NATURAL HISTORY OF THE BAY SCALLOP[1]

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INTRODUCTION

The bay scallop, *Pecten irradians*,[2] is one of the few commercial, edible bivalves of our Atlantic coast. In North Carolina, where it is of considerable national and very great local importance, it had received almost no scientific study previous to these investigations. Accordingly an investigation was undertaken at the United States Bureau of Fisheries station, Beaufort, N. C., which is in the heart of the scallop-producing area in this State. Work was begun in the summer of 1925 and continued into 1928.[3]

Effort was concentrated on those aspects of life history which it was thought would yield knowledge of greatest usefulness for conservation. However, during certain periods, time was found for anatomical and other studies. Because of the

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[2] Also known as *Pecten gibbus*. See discussion under "Classification and relationship."

[3] I wish to thank Capt. John A. Nelson, commissioner, and others of the division of commercial fisheries, Department of Conservation and Development, North Carolina, for much helpful service during these investigations.

economic importance of the form, its many points of interest, and the lack of a connected available account with a detailed description of the adult, the attempt has been made to make this account of the bay scallop reasonably complete and well rounded.

ECONOMIC IMPORTANCE

The bay scallop is an article of commerce in Massachusetts (the leading producer), Rhode Island, New York, Virginia, North Carolina, and, according to the Bureau of Fisheries latest statistics, Florida. In commercial value it ranks third among American mollusks, after the oyster and the hard clam, Venus. The accompanying table (Table 1) is compiled from data furnished by the division of fishery industries, and does not include an item of something over $11,000 for a closely allied but not identical west coast scallop. The large and commercially important giant or sea scallop of the Atlantic is also largely if not completely excluded. For comparison there are included Ingersoll's estimates for 1880 (Ingersoll, 1887).

TABLE 1.—*Quantities and values of bay scallops at early and recent dates*

State	Catch for 1880		Catch for most recent years[1]	
	Pounds	Value	Pounds	Value
Massachusetts	111, 600	$44, 640	1, 235, 304	$548, 348
Rhode Island	180, 000	72, 000	42, 870	28, 588
New York	288, 467	115, 387	209, 892	92, 253
Virginia	----------	----------	360, 732	74, 272
North Carolina	67, 500	27, 000	1, 394, 124	125, 845
Florida	----------	----------	14, 100	5, 000
Total	647, 567	259, 027	3, 347, 022	874, 306

[1] Statistics have not been collected annually in each State for any one recent year, so the statistics for the latest year are taken in each instance as follows: Massachusetts, Rhode Island, North Carolina, and Florida, 1928; New York, 1926; and Virginia, 1925.

In North Carolina, because it is limited to a small area with a meager population and because it offers the only opportunity for winter work for quite a proportion of the people of the scalloping area, the scallop fishery is of very great local importance.

LITERATURE

The old, colloquial name *Pecten* (which means comb) appears in pre-Linnæan scientific writings and was used by Linnæus although not formally adopted by that great naturalist (see Dall, 1898), who described numerous species of scallops under the generic name of *Ostrea*. Chiefly because of the adoption of its shell as a symbol of holy pilgrimage and its appearance in coats of arms, references to the scallop are frequent not only in zoological but also in popular literature, especially verse (see Ingersoll, 1887).

In general the numerous writings consulted will be referred to in later sections according to the subjects with which they deal. However, it may be worth while to note a few of the earlier works and some most used in the study on which this paper is based.

Poli (1795) described or figured the eyes, tentacles, gills, palps, fringed lips, foot, adductor muscle, kidneys, and rectum. His figure showing arrangement and appearance of soft parts of *Pecten jacobaeus* is very good and is still used (Pelseneer, 1906).

Another early investigator whose work is of notable interest is Garner, who described and figured the ocelli and nervous system (Garner, 1837, read 1834). He studied the circulatory system by means of injections (Garner, 1838–39, 1841) and attributed the great size of the adductor muscle to its use in clapping the shell in the swimming process. He suggested the importance of the gills for classification and discovered (see Kellogg, 1892) that the sexual products are discharged through the kidney.

