin which forms yolk protein. In males, the fast fraction was responsible for the increase, which could be due to the transport property of the fast fraction or it could be serving as a source of amino acids. An immature male with tail rot had low plasma protein concentrations of about one-half normal. Aging is associated with increased plasma protein concentration, especially of slow and

Table 12.—Blood chemistry values for winter flounder.

Component	Values			Miscellaneous	Source
Plasma chloride	149.7-158.4 mOsm/1 $\bar{x}$ = 154.2 mOsm/1				Grafflin (1935)
Plasma protein	3-4 g/100 ml				Pesch (1970)
Erythrocyte content	235-372 $mm^3/10^4$ $\bar{x}$ = 294 mm^3			Mean length of fish 203 mm	Eisler (1965a)
Hemoglobin	6.16-10.44 g/100 ml $\bar{x}$ = 8.93 g/100 ml				
	Summer		Winter		
Freezing point depression	$\bar{x}$ = −0.63°C		$\bar{x}$ = −1.15°C		Pearcy (1961)
Serum osmolality[1] (mOsm/1)	405.0 ± 7.0 (12)		[2]426.0± 6.0 (9)		Umminger and Mahoney (1972)
Serum sodium (mmoles/1)	185.8 ± 3.6 (12)		185.4 ± 4.5 (9)		
Serum chloride (mmoles/1)	157.9 ± 1.3 (12)		152.0 ± 3.5 (9)		
Serum potassium (mmoles/1)	5.2 ± 0.3 (12)		[2]4.0 ± 0.2 (9)		
Serum protein (g/100 ml)	5.5 ± 0.3 (12)		[3]3.1 ± 0.2 (10)		
Erythrocytes (× $10^6/mm^3$)	2.25 ± 0.19 (12)		2.01 ± 0.10 (10)		
Hematocrit (%)	22.3 ± 1.6 (12)		22.9 ± 1.2 (10)		
Hemoglobin (g/100 ml)	8.44 ± 0.16 (12)		[3]5.1 ± 0.40 (10)		
	Serum	Dialysed serum	Dialysate		
Freezing point (°C)	−1.37 ± 0.31?	−0.65	−0.72	March (water temp. −1.2°C, total no. fish 12)	Duman and De Vries (1974)
	−0.69 ± 0.07	—	—	August (water temp. +17°C, total no. fish 8)	
Melting point (°C)	−0.75 ± 0.03	−0.01	−0.70	March	
	−0.67 ± 0.07	—	—	August	
Melting point-freezing point (°C)	0.62 ± 0.35	0.64	0.02	March	
	0.02 ± 0.001	—	—	August	
Sodium (mMl^{-1})	250 ± 12	—	—	March	
	194 ± 6	—	—	August	
Chloride (mMl^{-1})	178 ± 6	0.0	172	March	
	147 ± 14	—	—	August	
% due to NaCl	58.1	—	—	March	
	94.0	—	—	August	

Table 12.—Continued.

Component	Values		Miscellaneous		Source
	Mean	Confidence limits	Number used		
Red blood cell count	1.81×10^6/mm^3	± 0.13	86	$\bar{x}$ SL of fish 24.7 ± 1.1 (98)	Horton et al. (1973)[4]
Hemoglobin concentration	5.5 g%	± 0.4	91	Total value	
Hematocrit	19%	± 2	92	Total value	
Thrombocyte count	135.5×10^3/mm^3	±26.6	26	Total value	
Erythrocytic sedimentation	1.4 cm/h	± 0.3	59	Total value	
Corpuscular volume (RBC)	112μ^3	±13	88	Mean value	
Corpuscular hemoglobin	34 picograms	± 3	88	Mean value	
Corpuscular hemoglobin concentration	31 g%	± 2	91	Mean value	
White blood cell count	40.8×10^3/mm^3	± 5.4	82	Total % of WBC	
Lymphocytes	51%	± 4	92	Total % of WBC	
Thrombocyte	39%	± 3	92	Total % of WBC	
Neutrophil	9%	± 2	92	Total % of WBC	
Basophil	<1%	±<1	92	Total % of WBC	
Blast form	<1%	±<1	92	Total % of WBC	
Mature erythrocyte					
Total	96%	± 2	92	% of RBC	
Winter	100%	±<1	37	% of RBC	
Spring	95%	± 4	55	% of RBC	
Immature red blood cell					
Total	4%	± 2	92	% of RBC	
Winter	<1%	±<1	37	% of RBC	
Spring	7%	± 4	55	% of RBC	
Clotting time	2.44 min	± 0.31		Whole blood from start of sample withdrawal	
Plasma protein concentration	5.22 g%	± 0.33			
Condition of fish (external)	2	±<1	91	Code 0-5 worst to best appearing	

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[1] Data expressed as mean ± standard error. Numbers in parentheses indicate the number of specimens used to obtain means.

[2] Highly significantly different ($P<0.0001$).

[3] Significantly different ($P<0.05$).

[4] Horton, D. B., D. W. Bridges, and J. J. Cech, Jr. 1973. First Annu. Rep. to Environ. Prot. Agency. Contract R-8003.

medium fractions (Pesch 1970). (In trout this is thought to be due to the increase in globulin antibody production as the animal is exposed to various diseases.)

Seasonal cycles in osmotic pressure of winter flounder serum and in four of eight blood characteristics (Umminger and Mahoney 1972) occur (Table 12). In winter flounder, serum osmolality was highest when they were sexually mature, which is opposite to the condition usually found in fishes.

Studies on laboratory acclimated winter flounder showed that temperatures ranging from −1° to 15°C had no effect on serum osmolality; therefore, seasonal change in serum osmolality of winter flounder in nature is probably not temperature controlled.

Pearcy (1961) found that the freezing point depression of winter flounder serum averaged more in winter than in summer. This seasonal difference was later verified by Duman and De Vries (1974) (Table 12). The possible adaptive value might be as protection against freezing in shallow water during cold weather.

3.46 Biochemistry

Brooke et al. (1962) did biochemical analyses of fish fillets and offal (bones, scales, and organs) and their seasonal variation in Gulf of Maine winter flounder (Table 13). Skeletal structure and scales are responsible for high ash in offal, and liver is important in high oil values.

The properties and composition of winter flounder oils were presented by Ackman and Ke (1968). There is some commercial value for the oil and it is sometimes used as a replacement for cod liver oil. It is chiefly notable for a low proportion of C_{22} relative to C_{20} and C_{16} (Table 14).

Table 13.—Biochemical analysis of winter flounder fillets (based on Brooke et al. 1962). Symbols: — = not related to season, * = higher than 5% confidence level, * = higher than 1% confidence level.**

	Protein (%)	Oil (%)	Ash (%)	Moisture (%)
Fillets	18.8 ± 1.5	0.15 ± 0.09	1.3 ± 0.14	79.9 ± 1.5
Offal	16.9 ± 1.6	3.20 ± 1.20	5.1 ± 0.1	74.2 ± 1.8
Seasonal variations				
Fillets	—	*	—	*
Offal	***	—	—	*

Table 14.—Properties and fatty acid compositions of commercially produced winter flounder oils (from Ackman and Ke 1968).

Oil		
Year produced:	1964(a)	1964(b)
Iodine value (Wijs):	141	150
Non-saponifiables (%):	1.14	1.03
Free fatty acid (%):	2.84	1.35
Composition in terms of major chain lengths and certain ratios of fatty acid types		
Chain length	1964(a)	1964(b)
C_{14}	5.9	6.6
C_{16}	28.3	25.4
C_{18}	22.9	23.2
C_{20}	23.8	25.5
C_{22}	15.9	15.3
% polyunsaturates		
Experimental[1]	25.3	27.2
Calculated[2]	24.9	27.6
16:0 as % of saturated	52.2	46.4
16:1 + 18:1	32.2	29.1
16:0/(16:1 + 18:1)	0.32	0.34

[1] By gas layer chromatography (GLC).

[2] From formula: % poly = 10.7 + 0.337 (oil I.V. - 100).

3.5 Behavior

3.51 Migration and local movements

McCracken (1963) has done a great deal of work on migration of winter flounder in Canadian waters and has summarized the work of Lobell (1939), Perlmutter (1947), and Merriman and Warfel (1948), showing that winter flounder make regular migrations.

During summer, mature flounders leave the shore zone in areas where temperatures rise above about 15°C but not where bottom temperatures do not reach this level. This movement toward cooler water is restricted to depths at which the temperature does not go below 12°C. Flounders return to the shore zone in fall after the temperature decreases below 15°C. In spring, immature and mature fish are both along shore with spawning fish concentrated in shallow water when the temperature warms to 3°-4°C.

North of Cape Cod flounders move deeper in winter. To the south, spawning condition is reached earlier, and mature flounders may remain in shallow water during the cold period. Figure 11 shows depth distribution by depth, age, and month of immature and mature flounders caught in Passamaquoddy Bay.

Aside from local onshore-offshore migration, results of tagging experiments have shown that the winter flounder is a stationary fish. Lobell (1939) showed summering concentrations in the Block Island region are composed of individuals from Long Island bays and sounds. Perlmutter (1947) compared fish north and south of Cape Cod and from Georges Bank meristically and found there was little intermixing. He concluded that most populations are the result of local spawning and comprise more or less discrete populations.

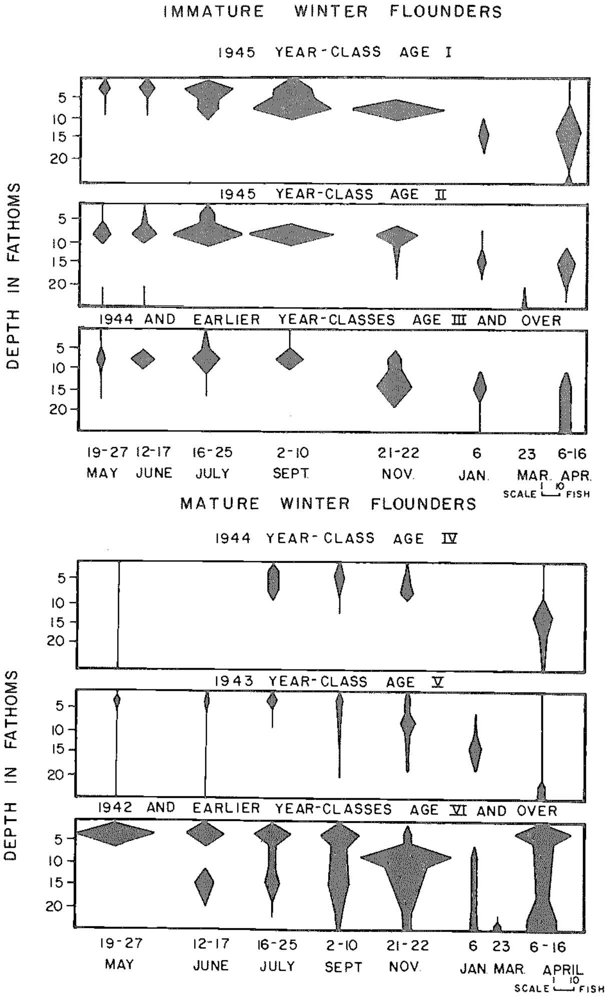

Figure 11.—Depth distribution of immature and mature winter flounder in Passamaquoddy Bay, April-May 1947, by age, month, and depth (from McCracken 1963).