Modern studies which have been especially useful are the account of the scallop fishery by Ingersoll (1887) in The Fishery Industries of the United States; papers by Jackson (1890) and Kellogg (1892 et. seq.); the Memoirs by Drew (1906) and Dakin (1909); and the account by Belding (1910).

CLASSIFICATION AND RELATIONSHIP

Among the schemes of classification of lamellibranchs, that employing the structure of the gills is the simplest and seems to be gaining most favor among students of recent forms. The possibility of such a scheme was suggested by Lankester in 1883. Development is due to various workers, notably Pelseneer, Menegaux, and Ridewood. Pelseneer's classification of orders (1906) is essentially that of Ridewood (1903); but with certain order names previously given by Pelseneer used instead of the new names proposed by Ridewood, and with the Septibranchs retained as an order. Under this scheme forms with flat, platelike, unreflected gill filaments (Protobranchia) are regarded as most primitive; those with reflected filaments held together in lamellae by interlocking cilia (Filibranchia) as higher in advancement; those with reflected filaments joined one with the other by vascular connection (Eulamellibranchia) as having attained the highest development; and the Septibranchs as being forms with degenerate gills.

In such a classification the scallops belong with the Filibranchia but evidently are close to the Eulamellibranchia, because vascular filamentary connections are found in the giant or sea scallop (*Pecten tenuicostatus* Mighels, as employed by Drew but, according to Dr. Paul Bartsch, in correspondence, *Pecten grandis* Solander).

Cooke (1895) and also Parker and Haswell (1897) employ a somewhat different classification with an intermediate order, the Pseudolemellibranchiata, in which are placed the oysters and the scallops with a few others. Although, as previously noted, the intermediate position for the scallop is indicated, the oysters would seem clearly to belong with the Eulamellibranchiata, and it may be questioned whether this intermediate order does not increase rather than decrease the difficulties.

In its main outline, classification according to the gill structure has the advantage of being a simple, logical, readily understandable one, which presents a reasonable interpretation of phylogenetic relationship. It seems the most useful scheme developed. Undoubtedly the understandable logic of the main outline of classification according to gill structure has had much to do with its favorable reception and may have unduly influenced zoologists. In the classification which Dall (1895) introduced after many years of study, the attempt is made to take into consideration all structural evidence. In this classification Pectinacea is constituted quite differently and placed with groups including Solenomya, Ostrea, and others in the order Teleodesmacea. The class is termed Pelecypoda. See also Rice (1900, 1908) and Verrill (1899).

The bay scallop almost universally is placed in the genus Pecten, but as to the species there is some difference of opinion and usage. Dall (1898) placed what I term the bay scallop—ranging from Massachusetts to the Gulf of Mexico and even to Brazil—in one species. Davenport (1903), largely as a result of "ray counts," finds the Beaufort (N. C.,) scallops very close to those of Cold Spring Harbor, N. Y., and noticeably different from those of Tampa, Fla., but admits the possibility of intergrades. The modal number of shell rays or ribs is given as follows: Cold Spring Harbor, 17; Beaufort, 17; and Tampa, 20. It is not clear from the context how the number for Beaufort was obtained, although abundant data for the other points are given. I made a count of rays on Beaufort shells and found 18 most prevalent, but with 17 nearly as numerous. The extremes in this count, which included 150 right valves and 46 left valves, were 16 and 20. (See Table 2.) The number was determined by counting the inner grooves much as was done by Davenport, except that two half grooves were not taken to equal one full groove. Jacot (1921), presumably counting the outer ribs instead of the inner grooves, found two subspecies, one commonly with 19 ribs (18–20) the other with 20 (19–22).

TABLE 2.—*Counts of rays or ribs on scallop shells from Beaufort and vicinity*

	16 rays	17 rays	18 rays	19 rays	20 rays
Right valve	10	52	68	16	4
Left valve	4	13	21	9	1
Total	14	65	89	25	5

Like Davenport, I hesitate to pass on the question of species. I accept Dall's decision in favor of one species for our Atlantic coast and consider that the available morphological evidence is strongly in favor of the view that the bay scallops, at least of the important commercial centers (North Carolina, New York, Virginia, and Massachusetts) are specifically the same. In Bulletin No. 37 Dall (1889) employed the name *Pecten irradians* Lamarck. In the "Tertiary Fauna of Florida" (Dall, 1898), on the ground of integradation with the Jamaican scallop which Linnæus described as *Ostrea gibba,* he employs the name *Pecten gibbus* Linné with *irradians* as a subspecies. Kellogg, Drew, and Belding use *P. irradians.* In correspondence, Dr. Paul Bartsch expressed himself in favor of that name, in the belief that our scallop is distinct from that of Jamaica; and Dr. H. A. Pilsbry favors it if the binomial is used. The name *Pecten irradians* Lamarck is here employed.

Although on morphological evidence the Beaufort and Massachusetts scallops are held to belong to one species, it is perhaps worthy of note in this connection that in one important biological aspect—spawning—the Beaufort scallops differ markedly from those of northern waters. The Beaufort scallops spawn principally in the fall when water temperature is falling; the others, according to Risser (1901) and Belding (1910), in the spring or early summer when the temperature is rising.

HABITAT AND DISTRIBUTION

According to Dall (1889) the range of *Pecten irradians* is from Nova Scotia to Tampa, Fla. Later (1898) he concluded that West Indian scallops were specifically the same as those of our Atlantic coast and that the species extended to Brazil. Kellogg (1910) reports it from the vicinity of the Chandeleur Islands in the Gulf of Mexico, and gives the range as Cape Cod to Texas. Belding (1910) states that it occurs from Massachusetts Bay to the Gulf of Mexico, but adds that a few are reported to be found in some of the warm bays of the Maine coast. Ingersoll (1887) found it rare or local "north of that great dividing point"—Cape Cod. In important commercial abundance it occurs so far north as Cape Cod and at least as far south as