Howe and Coates (1975) reported results of a 10-yr tagging study off Massachusetts. Flounder tagged at 21 locations showed the following movements: north of Cape Cod they were localized and confined to inshore waters, south of Cape Cod seasonally dispersed in a southeast direction beyond the territorial limit, and little mixing between Georges Bank and inshore area. Movements appear to be related to water temperature; they moved out when water temperatures climbed above 15°C. The steep continental shelf east of outer Cape Cod appears to limit winter flounder distribution to within 5 km of the coast.

Massachusetts Division of Marine Fisheries (1961)[10] tagging program in Quincy Bay showed that large fish ($\bar{x}$ = 350 mm TL) congregate in shoal water for spawning. As the temperature increased in summer, they dispersed

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[10] Massachusetts Division of Marine Fisheries. 1961. Annual report fiscal year July 1, 1960-June 30, 1961. Submitted by the director to the commission and Board of Natural Resources, Commonwealth of Massachusetts, 70 p.

to deeper waters. Young up to age IV remained in the harbor but moved deeper in summer. Fish 5 yr old or more (over 350 mm) tended to move out of the harbor completely in summer, and some travelled a long distance to form offshore populations.

A report (Anonymous 1964) described winter flounder populations containing a large number of abnormally pigmented individuals, all of the same age. This isolated group supports the fact that a population remains together and does not migrate.

Tyler (1972a) studied surges of winter flounder into the intertidal zone in the Passamaquoddy Bay region by means of underwater television. He found that they entered the intertidal zone with the rising tide. Peak movement occurred 2.0-2.5 h after low tide and fell off 3.5 h after the tide began to rise. Flounder occupied the area for 0-8 h then surged back to the sublittoral 2.5-0.5 h before the next low tide. Small (40-150 mm) and large (250-490 mm) flounders moved with the same synchrony but small ones tended to make short movements up and down the beach with net movement away from shore when the tide is falling, while large ones were more strictly directional. Intermediate sized flounder were absent from the intertidal region. He suggested that the adaptive value of this movement is that the intertidal zone is a good feeding area.

Saila (1961) conducted tagging experiments at Green Hill Pond, Charlestown, R.I., in an attempt to explain return of winter flounder to coastal breeding grounds on the basis of a model for diasporic nonoriented migration (a reassembly of animals dispersed over a strip of ocean bounded on one side by a straight coast running east-west and on the other by a reflecting barrier, the 20-fathom depth contour, beyond which no tagged fish were recaptured). The results showed flounder return to the same area to spawn each year. Approximately 75% returns to shore were achieved after 90 days of searching with a maximum strip width of 15 mi. If the barrier is 10 mi, the probability is 90% return after 90 days. This time period was within the time flounder were observed to enter Green Hill Pond and is less than the observed breeding season; therefore, diasporic migration with no assumptions about orientation to outside stimuli seems a reasonable explanation for movement back to the coast.

3.52 Schooling

Winter flounder do not school.

3.53 Response to stimuli

Response to light may affect depth distribution. McCracken (1963) showed from evidence in the laboratory and distribution of fish in Passamaquoddy Bay, that immature flounder of intermediate size perferred lower light intensities than mature or small immature flounder, and suggested that behavior in relation to light may change at sexual maturity.

Pearcy (1962a) found that small 0 group flounder are least photonegative and that age group I, during summer, showed a photonegative response. He thought light intensity might be another factor which is related to movement of young fish out of the shoals in fall and winter, or to differences in vertical distribution.

Sullivan (1915) found larvae strongly phototactic.

Olla et al. (1969) found a relationship between ambient temperature and activity. Divers observed flounder in Great South Bay, Long Island. Bottom temperatures ranged from 17.2° to 24.0°C. Flounders were active up to 22.2°C, but became inactive at higher temperatures with heads resting on the bottom. At 23°C all flounders found at 1100 h were buried in the sand with only their eyes protruding. Temperatures 50-60 mm below the sand surface were 19.8°-20.0°C, even in the shallowest part of the basin. Flounder evidently avoid high temperatures by burying themselves in the sand.

Radle (1971) showed that high temperatures near thermal effluent from a power plant in Indian River Bay, Del., estuary inhibited feeding of juvenile flounder. Those collected from stations with bottom temperatures 26.5°-27.0°C had less full stomachs than flounder from those stations with lower temperatures. Flounder from stations with temperatures 27.0°-27.5°C were not feeding at all.

Sherwood and Edwards (1901) observed a sudden fall in water temperature at Great Harbor and Waquoit Bay (Cape Cod region) on 23 February 1900 from 1° to −2.7°C. The flounder then disappeared from the harbor and none were taken again until 6 March when the water temperature rose to 0°C again.

Beamish (1966) tested swimming endurance of winter flounder at different temperatures against currents of different velocities (Table 15). Endurance was measured as the time a fish maintained its position against a current of known velocity.

Davis and Bardach (1965) reported on prefeeding activities of some marine fishes which had been conditioned to feed at certain time of day shortly after the start of their light period. After acclimation, most fishes increased locomotion 1-3 h before feeding. Trials with winter flounder showed that they did not exhibit this response, even after having been conditioned to feed at one particular time for over 23 days.

Table 15.—Swimming endurance of winter flounder at different current velocities (from Beamish 1966).

Temp. tested (°C)	Swimming speed (cm/s)	Endurance ± SE (min)
14	75	25.4 ± 3.3
	135	5.3 ± 1.2
11	75	10.0 ± 1.2
	105	3.2 ± 0.4
	135	1.4 ± 0.2
8	75	10.3 ± 1.0
	105	5.8 ± 0.7
	135	1.7 ± 0.2
5	75	14.1 ± 1.5
	105	5.8 ± 0.6
	135	1.9 ± 0.3

Sutterlin (1975) tested the attractiveness of 25 different chemical compounds to winter flounder by releasing seawater solutions of the compounds (10^{-3} molar concentration) through a plastic delivery tube in an area in front of the Biological Station in St. Andrews, New Brunswick, where winter flounder feed. Behavior of the flounder upon exposure to these compounds was monitored by an underwater television camera and the observers comments recorded on tape. Glycine was the most effective compound tested followed by alanine, methionine, asparagine, cysteine, glutamic acid, and leucine to a lesser extent. No amines or amino alcohols tested were attractants to flounder. During the fall the flounders were not attracted to any of the chemicals, probably as a result of behavioral or physiological states. Attraction was manifested by the fish circling the delivery tube, picking up pieces of clam shell and ejecting them, making digging undulations, or snapping at the spout.

Huntsman and Sparks (1924) studied temperature resistance ability of winter flounder of different sizes. They found that lethal temperature varied with age. Although differences were not great, there was an increase in susceptibility to high temperature with increase in size (100-200 mm, 29.1°-30.4°C; 200-300 mm, 27.8°-29.8°C).

Battle (1926) studied the effects of heat stress on the loss of functional activity in the muscle tissue of large and small winter flounder. She found in both large and small individuals: 1) an automatic mechanism of the heart was lost first, 2) cessation of propagated wave in the heart and peristalsis in smooth muscle of the stomach and ilium occurred second, and 3) finally, loss of functional activity upon electrical stimulation, in order, of somatic muscle, smooth muscle, and cardiac muscle.

Hoff and Westman (1966) calculated temperature tolerance of winter flounder by calculating median tolerance limits for various exposure times over a range of acclimation temperatures, and plotting lethal temperatures against acclimation temperature: cold limits 0°-1°C; heat 29.3°C total lethal maximum (TLM) at 48 h.

The behavior of fish when transferred from the acclimation tank to the high temperature tank was: 1) increase in general activity, 2) disturbances in equilibrium, and 3) increased respiratory movement. The behavior of fish transferred to cold temperature was: 1) loss of equilibrium, 2) initial increase in respiratory movements, and 3) violent convulsive spurts and spasms. Winter flounder frequently recovered from cold shock but never from heat shock.

Duman and De Vries (1974) examined freezing-melting point behavior of serum from winter flounder collected in St. Margaret's Bay, Nova Scotia, to determine the mechanism of freezing resistance. Freezing-melting points were determined by a capillary technique. For a NaCl solution the temperatures of freezing and melting points were within 0.02°C of each other. Winter flounder serum collected in March had widely separated freezing and melting points (thermal hysteresis). Serum collected in August did not show this property (Table 12). The serum of an Antarctic fish (*Trematomous borchgrevink*) has an unusually low freezing point because a group of glycoproteins act as an antifreeze. Winter flounder serum was examined to see if such compounds were responsible for the low winter freezing point since increased NaCl could only account for 58% of the serum freezing point depression. The antifreeze compound was associated with the colloidal portion of serum. It was stable at a temperature of 100°C, soluble in 10% trichloracetic acid, and had a molecular weight greater than 3,500 daltons. The mechanism of action of the compounds was similar to that of glycoproteins of the Antarctic fish; however, results of gel electrophoresis and amino acid analysis indicated they were not the same chemically.

4 POPULATION

4.1 Structure

4.11 Sex ratio (Table 16)

Table 16.—Sex ratio of winter flounder.

Sex ratio ♀ : ♂	Area of Capture	Number of fish	Source
7:3	Green Hill Pond, Charlestown, R.I.	601	Saila (1962a)
3:2	Narragansett Bay, R.I.	940	Saila (1962b)
3:1	Fishing grounds south of Rhode Island and Mass.	2,118	Lux (1969)
1:1	Long Pond, Newfoundland	227	Kennedy and Steele (1971)
1:1	Mystic River, Mass.		Haedrich and Haedrich (1974)
2.3:1	Massachusetts	12,151	Howe and Coates (1975)

Saila (1962a, b) compared sex ratios of fish in Narragansett Bay, R.I., with those from Charlestown Pond, R.I., and concluded that the higher proportion of females was due to catch selectivity for larger fish, since females were considerably larger and market preference is for large fish.

4.12 Age composition

Age composition has been studied by a number of authors based on analysis of otoliths (Table 17).

4.13 Size composition

Numerous authors have presented data on length frequencies of winter flounder from different areas. One of the most extensive works was done on the Canadian Atlantic area by Kohler et al.[11] This work is too long to con-

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[11] Kohler, A. C., D. N. Fitzgerald, R. G. Halliday, J. S. Scott, and A. V. Tyler. 1970. Length weight relationships of marine fishes of the Canadian Atlantic region. Fish. Res. Board Can., Tech. Rep. 16, 199 p.

Table 17.—Calculated age distribution of winter flounder population.

Age	Saila et al. (1965) Charlestown Pond		Narragansett Bay		Poole (1966b) Long Island bays Great South	Moriches	Shinnecock	Peconic	Dickie and McCracken (1955) St. Marys Bay, N.S. 1948-53	Kennedy and Steele (1971) Newfoundland Nov. Dec.	Mar.	Apr.	May-June	July	Sept.-Oct.
I	0	1	56	89	3	1	0	2							
II	15	78	159	199	29	50	22	26					1%		
III	95	236	211	316	126	69	98	54	42				5%	6%	4%
IV	100	241	171	312	82	77	99	86	110	18%	18%		12%	17%	2%
V	45	82	110	128	17	35	38	62	137	19%	45%		20%	25%	16%
VI	16	25	25	37	5	7	3	11	136	22%	28%	2%	12%	23%	22%
VII	4	7	13	27	0	1	0	2	103	17%	5%	10%	23%	4%	18%
VIII	1	5	1	12					68	15%	2%	10%	13%	4%	23%
IX	12(9+)	8(9+1)	14	26					41	14%	2%	45%	5%	15%	12%
X									14			30%	4%	5%	1%
X									14	2%		3%	6%	1%	1%
										Σ(76)	(35)	(27)	(179)	(49)	(66)

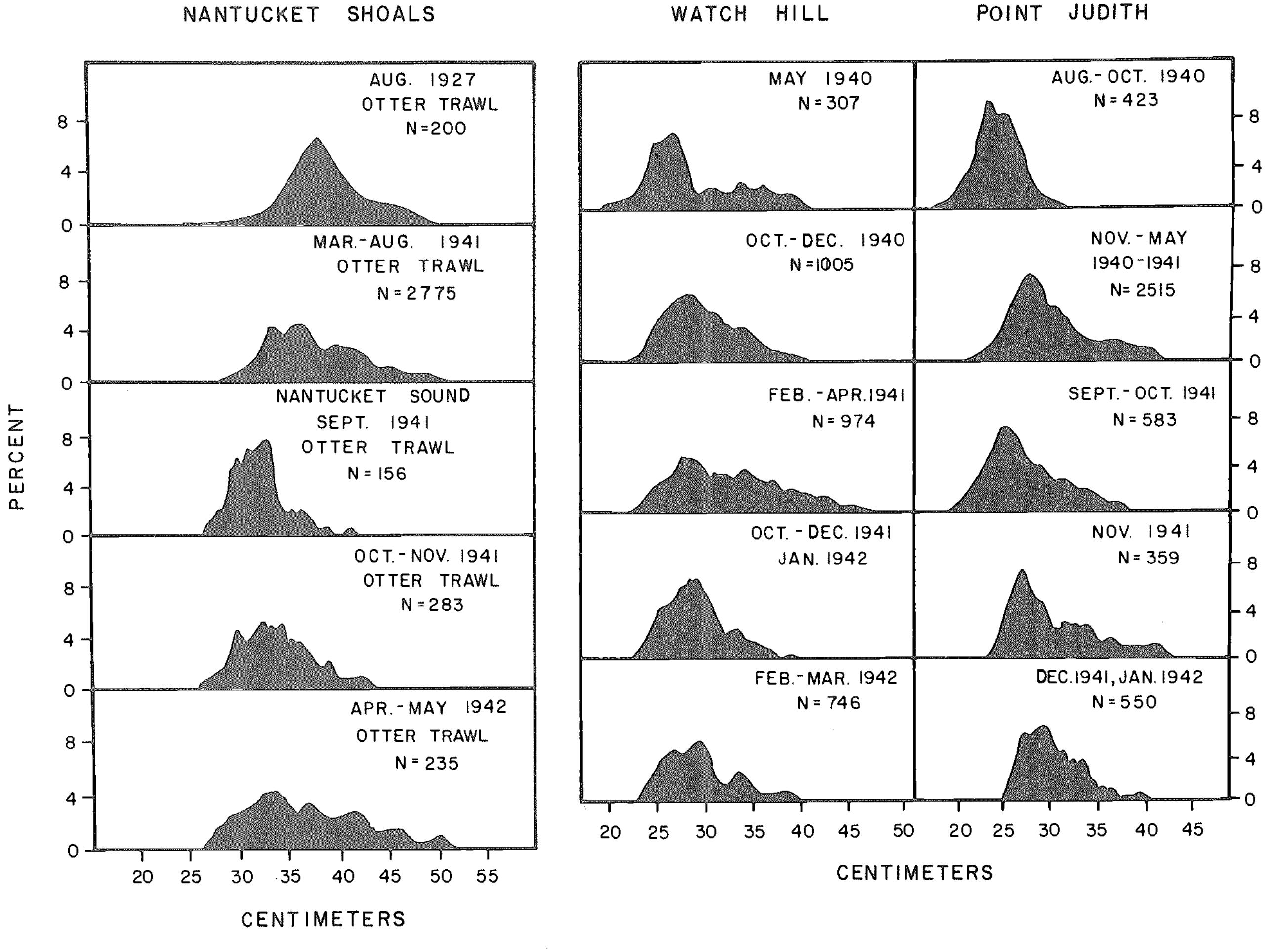

Figure 12.—Size composition of winter flounder from Nantucket Shoals, Watch Hill, and Point Judith, R.I. Data smoothed by moving average of threes (from Perlmutter 1947).

dense; therefore, interested readers should consult the original reference. Other work has been done by Perlmutter (1947) (Fig. 12), de Sylva et al. (see footnote 3), Lux (1969), Tyler (1972a), and Kennedy and Steele (1971) (Fig. 13). Changes in length composition with depth were calculated by McCracken (1963) and are also discussed under sections 2.2, 2.3, and 3.1 (Fig. 14).

4.2 Abundance and density

4.21 Average abundance

The results of authors who estimated average abundance of winter flounder are summarized in Table 18.

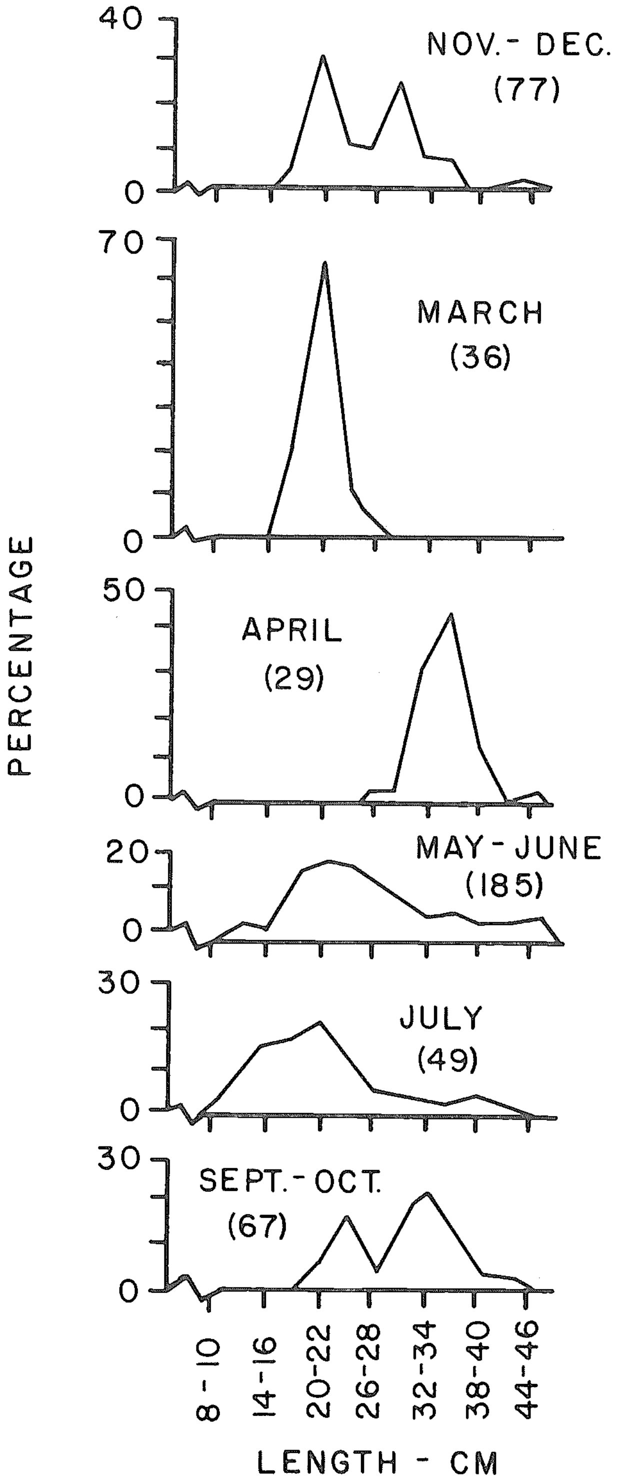

Figure 13.—Size composition of winter flounder from Newfoundland (from Kennedy and Steele 1971).

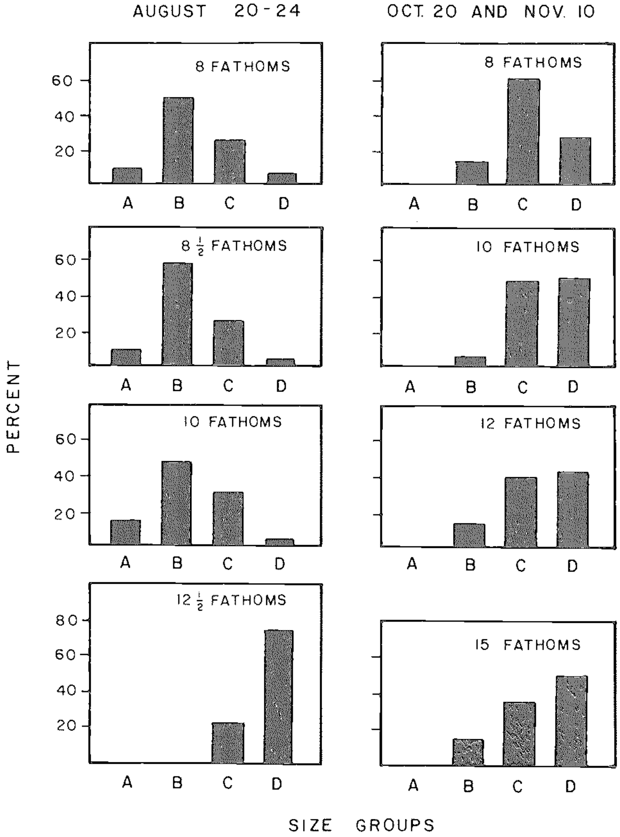

Figure 14.—Changes in length composition with depth of winter flounder in Northumberland Strait. Size groups are: A = 10-19 cm; B = 20-24 cm; C = 25-29 cm; and D = 30 cm and over. (From McCracken 1963.)

Oviatt and Nixon (1973) determined by multiple regression analyses of fish numbers and biomass on 14 environmental variables that only temperature and depth were factors influencing winter flounder abundance. This is a reflection of tendency for fish to move out of the shallow waters as temperature warms in summer and back in as the water cools in winter.

Jeffries and Johnson (1974) reported on 7-yr variations in winter flounder abundance in Narragansett Bay. The relative abundance appeared to be associated with climatic trends but not with fishing pressure, but the annual abundance in the bay is reflected 2 to 3 yr later in the commercial catch. A major reduction in abundance of winter flounder was statistically related to a seemingly insignificant trend of temperature increase. Increased average temperatures in April were associated with a decrease in future catch, the 2- to 3-yr lag being almost equal to the period required for flounder to grow from larvae to catchable size. Jeffries and Johnson (1974) suggested that the chief effect of the temperature increase might be to hasten metamorphosis which takes place in April. This would cause the flounder to leave the plankton earlier and thereby encounter a set of predators qualitatively or quantitatively different from those experienced by juvenile flounders of previous years. When a small change in the physical environment occurs over a period of several generations there is a much greater set of consequences resulting than would be predicted from physiological tolerances of each species involved.

Table 18.—Average density estimates of winter flounder.