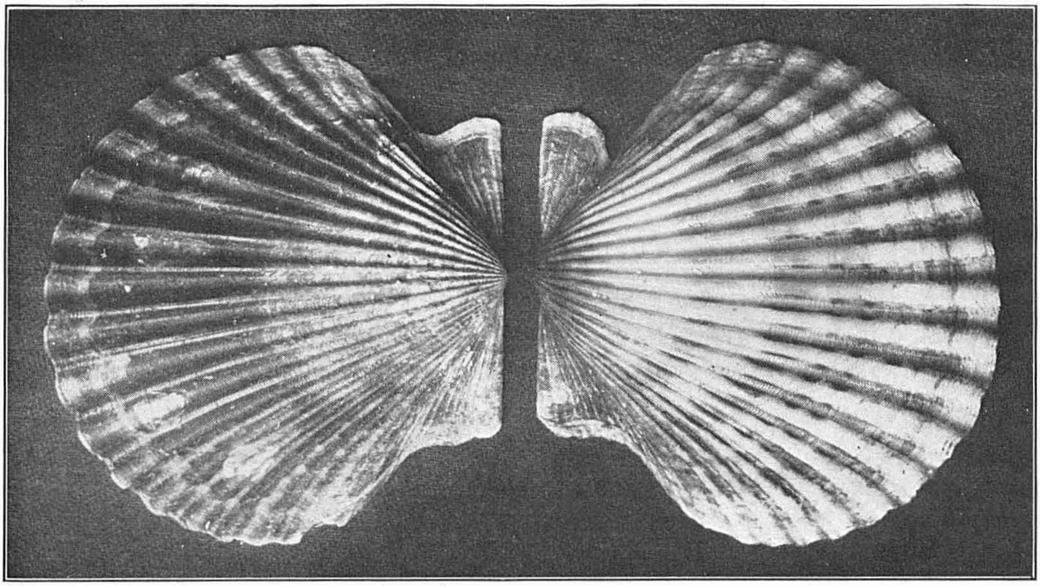

Figure 1.—Shell of bay scallop. Exterior view of left and right valves

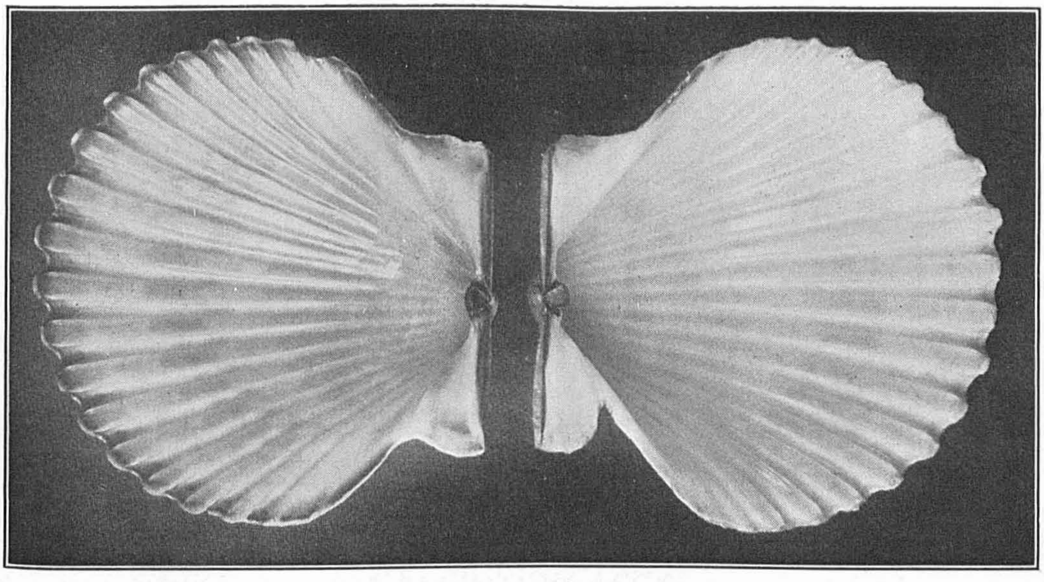

Figure 2.—Interior view of left and right valves. The lower or right valve, shown at right, is marked by the byssal notch