Area	Life stage	Density estimate			Author
Narragansett Bay	Larvae	0.0068/m³			Herman (1963)
Long Pond, Newfoundland	Adults	14.9 catch/man-h			Kennedy and Steele (1971)
Narragansett Bay	Larvae	$\bar{x}$ = 54.09/100 m³ Range (11.1-107.1)			Marine Res. Inc. (1974)[1]
Mystic River, Boston, Mass.	Adults	Mar.	153/ha	15,300/km²	Haedrich and Haedrich (1974)
		June	37/ha	300/km²	
		Aug.	180/ha	18,000/km²	
		Nov.	368/ha	36,800/km²	
Delaware, Indian River	Adults	241,776			Radle (1971)
Cape Cod Canal	Eggs	Mar.-1 June		0.450/m³	Fairbanks et al. (1971)
	Larvae	Mar.-May		0.035/m³	
Buzzards Bay	Eggs	Feb.-May		0.074/m³	
	Larvae	Mar.-June		0.113/m³	

[1] Marine Research Inc. 1974. 19th Rome Point Investigations, Narragansett Bay Ichthyoplankton Survey Final Report to the Narragansett Electric Company.

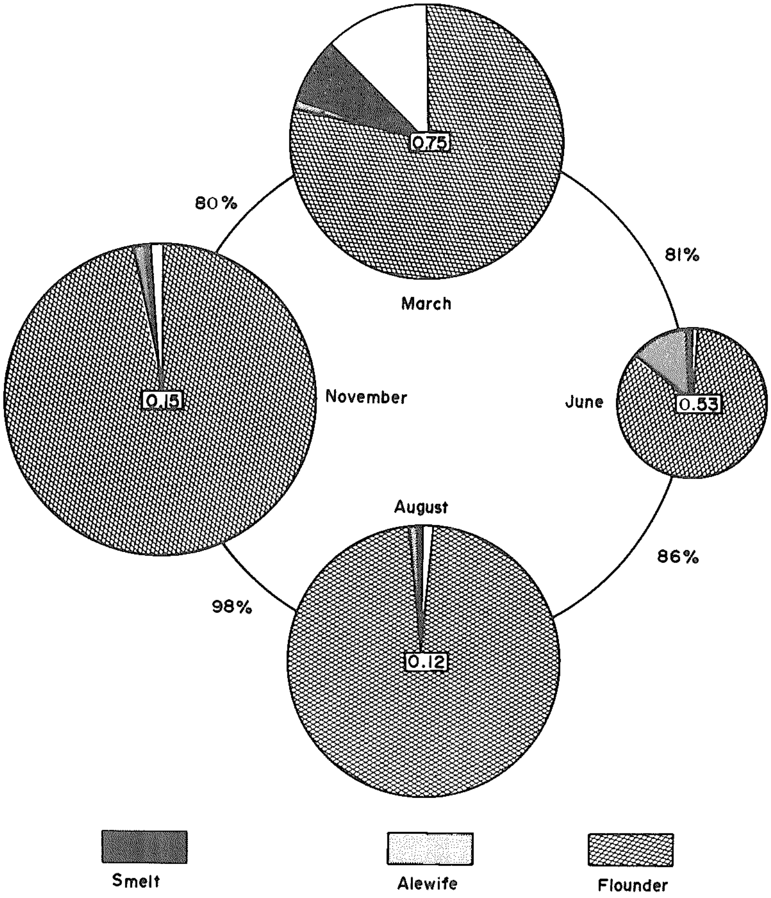

Figure 15.—Annual cycle of fish biomass in Mystic River, Mass. (from Haedrich and Haedrich 1974).

4.22 Changes in abundance

Seasonal abundance varies for reasons discussed in sections 2.2, 2.3, and 3.5.

4.23 Density

Greatest density of eggs occurs in February and March, of larvae in April and May, and of adults in winter and spring (Table 18).

4.24 Changes in density

Haedrich and Haedrich (1974) (Fig. 15), Oviatt and Nixon (1973) (Fig. 16) and Pearcy (1962a) (Fig. 17) calculated seasonal changes in density of flounder populations in the Mystic River, Mass., Narragansett Bay, and Mystic River, Conn., respectively.

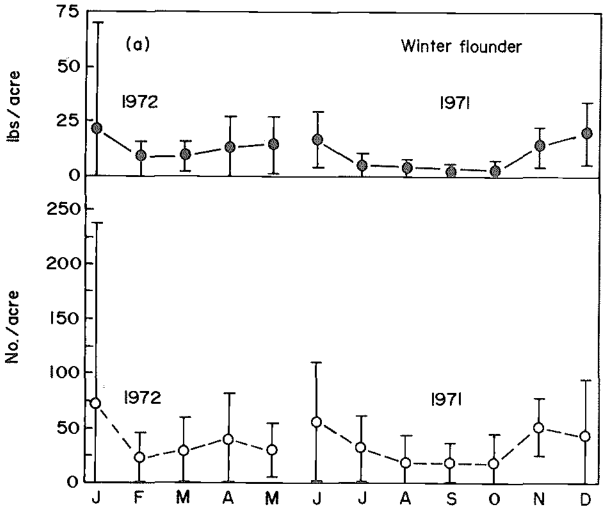

Figure 16.—Biomass and numbers of winter flounder in Narragansett Bay (from Oviatt and Nixon 1973).

4.3 Natality and recruitment

4.31 Reproduction rates

See section 3.1.

Survival rates—Figure 18 is a survival curve for larval and juvenile winter flounder from Pearcy (1962a).

4.32 Factors affecting reproduction

Tyler and Dunn (1976) studied growth and measures of somatic and organ condition in relation to meal frequency. Six ration levels were established by feeding fish a mixed diet of whole chopped clams and beef liver cubes at the following frequencies: one meal per day, one meal every other day, every 4th day, every 8th day, every 16th day, no food. The testing period was July through December. Food was supplied in excess of quantities eaten at each meal, water temperature was 7°C. Decrease in feeding frequencies resulted in increase in food consumption per meal but less food consumption per month. At two meals per month, fish did not eat more per meal.

The maintenance ration was 7.9 cal/g per day. Weight loss during starvation equalled 2.14-2.05 g cal/g per day. Gross conversion efficiency ranged from 1 to 16% and was positively correlated with ration. Net conversion efficiency averaged 24.3% and was not related to ration. Condition, liver weight, percent fat in the liver, and percent ovarian follicles with yolk were positively cor-

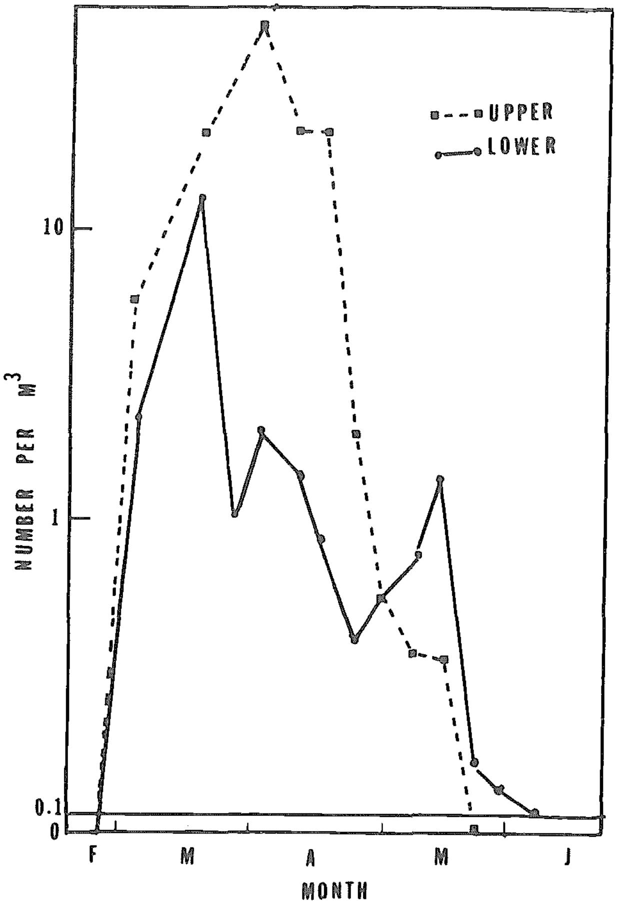

Figure 17.—Average density of flounder in Mystic River, Conn. (from Pearcy 1962a).

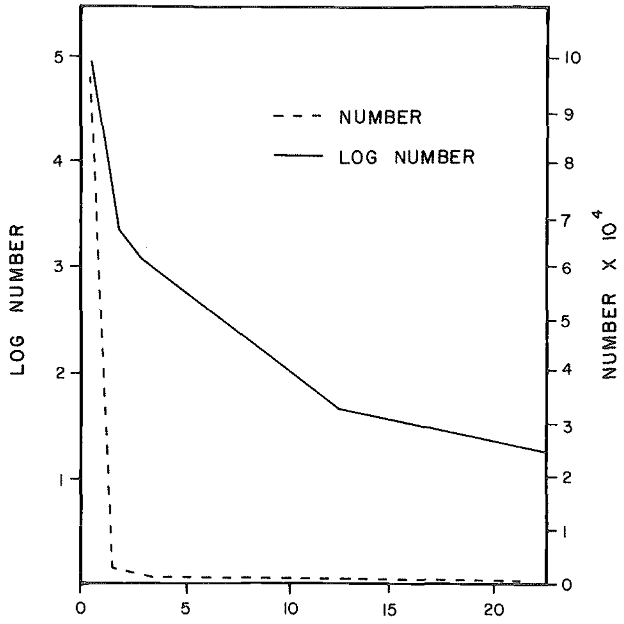

Figure 18.—Survival curve for larval and juvenile winter flounder, Mystic River estuary, Conn. (from Pearcy 1962a).

related with mean calories consumed per day. The smaller proportion of oocytes with yolk in fish with decreased rations was due to the decrease in the numbers of oocytes starting vitellogenesis. The field population from Passamoquoddy Bay, N.B., showed the same negative correlation between condition index and percent oocytes not undergoing vitellogenesis. This indicated that field fish were not getting all the food they could use, and the adaptive reproductive strategy in the face of the lack of food was to sacrifice egg production and maintain body weight so that when a good year came their bodies would be large and able to carry a large ovary.

4.33 Recruitment

Age or length at which flounders are recruited into the fishery varies. Briggs (1965) calculated sports fishery recruitment at 200 mm TL for South Shore bays, Long Island, and 260 mm TL for Gardeners and Peconic Bays. Dickie and McCracken (1955) gave commercial fishery data for St. Marys Bay, Nova Scotia, 3-4 yr, 363 g. Perlmutter (1947) reported commercial and sport data for Long Island and New York, 180-200 mm, and Watch Hill and Point Judith, R.I., 170-220 mm. Saila et al. (1965) gave commercial data for Narragansett Bay and offshore waters in Rhode Island: 18 mo (first entry) age III fully recruited and 250 mm. Factors influencing recruitment were size selection by fishermen, differences in depth distribution with age, mesh size of fishing net, and market preferences.

See also section 4.5.

4.4 Mortality and morbidity

4.41 Mortality rates

Pearcy (1962a) estimated loss rate for small larvae in a Connecticut estuary as 20%/day compared with 4%/day for postlarvae. Juvenile mortality rates were 0.31/mo for age 0 and 0.084/mo for age I. Total mortality during larval and juvenile stages is approximately 99.98-99.99% (Table 19).

A summary of mortality rate values for adult winter flounder calculated by several authors is presented in Table 20.

Table 19.—Provisional life table for larval and juvenile stages of winter flounder (from Pearcy 1962a).

	Age in months	Survivors	Numbers dying	Mortality rate × 100
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

4.42 Factors causing or affecting mortality

Pearcy (1962a) found that the most important factors affecting mortality of larvae were translocation and natural mortality. Translocation out of the estuary by seaward drift was significant and though little is known of the fate of these larvae, conditions were surmised to be more unfavorable offshore for larvae because of lack of suitable food. Predation was also thought to be the major cause of juvenile and larval mortality. There was no indication of accelerated mortality during the period of metamorphosis for the winter flounder (see Table 19) as mortality rates on a percentage basis were about the same. Mortality rates decreased with age. The average monthly survival rate for age group 0 was about 69%; for age group I it was 92% (Fig. 18).

Dickie and McCracken (1955) found that the leading cause of natural mortality of adult flounder in Passamaquoddy Bay was predation. The winter period was the most dangerous as 30% of the mortality occurred from November to April.

Table 20.—Summary of mortality rate data of winter flounder.

Natural mortality rate	Fishing mortality	Total annual mortality	Geographic location	Year	Source
0.54	0.24	0.78	Long Island Sound & bays	1937	Perlmutter (1947)
0.33	0.43	0.76	Long Island Sound & bays		Figures calculated by Poole
	(instantaneous rate)				
0.321	0.475		St. Marys Bay, Nova Scotia	1949-50	Dickie and McCracken (1955)
0.296	0.272		St. Marys Bay, Nova Scotia	1952-53	
	Males	Females			
	0.56	0.65	Charlestown Pond, R.I.		Saila et al. (1965)
	0.51	0.58	Narragansett Bay		
0.50	0.22	0.72	Great South Bay, N.Y.	1964	Poole (1969)
0.52	0.21	0.73	Great South Bay, N.Y.	1965	
0.52	0.20	0.72	Great South Bay, N.Y.	1966	
	(instantaneous rate)				
0.273	0.271	0.474	South of Cape Cod	1964-66	Howe and Coates (1975)

4.5 Dynamics of the population as a whole

Dickie and McCracken (1955) analyzed a population of winter flounder in St. Marys Bay, western Nova Scotia, where a commercial flounder fishery began in 1948. This fishery showed a rapid rise in landings, a subsequent drop, and a stabilization as the catch appeared to reach a state of balance with production. Formulas used to calculate yield isopleth diagrams are:

Growth

$$W_{t-t_0} = W\infty\,(1 - \exp[-k\,(t - t_0)\,]^3$$

where W = weight in pounds
$W\infty$ = upper asymptote of growth curve (2.43)
k = slope (0.40)
t = any age in years
t_0 = time when length theoretically is 0.

Values obtained

$$W_{t-t_0} = 2.38\,(1 - \exp[\ -0.39(t - t_0)\,]\,)^3.$$

Initial population size

$$P = Y/\mu$$

where P = population size
Y = catch (weight in pounds)
μ = rate of exploitation.

Yield equation

$$Y_w = FRW\infty \exp[-M\,(t_{p'} - t_p\,)\,]\sum_{n=0}^{3}\frac{\Omega n \exp[-nK(t - t_0)\,]}{F+M+nK}$$

$$\cdot \left(1 - \exp[-(F+M+nK(t_\lambda - t_{p'})\,)\,]\,\right)$$

where $\Omega_0 = +1, \Omega_1 = -3, \Omega_2 = +3, \Omega_3 = -1$
F = instantaneous fishing mortality rate (0.251)
R = recruitment (1,000,000 fish/yr)
M = instantaneous mortality coefficient (0.36)
$t_{p'}$ = age of recruitment (3.0 yr)
t_λ = maximum age by which time all flounders die (18 yr)
K = growth coefficient.

The yield-isopleth diagram (Fig. 19) represented the situation believed to be closest to that of St. Marys Bay fishery. The sustained annual yield of over 0.5 million pounds predicted by the model agrees with the observed total landings for the past 3 yr. The model showed that catches will increase only if flounders are captured at smaller sizes and fished harder than at present. Therefore, there was little basis for restrictive regulation of the fishery as this would tend to lower the annual yield. Total fishing effort in the bay was limited by returns per unit effort. Therefore, St. Marys Bay flounder fishery is probably realizing the maximum sustained yield possible under present market conditions.

Saila et al. (1965) utilized available data on winter flounder vital statistics to get a preliminary theoretical estimate of the size of a population of juvenile winter flounder necessary to sustain or increase the yield of a commercial fishery for the species in Rhode Island Sound. Equations used to estimate equilibrium yield are:

$$Y_E = \overset{T=T}{\underset{T=T_r}{}}\ \frac{F_T P_{T(0)}\,(1 + \exp[g - ZT])}{2}$$

Y_E = equilibrium yield
T = successive intervals or periods in the life of the fish
T_r = the first period under consideration
T = the last period under consideration
F = instantaneous rate of fishing mortality
Z = instantaneous rate of total mortality
g = instantaneous rate of growth in weight.

Coefficient values were derived from the data of Saila et al. (1965) and Pearcy (1962a). Fishing mortality was calculated on the basis of Rhode Island trawl landings for a 10-yr period. Figure 20 illustrates three surfaces representing the stock weights (in grams) of winter flounder at 5 mo of age necessary to produce an equilibrium yield of approximately 2 million pounds. The lowest surface uses a conservative estimate of Z, the middle surface an average value, and the upper surface a slightly higher one.

The stock weight of newly metamorphosed juveniles necessary to sustain the empirical average yield under average mortality coefficients for all life history stages was 6.5×10^6g or 1.8×10^{10} individuals. The stock weight of juvenile flounder at an age of 5 mo was a significant proportion of the equilibrium yield. Growth appeared to be very rapid during the early life history stages and this provided for a significant early increase in biomass over and above the amount removed by natural mortality. The effect of natural mortality is more significant than the fishing mortality, and research on increasing the basic productivity of nursery areas would have a high probability of success in terms of improving the fishery.

4.6 The population in the community and the ecosystem

Dexter (1944) classified the winter flounder as a dominant which exerts control over the *Strongylocentrotus-Buccinum* community by occupying and holding space. The community extends from spring low water to a depth of about 27 m and latitudinally from the northern part of Cape Cod to the boundary of the cold Labrador Current off the coast of Maine. It is characterized by echinoderms, large gastropods, skates, sculpins, flounders, and decapod crustaceans.

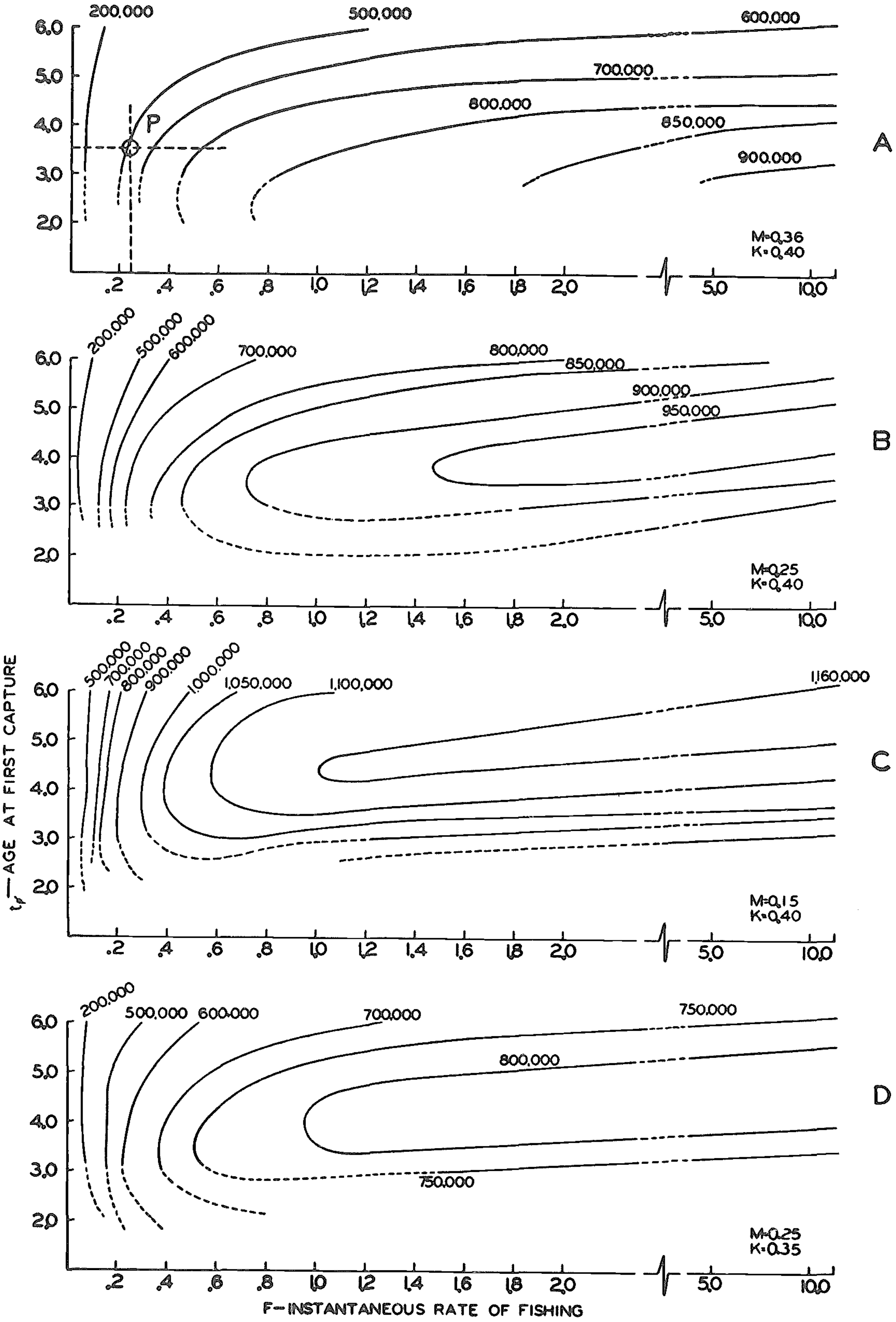

Figure 19.—Yield isopleth diagrams for the St. Marys Bay flounder fishery (from Dickie and McCracken 1955).

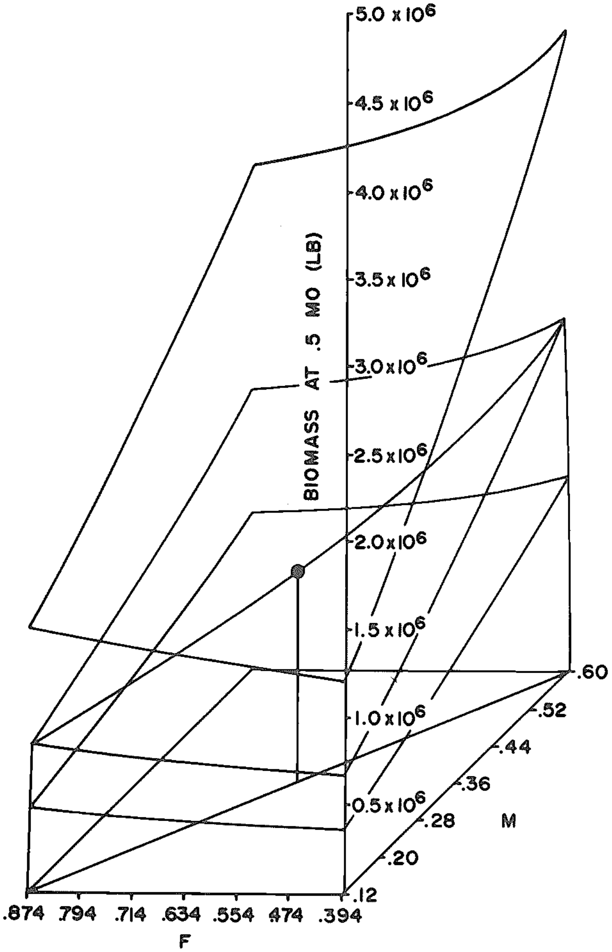

Figure 20.—Stock weights of winter flounder at age 5 mo required to produce an equilibrium yield of approximately 2 million pounds for three values of Z for the first 5 mo. Lowest surface, Z = 1.655; middle surface, Z = 1.855; and upper surface, Z = 2.055. (From Saila et al. 1965.)