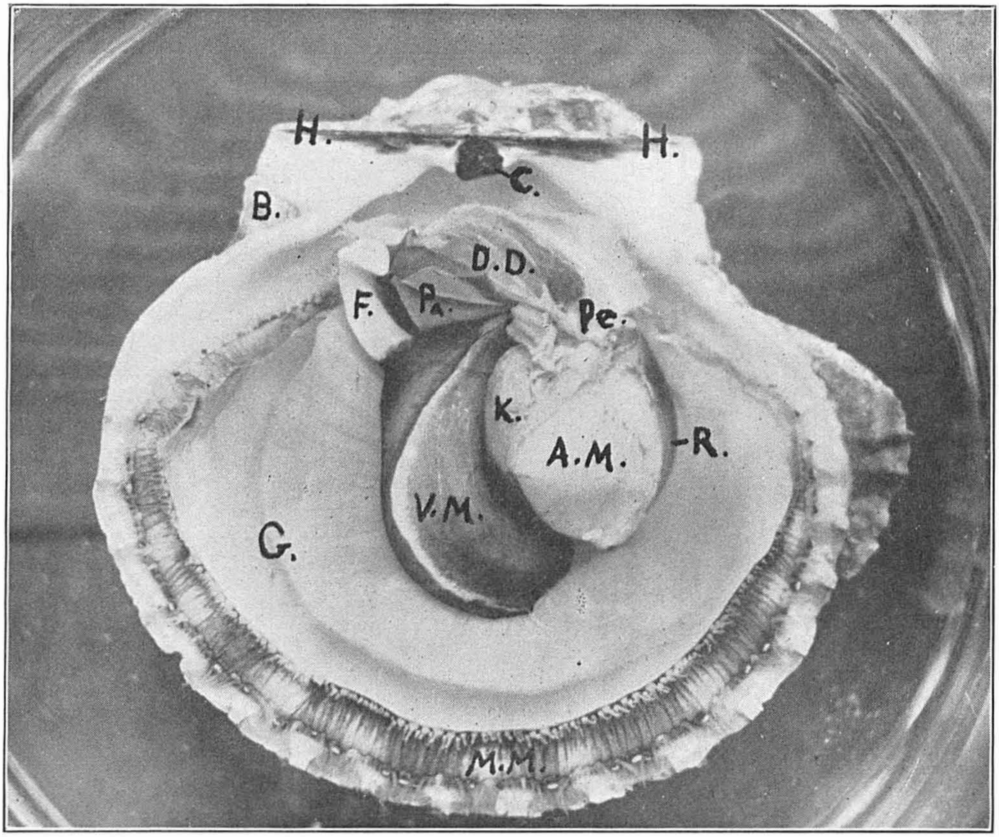

FIGURE 3.—Bay scallop lying on its right side, with left valve, left gill, and most of left mantle lobe removed. *A. M.*, adductor muscle; *B.*, byssal notch (overgrown by *Ostrea equestris*); *C*, cartilage; *D. D.*, digestive diverticula overlying stomach; *F.*, foot; *G.*, gill; H., hinge; K., execretory organ or kidney; *M. M.*, mantle margin with eyes and sensory tentacles along outer edge and guard tentacles along inner edge; *Pa.*, palps; *Pe.*, pericardium; *R.*, rectum; *V. M.*, visceral mass

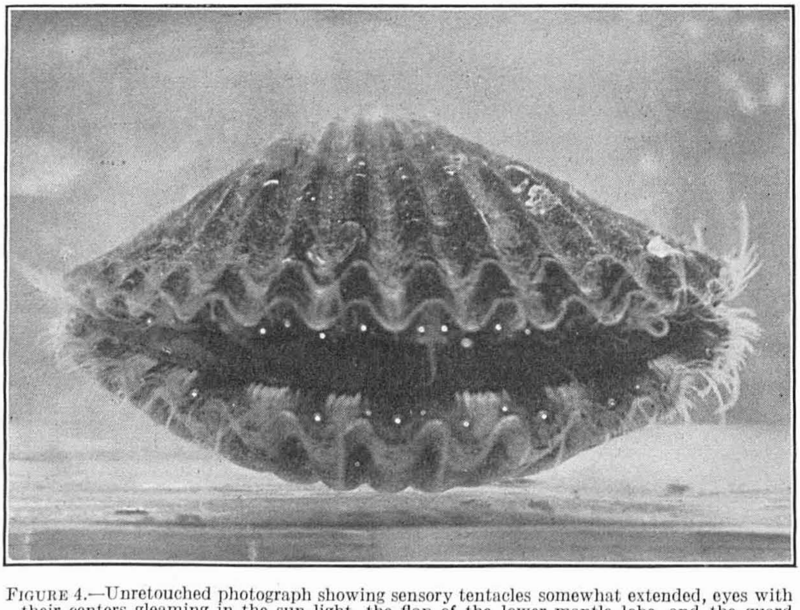

FIGURE 4.—Unretouched photograph showing sensory tentacles somewhat extended, eyes with their centers gleaming in the sun light, the flap of the lower mantle lobe, and the guard tentacles of both flaps

Bogue Sound, N. C. A small commercial catch is recorded for Florida in 1928. Areas famous for the abundance (past or present) of scallops are: The south shore of Cape Cod and Buzzards Bay, Mass.; Greenwich Bay, R. I.; Long Island Sound, particularly sections of the Connecticut shore (unproductive since an early date); Peconic Bay, Long Island, N. Y.; and Bogue Sound, Core Sound, and Beaufort Harbor in North Carolina. In suitable coastal areas between Long Island and North Carolina it occurs, or has occurred, sometimes in commercial numbers. Of recent years important catches have been taken near Chincoteague, Va.

The range in depth is from that of flats with only a foot or so of water over them at ordinary low water (bare at extreme low water) to as much as 60 feet (Belding, 1910). In North Carolina, where the sounds are very shallow, comparatively few scallops are found at a depth of much more than 6 feet.