Richards (1963) analyzed the demersal fish population of Long Island Sound from a sand-shell bottom and a mud bottom. The 10 most common species (of 37 species, 3,949 individuals) constituted 93% of the total standing crop. The winter flounder was the most abundant species composing 67% of the standing crop in both bottom types. There were two groups of species, residents and migrants. The chief residents besides winter flounder were the windowpane, *Scophthalmus aquosus*, and the hake, *Merluccius bilinearis*. The chief migrant was the scup, *Stenotomus chrysops*. In general, fishes were more abundant in fall, decreased early in winter, increased in late winter, and reached a low in summer.

The sand-shell station was characterized by a high percentage of sand and gravel. It was occupied by a biomass of epifauna five times that of infauna of which the epifauna dominates the diets of prey species. Winter flounder dependence on polychaetes separated it from most other predators, and its omnivorous tendencies precluded extensive competition. Immigration of migratory predators increased chances for interspecific competition, but this was kept to a minimum (except for *S. aquosus*) by the abundant and well distributed food resources and absence of territoriality among the predators. The community was heterogeneous. Juvenile production was 0.06 g/m^2 per year. Trophic level conversion figures based on consumption of epi- and infauna showed infauna productivity was sufficient to support the species without additional epifauna but efficiency of food conversion was low, and it did not appear to make maximum use of available food (Richards 1963).

Tyler (1971) described periodic and resident components of a northern Atlantic fish community located in Passamaquoddy Bay, New Brunswick. Temperature ranges for this area were 1.2°-10.1°C, salinity 29.5-22.3°/oo. The bottom was sloping, 38-55 m in depth, and covered with brown mud. Tyler concluded that in temperate regions, inshore deepwater fish communities are made up of three groups of species—one present during winter only, one during summer only, and a third throughout the year. The winter flounder was one of the most numerous members of the resident community. The population exhibited seasonal fluctuations in abundance related to spawning time, the maximum occurred in April and May. Tyler believed formation of temporal groups was mainly related to temperature regime, the greater the annual temperature fluctuation the more species in the temporal and the less in the regular component. Thus community stability was directly related to temperature stability. This was a food limited production system (Tyler 1972b) and there was, in general, overlap in diets of the principal species of the community. The principal prey of the year-round residents were the same during the summer and winter except that four additional prey species were taken in summer. When winter seasonal species emigrated, the prey species were exploited by summer and year-round residents. When summer seasonals left, the principal species unique to them were unexploited.

Derickson and Price (1973) studied the shore zone of Rehoboth and Indian River Bays, Delaware River. They collected 46 species and 41,286 individuals. The five most ecologically important species in order of abundance were *Fundulus majalis*, *Menidia menidia*, *Fundulus heteroclitus*, *Pseudopleuronectes americanus*, and *Anchoa mitchilli*. Combined average biomass estimates for the five species were 5,500 kg/km^2 and 2,800 kg/km^2 for Rehoboth Bay in 1968 and 1969, respectively, and 7,600 kg/km^2 and 3,700 kg/km^2 for Indian River Bay in 1968 and 1969, respectively. Greatest species diversity and abundance occurred in summer, probably because the bays were used as a nursery and feeding grounds. The numbers of individuals and species showed a direct relationship to seasonal temperature. Winter flounder abundance showed no relationship to substrate type, vegetation, and water current velocity, but water depth and temperature were important to various life stages of flounder.

Oviatt and Nixon (1973) described the community structure in Narragansett Bay. The 10 most important species made up 91% of the catch (Table 21). Winter flounder was the most abundant species. There was no clear pattern of fish abundance except for higher diversity at the mouth of the bay. Bay characteristics were: relatively unpolluted, covers 259 km^2, has a small salinity range (24-30‰), temperature range from −0.5° to 25°C, weak seasonal stratification, and depths up to 40 m. East Passage is deeper than West Passage. Both were dominated by fine sediments with sand present at the mouth of the Bay and upper West Passage. The only year-round residents of the Bay were winter flounder and sand dab (windowpane). Scup, butterfish, weakfish, and sea robin were summer species only; winter species were sea herring, blue back herring, tom cod, and sculpin. The total species diversity expressed as the Shannon Weiner Index was 3.22. The high was in October and the low in January which is opposite to tnat reported by McErlean et al. (1973) for Chesapeake Bay.

Table 21.—**Important fish species by number and percent of two ecosystems. Species rank for 101 trawls at regular stations throughout the year.**

Common name	Scientific name	Percent of total	Total number
	Narragansett Bay, R.I.[1]		
Winter flounder	*Pseudopleuronectes americanus*	36	3,361
Windowpane	*Scophthalmus aquosus*	14	1,287
Scup	*Stenotomus chrysops*	10	915
Butterfish	*Peprilus triacanthus*	9	871
Weakfish	*Cynoscion regalis*	8	718
Northern sea robin	*Prionotus carolinus*	6	563
Red hake	*Urophycis chuss*	3	272
Barred sea robin	*Prionotus martis*	2	186
Cunner	*Tautogolabrus adspersus*	2	179
Little skate	*Raja erinacea*	1	126
	Mystic River estuary, Mass.[2]		
Winter flounder	*Pseudopleuronectes americanus*	53	1,465
Rainbow smelt	*Osmerus mordax*	32	890
Alewife	*Alosa pseudoharengus*	7.6	186
Atlantic herring	*Clupea harengus*	5.9	163
Atlantic menhaden	*Brevoortia tyrannus*	0.9	27
Blueback herring	*Alosa aestivalis*	0.7	19
Ocean pout	*Macrozoarces americanus*	> 0.1	4
Grubby	*Myoxocephalus aenaeus*	> 0.1	3
Cunner	*Tautogolabrus adspersus*	> 0.1	3
Atlantic mackerel	*Scomber scombrus*	> 0.1	3

[1] Oviatt and Nixon (1973).
[2] Haedrich and Haedrich (1974).

The winter flounder population was not aggregated ($K = 1$) and the maximum K value (a measure of aggregation) of 7.3 occurred in the fall. There was little difference in seasonal means (spring 8,151/km^2, summer 6,669/km^2, fall 7,163/km^2, and winter 11,856/km^2). Trophic relationships were such that the two major species, winter flounder and windowpane, did not compete for food. The mean annual biomass of demersal fishes was 31,876 kg/m^2. Although the abundance of demersal fishes was small with respect to other parts of the system, they might be important in regulating diversity and abundance of other members of the benthos.

Haedrich and Haedrich (1974) surveyed fishes in the Mystic River estuary, Mass. It is a mixed, almost homogeneous estuary with a tide range of 2-4 m, salinity 29-32‰, and temperature 5°-18°C (bottom 3°-14°C). The lower 2 km of the estuary has been dredged. A power plant was located on the upper end of this stretch; heating effects are minimal, but discharge may be 10° higher than the intake temperature. The midstream temperature of water near the plant was rarely higher than 1° of that downstream. The estuary was highly polluted: DO 1-6.8 ppm but generally less than 50% saturated, pH 6.5-8.0 with a high concentration of organic nutrient, and coliform counts in concentrations as high as 30,000 cells/100 ml. Oily residues and hydrogen sulfide were present in the sediments. A benthic community analysis showed very low diversity dominated by the polychaete, *Capitella capitata*, a pollution indicator organism. Total number of fishes caught was 2,778 of 23 species; total weight was 1,631 kg. The 10 most abundant species are given in Table 21. This assemblage was similar to other northern fish communities with periodic and resident species; the winter flounder was a resident, completing its entire life cycle in the estuary. Catch rates for the estuary were lowest in June by numbers and weight and increased, thereafter, throughout the year. The mean rate of biomass caught was 24 kg/h or 2 g fish/m^2. Diversity in numbers was at its highest in June and lowest in August; species diversity was greatest in November (see Fig. 15).

Biomass diversity indicates complexity of energetic relations in the food web; in this estuary, diversity was low and winter flounder were major channels of energy flow at the fish trophic level. The community had a dynamic period from November to August and a static one from summer to early winter. Food competition between major species was not likely as the three major fish species have very different food habits. They do not compete for space and the breeding time is different for all three species. Pooled annual diversity, a measure of community structure designated H, was 1.19 on numbers and 0.71 on weight. These values were low, but close to those obtained by McErlean et al. (1973) from the Patuxent River, Md.; suggesting this diversity level might be characteristic of temperate estuaries.

5 FISHING

5.1 Fishing equipment

5.11 Gears

The most common gear used in the winter flounder fishery is the otter trawl (No. 35 Yankee). Dickie and McCracken (1955) gave the mesh size in the belly as 4 in (10.2 cm) between knot centers as purchased and in the cod end about 3 in (7.6 cm). Motte et al. 1973[12] described

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[12] Motte, G. A., A. J. Hillier, and R. P. Beckwith. 1973. Bottom trawl performance study. Univ. R.I. Mar. Tech. Rep. Ser. No. 7. Unpaged.

the trawl in detail (Table 22). Although there is a pound net fishery in the Chesapeake area and a fyke net fishery in the Middle Atlantic region, these fisheries are declining.

Perlmutter (1947) gave a history of the development of the fishery in the New York area. Before 1895 fish were taken by fyke net and traps. As consumer demand increased, more efficient gear was used. In 1895 the beam trawl was introduced in the flounder fishery of Massachusetts. By 1915, the Cape Cod fishery had changed to otter trawls and there was a shift from sail to gasoline and diesel engines which made it possible to fish a greater area. By 1920 the winter flounder fishery was at its peak, but during the 1930's fishermen reported decreasing catches on major grounds; therefore, a market developed for yellowtail flounder, *Limanda ferruginea*. During the 1960's the winter flounder fishery increased again.

Table 22.—Description of Yankee 35 Otter Trawl (Motte et al. 1973[1]).

Line	Length × diameter	Material	Attachments
Headline	52 ft	Combination	Floats: 8 or 19 × 8 in. diam. plastic
Bosom	12 ft × 5/8 in		
Each wing	20 ft × 5/8 in		
Footrope	72 ft	Chain	Bobbin gear: 4-in diam. rubber discs, full length of footrope
Bosom	10 ft × 3/8 in		
Each wing	31 ft × 3/7 in		
Hanging line	89 ft × 5/8 in	Polypropylene-Dacron	
Wing lines	6 ft × 5/8 in	Polypropylene-Dacron	
Wing bridles			
Upper	60 ft × 3/8 in	Steel wire chain	
Lower	60 ft × 3/8 in		
Door legs			
Upper	7 ft × 5/16 in	Chain	Doors: standard rectangular 3 ft × 6 ft × 1½ in 236 lbs
Lower	7 ft × 5/16 in	Chain	
Towing warps	7/16 in	Steel wire	

[1] Motte, G. A., A. J. Hillier, and R. P. Beckwith. 1973. Bottom trawl performance study. Univ. R.I. Mar. Tech. Rep. Ser. No. 7. Unpaged.