As its name implies, the bay scallop is principally an inhabitant of inclosed waters—bays, harbors, estuaries, and sounds. These may be either of ocean saltness or decidedly brackish. Belding (1910) states that the density (temperature not given) may be as little as 1.010. In North Carolina scallops occur in commercial abundance in water ordinarily ranging in salinity from about 20 parts per mille (possibly decidedly less for brief periods) to 38 parts per mille. There may be a strong tide, a moderate tide, or almost none. Ordinarily scallops occur amid a growth of eelgrass (Zostera) or other vegetation. This plant growth may be long and heavy or short and sparse. The type of bottom varies from soft mud to hard sand (but not shifting sand).

ORGANIZATION AND MODE OF LIFE

SHELL

The general outline and appearance of the shell of an adult scallop are shown in accompanying photographic illustrations. (Figs. 1 and 2.) In addition, Figure 5*a* illustrates the cross sectional shape of the ribs and Figure 5*b* that of the shell, through center of umbo, fossette, and central rib. The umbos are straight (nonspiral) and approximate and directed at right angles to the hinge, near the center of which they are located. The central position of umbos relative to the anterior and posterior portions has, in an allied species, led Dakin (1909) to term the shell equilateral, although there are small posterio-anterior differences which strictly make it inequilateral. The deeper cupping of the lower right valve makes the shell inequivalve, a condition found in comparatively few lamellibranchs and doubtless an adaption to a lateral position in life. The deep byssal notch in the right valve is anterior, and the fossette or cartilage box points somewhat anteriorly. The adductor muscle impression is posterior but very faint, as is also the pallial line (without sinus). The shapes of the auricular regions or "ears" are well shown in the photographs. (Figs. 1 and 2.) The posterior auricular margin is slightly obtuse, the anterior reflected.

The long, thin external ligament (the ligament proper) extends the length of the hinge either side of the umbos (the type termed by Dall (1895) amphidetic) and holds the valves together along the hinge line. The cartilage (or so-called internal ligament, the resilium of Dall), roughly pyramidal in shape and well supported in its fossette or box, adds considerably to the strength of the hinge but has the primary function of tending, like a compressed spring, to open the shell. Cooke (1895) states that the ligament is inelastic and insoluble in caustic potash, the cartilage very elastic and soluble in caustic potash. The cartilage, in thin pieces, is a clear red amber and of a gelatinous appearance but is readily split into horizontal right and left layers of fine fibers. At each end of the clear portion of the cartilage is a whitish, opaque pad, presumably a layer of cartilage impregnated with lime.

The hardness and brittleness of the scallop shell make difficult the preparation of sections for the study of calcareous structure. Dakin (1909), who made sections, states that prismatic and nacreous layers can not be definitely distinguished, that an irregular arrangement of crystals (chiefly aragonite) representing both these layers makes up the calcareous portion of the shell. In addition he found a trace of periostracum. Jackson (1890) states that the prismatic layer is present in the early dissoconch shell, but wanting in the adult. Drew (1906) found only the nacreous layer present in the shell of the giant scallop of commerce. Belding (1910), on the other hand, states that both nacreous and prismatic layers are present.

The present writer has examined numerous shell fractures instead of sections. A fracture along a rib of an upper valve ordinarily shows an outer white area, an intermediate dark area, and an inner white area. A fracture across the ribs shows the intermediate dark area divided by narrow, white areas at the edges of the ribs, connecting the outer and inner white areas. (See fig. 5*a*.) Occasionally a rib is found which has no evident outer white surface. The inner white surface does not extend quite to the tips of the dark ribs.