5.12 Boats

Dickie and McCracken (1955) described boats used in the Newfoundland winter flounder industry. Originally there were two types of boat: 1) large boats 40-45 ft long with gasoline engines, about 100 hp, which towed 50 ft "flounder drags" or No. 35 Yankee trawls; these boats began fishing earlier in spring, and 2) smaller Cape Island type open boats 30-40 ft long with gasoline marine engines and power-driven winches. By 1951 the large boats stopped fishing for winter flounder.

Olsen and Stevenson[13] described commercial fishing boats used in Rhode Island waters. There were three groups of trawlers: 1) day boats 40-60 ft long fishing the nearshore grounds with a three-man crew, which leave and return to port the same day, 2) short-trip boats, essentially the same as day boats but making trips of 1-3 days, and 3) long-trip boats 55-85 ft long fishing the offshore grounds such as Nantucket shoals and Georges Bank, carrying a three- to six-man crew and making 3- to 6-day trips. These boats had larger engines and were usually equipped with radar.

5.2 Fishing areas

5.21 General geographic distribution

The general geographic distribution is the northwest Atlantic (FAO Statistical Area 21) on the coast of North America from Labrador to Cape Hatteras, N.C. (Fig. 2).

5.22 Geographic range

Winter flounder are found within 15 mi (24.2 km) of the shore and on offshore banks. They enter estuaries and may be found in brackish waters of many rivers. They are most abundant from Nova Scotia to New Jersey in inshore waters (Perlmutter 1947). There are also large populations on Georges Bank and Nantucket Shoals.

5.23 Depth range

Tide mark to 20 fathoms (40 m), they extend to 50 fathoms on the offshore banks. The depth record is 70 fathoms (Bigelow and Schroeder 1953). Variations of density with depth have been discussed in sections 4.12 and 4.24.

5.24 Conditions of the grounds

Olsen and Stevenson (see footnote 13) stated that in Rhode Island waters, winter flounder can be caught over all types of bottom, but in salt ponds and estuaries they preferred muddy sand. Bigelow and Schroeder (1953) reported that on offshore banks they were common on hard bottom.

5.3 Fishing seasons

5.31 General pattern of seasons

Early spring to late fall.

5.32 Dates of beginning, peak, and end of season

See Table 23.

5.33 Variation in date or duration of season

The season generally begins after adults have spawned and begun to move into deeper water. Factors affecting this are covered in sections 3.16 and 3.51.

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[13] Olsen, S. B., and D. K. Stevenson. 1975. Commercial marine fish and fisheries of Rhode Island. Univ. R.I. Mar. Tech. Rep. 34, 117 p.

Table 23.—Fishing seasons for winter flounder.

Area	Season	Peak	Minimum	Author
Long Island	Feb.-June	Apr.-May	—	Lobell (1939)
Rhode Island	Year-round	May-July	Winter	Olsen and Stevenson (1975)[1]
St. Marys Bay, Nova Scotia	Mar.-Winter	Apr.-July	Winter	Dickie and McCracken (1955)
Long Island sports fishery	Mar.-Nov.	Apr.-May	Winter	Briggs (1965)

[1] Olsen, S. B., and D. K. Stevenson. 1975. Commercial marine fish and fisheries of Rhode Island. Univ. R.I. Mar. Tech. Rep. 34, 117 p.

5.4 Fishing operations and results

5.41 Effort and intensity

Dickie and McCracken (1955) calculated fishing effort in the St. Marys Bay, Nova Scotia, fishery by compiling average catch per 50-ft net per hour from boats which fished exclusively for flounder. To compare the drop in catch per effort with the history of the fishing intensity they divided the total landings of flounders from the catch by the catch per unit of effort by 50-ft nets.

Edwards (1968) computed exploitation rate by calculating the average catch in pounds per tow for ICNAF Subarea 5 (New England) made by the 1963-66 groundfish survey using a 36 Yankee Trawl with a 0.5-in (1.3-cm) cod end liner. The trawl had a bottom spread 35-40 ft (10.7-12.2 m) and a maximum height of 7 ft (2.1 m) at the middle. Biomass was calculated by applying a correction factor of the number of square miles for the zone divided by area the net sweeps each tow (0.016 mi^2) to the catch per tow in pounds.

Results of both calculations are presented in Table 24.

Briggs (1965) calculated catch per unit effort of winter flounder by sportsmen fishing from five different facilities (bank and pier, rowboat, open boat, charter boat, and private boat) in four different locations around Long Island (Great South Bay, Shinnecock Bay, Gardiners Bay, and Moriches Bay) for each month in 1961-63. Open boat and charter boat anglers had the best catch per unit effort in the bays. Catch was highest in spring and lowest in summer (16-20 fish per angler per trip in spring, 10 or less in summer). Bank and pier anglers had the lowest catch per unit of effort.

Table 24.—Fishing effort for winter flounder in St. Marys Bay and ICNAF subarea 5.

Year[1]	Landings by 50-ft nets[1] Total	Landings by 50-ft nets[1] Catch/h in lbs	Landings by all nets[1] (lbs)	Proportion taken by 50-ft net[1]	Total effort by 50-ft net[1]
1953	253,111	110	421,071	0.60	3,828
1952	152,047	105	369,262	0.41	3,517
1951	99,636	152	586,111	0.17	3,856
1950	487,656	188	1,299,176	0.38	6,911
1949	354,024	415	737,403	0.48	1,777
1948	272,018	476	294,000	0.93	626

Catch per unit tow in pounds[2]

Southern New England		Georges Bank		Gulf of Maine			Browns Bank
Inshore	Offshore	Shoal	Offshore	Shallow	Middle	Deep	
8.01	—	4.99	0.01	11.44	0.55	0.09	0.13

[1] Dickie and McCracken (1955).

[2] Edwards (1968).

5.42 Selectivity

Dickie and McCracken (1955) stated that nets with a mesh size of 4 in (102 mm) between knot centers in the belly and 3 in (76 mm) in the cod end take flounder down to 200 mm in size, but in the Nova Scotia fishery, fish plants place a minimum of 300 mm on flounder size.

5.43 Catches

Total annual yields in Table 25 include the world yield and the U.S. yield by states. For maximum equilibrium yield see section 4.5.

Table 26 is the sports fishery yield of the United States by geographic section.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

Poole (1969) reported the State of New York Fish and Game Law prohibits buying, selling, or offering for sale, winter flounder less than 8 in (206 mm) long.

Howe and Coates (1975) reported Massachusetts prohibits otter trawling at all times north of Boston and in Buzzards Bay. In most other areas trawling is prohibited from 1 April or 1 May to 31 October.

Trawl regulations by the International Commission for the Northwest Atlantic Fisheries in relation to bottom fisheries, prohibit use of trawl nets with cod end meshes of dimensions less than 130 mm in manila twine netting or the equivalent when materials other than this are used to take winter flounder in subarea 4 (Bogdanov and Konstantinov 1973). See Figure 2.

6.3 Control or alteration of chemical features of the environment

Eisler (1965b) studied acute toxicity of alkyl benzene sulfonate (ABS), a surfactant present in detergent, to five estuarine fish species. The fishes, *Menidia menidia*, *Fundulus heteroclitus*, *Mugil cephalus*, *Anguilla rostrata*, and *Pseudopleuronectes americanus*, were collected from New Jersey. Tide detergent, used as a source of ABS, contained 30.3% ABS. The winter flounder was intermediate in susceptibility; 8.2 ppm detergent was the LC_{50} after 96 h exposure at 20‰ salinity and 20°C. After 12 wk in solution, the detergent retained its toxicity.

Sprague and Carson[14] did preliminary screening tests

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[14] Sprague, J. B., and W. B. Carson. 1970. Toxicity tests with oil dispersants in connection with oil spills at Chadabucto Bay, Nova Scotia. Fish. Res. Board Can., Tech. Rep. 201, 30 p.

Table 25.—Annual yield of winter flounder in world and U.S. commercial fisheries.[1]

	1965	1966	1967	1968	1969	1970	1971	1972	1973
	1,000 t								
Canada	5.2	3.3	2.7	1.2	2.5	—	—	—	—
U.S.	11.6	14.7	12.3	9.5	11.3	12.1	11.6	7.2	9.7
Total	16.8	18.0	15.0	10.7	13.8	12.1	11.6	7.2	9.7

Year	Maine	New Hampshire	Massachusetts	Rhode Island	Connecticut	New York	New Jersey	Delaware	Maryland	Virginia
	1,000 lbs									
1973	186	8	10,914	4,414	844	1,661	160	2	2,200	900
1972	280	10	11,344	4,634	38	1,429	94	2	3	21
1971	146	7	14,542	5,275	817	1,660	79	5	17	55
1970	298	8	15,898	5,301	789	1,692	146	3	21	123
1969	96	4	15,616	4,300	931	1,444	268	2	60	394
1968	45	—	11,996	3,362	1,041	1,826	422	3	74	824
1967	103	—	16,419	3,844	886	2,931	366	19	178	798
1966	92	—	21,085	4,275	831	3,259	438	50	91	220
1965	69	—	16,520	3,638	727	2,245	279	38	62	122
1964	75	—	13,901	4,080	957	1,441	357	48	26	68
1963	45	—	11,786	2,918	983	1,834	185	37	10	2
1962										
1961	158	—	11,934	2,028	980	1,695	152	20	3	1

[1] From *Fishery statistics of the United States*. National Marine Fisheries Service, Statistical Digest numbers 54-56 for the years 1961-73.

Table 26.—Sports fishery statistics for winter flounder in 1970 and 1965 by survey region (from Deuel 1973 and Deuel and Clark 1968).

	Region I North Atlantic New England-New Jersey			Region II Middle Atlantic New Jersey-Cape Hatteras			
Year	No. anglers	No. fish	Wt. of fish (1,000 lbs)	No. anglers	No. fish	Wt. of fish (1,000 lbs)	Total
1970	563	42,949	24,684	402	18,632	12,801	
1965	579	40,014	21,838	277	7,256	6,935	
Number of fishes of all species caught by U.S. salt water anglers in 1970							
		21,581			7,496		29,077

of oil dispersants, manufactured for use in cleaning up oil spills, for acute toxicity to aquatic life. The test procedure used a static system with a given concentration of test mixture. Exposure continued for 7 days, after which several fish were removed and held in clean running water for 7 more days to check for delayed mortality. Test results gave an indication of acute lethal effect only. There may be long-term or sublethal effects at concentrations of oil dispersants lower than those discussed (Table 27). A classification scheme for "grade of toxicity" adapted from a report by the Joint Group of Experts on the Scientific Aspects of Marine Pollution (1969) was employed to describe toxicity (Table 27).

Bunker C oil was "practically nontoxic" by 4-day criteria, but in 7-day tests, including 7-day postexperiment mortality, it was "slightly toxic" to winter flounder (5°C 1,000-3,000 mg/liter). Corexit 8666 was "practically nontoxic" as was its dispersion with Bunker C oil. An apparent toxicity during degradation should be investigated before Corexit 8666 is considered for widescale use. Fish which died in Corexit alone had gill rakers and throats covered with white particles, apparently Corexit in mucus. This suggested Corexit caused mucus secretion around the affected areas and could be a factor

Table 27.—Four-day median lethal concentrations of various oil dispersants, alone or mixed with Bunker C oil, to winter flounders and grading system used to describe toxicity at 5°C (from Sprague and Carson 1970).[1]

Bunker C oil	> 10,000 mg/l
Corexit 8666	> 10,000 mg/l
Corexit 8666 and oil	> 10,000 mg/l
BP 1100 + oil	32 mg/l
Disperaol SD	> 1,000 mg/l
Grade 0 "Practically nontoxic"	Acute toxicity threshold above 10,000 mg/l
Grade 1 "Slightly toxic"	Threshold 1,000-10,000 mg/l
Grade 2 "Moderately toxic"	Threshold 100-1,000 mg/l
Grade 3 "Toxic"	Threshold 1-100 mg/l
Grade 4 "Very toxic"	Threshold below 1 mg/l

[1] Sprague, J. B., and W. B. Carson. 1970. Toxicity tests with oil dispersants in connection with oil spills at Chadabucto Bay, Nova Scotia. Fish. Res. Board Can. Tech. Rep. 201, 30 p.

in mortality, but this could also have happened after the fish began dying.

Smith and Cole (1970) examined the effects of chlorinated hydrocarbons DDT, heptachlor, dieldrin insecticide residues, and two related breakdown products DDE and heptachlor epoxide, on winter flounder juveniles and adults from the Weweantic River estuary, Mass. Topp (1968) compared larval mortality of winter flounder in the Weweantic to that data compiled by Pearcy (1962a) for the Mystic River estuary, Conn., and found excessive mortality in the former. He felt this might be due to pesticide contamination which drained from cranberry bogs along the Weweantic River watershed and from county mosquito control programs.

Winter flounder contained residues of the above compounds in their tissues. In nonmigratory juveniles, seasonal patterns were demonstrated for DDT, heptachlor, DDE, and heptachlor epoxide. Peak concentrations of parent compounds were more closely associated with high runoff conditions than with specific applications of pesticides in the drainage system. Dieldrin was present uniformly throughout the year. Migratory adult flounder present from October to May contained heptachlor and heptachlor oxide levels similar to juveniles but significantly less DDE (Table 28). Comparisons of chromatographic patterns of these flounders with flounders from widely separated coastal populations and offshore Georges Bank flounders showed that the Weweantic population had a unique pattern quite dissimilar from other populations inferring that local pesticide levels can establish area specific chromatographic patterns. Adult female flounder sequentially concentrated DDT, DDE, and heptachlor epoxide in their ripening ovaries as spawning season approached (Table 28). Ovarian concentrations of insecticide residue may have caused the high larval mortality at final yolk sac absorption reported by Topp (1968), because residues were bound to yolk fats where they remained inactive until those fats were metabolized by the developing egg. At this time DDT would be released and would cause death.

Eisler (1970) reported juvenile winter flounder were intermediate in susceptibility to endrin, p,p'-DDT, and heptachlor on the basis of LC_{50} (96 h) tests conducted with 10 species of marine fishes.

Janicki and Kinter (1971) reported inhibition of ATP-ase activity by DDT and its commercial solvents cyclohexanone and DMF (N,N dimethylformamide) in winter flounder from the Gulf of Maine. They found measurable inhibition of Na^+, K^+, Mg^{++}, ATP-ase activity in the intestinal mucosa at 1 ppm concentration DDT which was linear through 50 ppm. The gills tested with DMF and 50% ppm DDT showed ATP-ase activity 54% inhibited. Cyclohexane completely inhibited activity. This inhibition of ATP-ase activity hindered active secretion of salt through gills which is important in maintaining tissue osmolarity. These observations may explain the sensitivity of teleosts to DDT.

Baker (1969) experimented on histological and ultrastructural effects of high (3,200 and 1,000 µg/liter), medium (560 µg/liter), and low (180 µg/liter) copper concentrations on several organs, and the relationship of these effects to medical knowledge of copper metabolism. The results showed that high and medium levels of copper resulted in fatty metamorphosis in the liver, necrosis in the kidney, destruction of hemapoetic tissue, and gross changes in gill architecture. Somatic muscle, heart, stomach, duodenum, intestine, eyes, and brain showed no morphological changes.

Pritchard et al. (1973) described metabolism and excretion of DDT and Mirex, two highly persistent organochlorine pesticides, in winter flounder. Fish were injected with sublethal concentrations (100 g/kg) of labeled pesticide. Tissue and body fluids were analyzed. Because there was limited metabolism of parent pesticides to less toxic derivatives (90% of the DDT and 100% Mirex were unaltered after 1 wk), and excretion of both was very slow because of plasma binding, they concluded winter flounder retain large fractions of pesticide which they are essentially unable to detoxify. Since fishes hold their pesticide burden primarily in muscle, the flesh of flounder from contaminated areas will be heavily loaded and is potentially dangerous for terminal consumers such as man.

Freeman et al. (1974) determined mercury levels in fish from the Canadian Atlantic Coast. These results were 0.17-0.18 ppm mercury with a mean of 0.17 ± 0.01 for dorsal muscle of male fish, 557 g average weight, and 0.11-0.20 ppm mercury with a mean of 0.17 ± 0.03 for

Table 28.—Average concentrations of insecticide residues in muscle tissue of winter flounder of various ages taken 25 January 1967, Weweantic River estuary (ppm wet weight). (From Smith and Cole 1970.)

Age	No. fish	DDT	DDE	Heptachlor	Heptachlor epoxide	Dieldrin
I	5	< 0.01	0.72	1.55	0.56	< 0.01
II	7	< 0.01	1.07	1.10	< 0.01	< 0.01
III	4	< 0.01	0.18	1.27	< 0.01	< 0.01
IV	3	< 0.01	0.21	0.62	< 0.01	< 0.01
			Ovarian tissue			
30 Oct. 1966	3	0.11	0.02	0.07	—	< 0.01
25 Jan. 1967	3	0.16	0.04	< 0.01	< 0.01	< 0.01
29 Mar. 1967	4	0.40	0.22	< 0.01	0.65	< 0.01

female dorsal muscle. There was no significant difference between mercury levels and sex or weight of the fish. Mercury limits allowed for commercial fish in the United States and Canada are 0.5 ppm.

6.4 Control or alteration of biological features of the environment

Hess et al. (1975) simulated the impact of the entrainment of winter flounder larvae at a nuclear power station, Millstone Point, Conn. Currents and water levels were simulated by a tidal hydrodynamic model, tidal currents, and diffusion by a computer. These provided input to a transport model which simulated the concentration of larvae to predict the numbers which could be entrained. Results indicated that the reduction in winter flounder larvae at the end of the pelagic stage when they are most likely to be entrained was less than 1% with the assumption that larvae will not return if lost from Millstone Bight. The effect of this 1% reduction in recruitment was simulated by a model in which year classes and total egg production were represented by compartments. Population parameters such as fecundity, natural and fishing mortality, and growth information was gathered from the literature. The effect of entrainment was incorporated by reducing the number of recruits to year class I that would result from a certain level of egg production. This indicated for a 1% reduction in recruitment, a potential 6% decrease in total population size after 35 yr of power plant operation (the average power plant life) (Fig. 21).

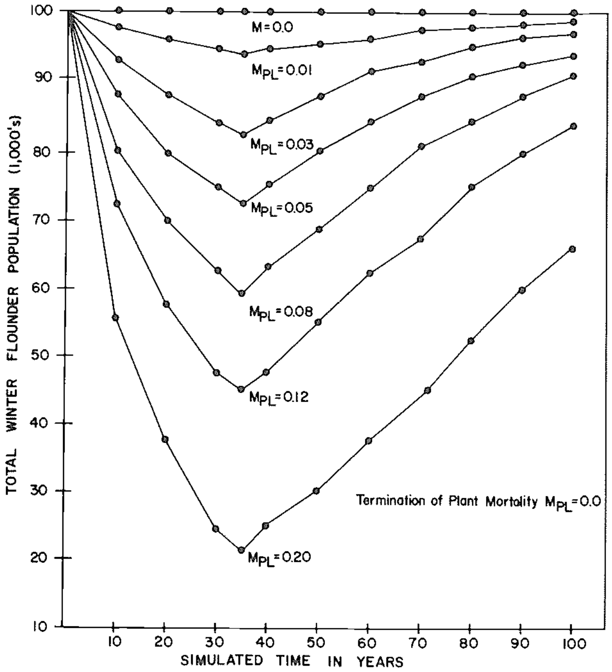

Figure 21.—Simulated total population of winter flounder breeding in Niantic River with various levels of entrainment mortality (Mpl) (from Hess et al. 1975).

Predicted values for which there was no local information such as currents, number of spawning adult winter flounder, and larval concentration are being verified by field work in progress.

An overall assumption is made that some of the flounder larvae spawned in the Niantic River and passing near the power plant will remain in the estuary. If all are lost to Long Island Sound the effect of entrainment of several percent of the larval population would be nil for winter flounder recruitment.

7 POND FISH CULTURE

Winter flounder were propagated and raised in fish hatcheries in the late 1800's in the United States because it was felt that the release of larvae would increase the flounder population, although the effectiveness was never established. The techniques for collecting adults, stripping and fertilizing eggs, and raising eggs and larvae were described by Brice (1898), Rathbun (1893), and Mead (1909). These techniques are mainly of historical interest, but they did have some interesting methods of dealing with the eggs which stick together in large clumps after fertilization.

Eggs may be prevented from clumping by coating with diatomaceous earth (Smigielski and Arnold 1972). Eggs were stripped into a polyethylene dishpan 35 × 30 × 14 cm. After the eggs were fertilized, they were covered by a dense slurry of diatomaceous earth suspension (50 g/l of sterile seawater) and swirled in the suspension for several minutes. They were then rinsed by repeated dunking in clean seawater to remove excess diatomaceous earth, placed in plastic dishpans with screens fitted over holes cut in the sides and bottom, and incubated in flowing seawater.

7.1 Procurement of stock

Field collections of gravid adults by otter trawl (Smigielski and Arnold 1972).

7.2 Spawning

Smigielski (1975) studied responses of winter flounder to human chorionic gonadotropin (HCG), oxytocin, pregnant mare serum gonadotropin (PMSG), deoxycortisone (DOCA), and freeze dried carp pituitary. Carp pituitary extract was successful, producing viable hatch in every case at dosages of 5 mg/454 mg body weight. The eggs and larvae were normal in every respect.

HCG sometimes was successful when water temperatures were below 6°C and dosages were over 200 International Units. In general egg quality was poor and survival low. The formation of membranous plugs and gross hydration caused death in several females.

PMSG, DOCA, and oxytocin occasionally produced hydration but no ovulation. Water temperature appeared to be the most critical factor in producing ovulation in winter flounder. The majority of fish did not hydrate at temperatures over 6°C and had gonadosomal indices less than 12% even with hormone treatment. Observations reported in Bigelow and Schroeder (1953) in the Gulf of Maine showed that extensive spawning does not occur at water temperatures over 6°C. Hormone treatment experiments at water temperatures of 6°-7.5°C suggest that temperature above 6°C inhibit maturation of winter flounder eggs. Past observations showed that gravid female flounder died in water temperatures of 10°C, and their ova were stunted and misshapen. Male flounders held under the same conditions suffered no ill effects.

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