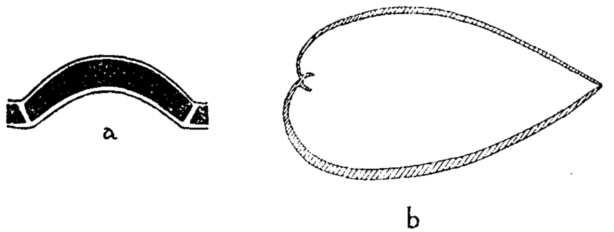

FIGURE 5.—Diagrams of shell structure: *a*, Cross section of rib and portion of adjacent grooves of left valve. (The upper white represents the outer white area which may be prismatic. The intermediate dark area (actually brown) and the inner white area are assumed to constitute the nacreous layer.) *b*, Cross section of shell through groove of upper (left) valve, rib of lower (right) valve, and "cartilage box"

In any fracture the shell appears laminated. When color is present there are the inner white laminæ, the intermediate brown laminæ, and the outer white lamina. No further lamination within this outer white layer has been distinguished, but in some fractures cross striæ have been seen. In fractures across the ribs the laminæ appear approximately parallel to the valve surfaces. In fractures along the ribs the brown laminæ are seen to extend at an angle and toward the ventral margin from the outer white layer to the inner white layer. The laminæ of the inner white layer are parallel to the inner surface. The layer (*Hypostracum* or *clear substance*) laid down at the end of the adductor muscle is relatively transparent and is clearly and regularly cross striated in fractures. In positions abandoned by the adductor in its advance, this clear layer is overlaid by the inner white layer, and near the umbos of some shells also by the brown layer.

Because of its distinctness from the underlying shell material, it is suggested that the generally thin outer white layer represents the prismatic. Seemingly the laminated structure, whether lying at an angle with or parallel to the inner white layer, and whether secreted within or without the pallial line, must be considered nacreous.[4] Because the brown material is found overlapping the clear layer, it is evident that the ability to deposit it is not confined to the mantle margin. From the slant of the brown laminæ, it seems, according to the accepted secretion theory, that for their deposition the outer or shell fold must be reflected sharply back over

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[4] According to Pelseneer (1906) the nacreous layer is composed chiefly of aragonite, of which, according to Dakin (1909) a scallop shell is mainly constituted. See also Horwood (1911, 1912).

the valve margin. The brown coloring has been found by Belding (1910) to be undestroyed by acid which removes other colors from the shell.

A thin, but definite, periostracum is present.

MANTLE

Morphologically the mantle is considered to be a fold of the integument of the dorsal portion of the molluscan body (Cooke, 1895). In the Lamellibranchia it consists typically of two equal portions or lobes which line the two valves, which they secrete, and surround the other soft parts and the mantle or pallial cavity. Because of their structure and blood supply they are held to be very important for respiration (Dakin, 1909, considered them the principal organs of respiration) or even to be the only important respiratory organs (Pantin, 1928).

In Pecten the mantle lobes differ somewhat in size and shape even as the valves differ. The margins of the two lobes are free from the shell and, except near the hinge line, not united one to the other. Anteriorly the united portion is very short, posteriorly about equal to the width of the shell ear. Not only are the pallial lobes largely ununited, except where contiguous along the dorsum, but they are generally free from the inclosed soft parts, being adnate in *Pecten irradians* only to the adductor muscle, the pericardium, a portion of the surface of the digestive deverticula, the cephalic extremity of the branchial axis, and a portion of each of the outer labial palps. The internal epithelium of the mantle is ciliated. The external epithelium, especially that of the free margin, secretes the shell (Cooke, 1895).

Except for the margins the mantle is very thin and transparent. Across it, nerves and even blood vessels may be plainly seen. The membranous structure and the elaborately branched vascular system indicate an important respiratory function.

The free, marginal portion (figs. 3 and 4) of the mantle, peripheral to the pallial line, is thick, tough, highly pigmented, and very complex. It is supplied with an elaborate system of radial and concentric muscles, many tentacles, ocelli, and a large nerve (the circumpallial) which functions as a ganglion. Three folds of the mantle margin are recognized. The *shell fold* may be taken as extending from the pallial line, demarking the free margin from the fixed portion of the mantle, to the periphery of the shell, where the mantle is reflected inwards, and ending in the periostrachal groove. Dakin (1909), working with the European *Pecten maximus* and *P. opercularis,* states that it bears long tentacles. None was observed in *P. irradians* or reported by Drew (1906) for *P. tenuicostatus* or *P. grandis* (see p. 571).

This fold is radially convoluted to form the ribs or rays of the shell.

The middle, sensory, or ophthalmic fold extends from the periostrachal groove to the base of the flap or *velar fold.* On it (figs. 3 and 4) are the ocelli and highly extensible and contractile tentacles in a band several tentacles wide. These tentacles are smallest next to the groove and largest next to the flap. Possibly the largest or most extensible of all occur near the ears. On occasion they are extended to the surprising length of about 2 inches. The ocelli, especially the larger ones, are generally in line with the larger tentacles, but are wanting in a section ventral to the ears. They vary considerably in numbers, and in adults are more numerous on the upper lobe. Because of the variations in numbers and size of eyes, it has been suggested (Drew, 1906) that new eyes are added with growth and that the number of eyes may be an indication of age. Drew worked with scallops not only of a different species but probably much longer lived. In *P. irradians* the quota, or very near it, for the lower lobe is attained early. Specimens a centimeter long possess but few less than those of full growth. However, for the upper pallial lobe the case is different. Specimens a centimeter or slightly greater in length have about the same numbers of ocelli below and above. The ocelli of the upper lobe continue to increase until (with 40 to 55 formed in those I examined) they are about one-fourth to one-half more numerous than those of the lower lobe. The ocelli of the ear section, rather small and few in number (about a dozen, chiefly at the posterior ear), are of interest because they are exposed when the shell is closed. Dakin (1909) noted that in various species the ratio of the number of eyes on the upper lobe to the number on the lower lobe increased with the relative flatness of the upper valve, but that even if the upper valve was the more convex the upper lobe had more eyes than the lower.

The abundance of scallop eyes and the unequal distribution between the two mantle lobes have led to considerable discussion. Patten (1886) has queried the scallop's need for many organs of vision if two suffice for other forms. Dakin believed numerous eyes were needed because they were not movable in various directions and images would be formed only of objects directly in front of an eye. A reasonable explanation for the greater abundance of eyes on the upper lobe seems more difficult to find. It is perhaps worthy of notice that this uneven distribution tends to equalize the light perception of the two valves.

The ocelli of Pecten have been the object of much study since Poli (1795) sketched their external appearance, recognized their resemblance to the vertebrate eye, and named some of the parts. Garner (1837) stated that scallops possess "small, brilliant, emeraldlike ocelli, which, from their structure, having each a minute nerve, a pupil, a pigmentum, a striated body, and a lens, and from their situation at the edge of the mantle, where alone such organs could be useful, and also placed, as in Gasteropoda, with the tentacles, must be organs of vision." Krohn in 1840, according to Sharp (1884) and Dakin (1910), greatly advanced knowledge of the structure of the ocellus which he designated a closed vesicle. Apparently he was the first to note the septum and the division of the nerve into two branches.

The "modern" period in the study is taken to begin with the paper by Hensen (1865), who not only advanced knowledge of eye structure but also proved something of a seer when, after remarking upon the clearness with which details of the eye may be observed, he asked "but how much toil (Mühe) will be necessary before the entire structure of this cubic millimeter will be understood?" In the many years that have elapsed a great amount of minute attention has been given the structure of this diminutive organ and presumably the end is not yet.

Among later accounts may be mentioned Hickson (1880), Patten (1886), Rawitz (1888), Schreiner (1896), Hesse (1900, 1902, 1916), Hyde (1903), Dakin (1909, 1910a), and Küpfer (1916). Of these only Hyde worked with *P. irradians* or other American scallop. Some of her findings were so different from those of other investigators that Dakin (1910a), working with European species, made special but unsuccessful efforts to confirm them. The retina evidently is very complicated and the chief cause of disagreement. The paper by Dakin (1910a) presents a clear, detailed, and very useful account based on extensive personal investigations and with a careful survey of the literature. The book by Küpfer (loc. cit.) is unusually elaborate and complete. Notable features are additions to the knowledge of the outer layer of the retina and of the development of the eyes, and a detailed comparative anatomical discussion. The recent account (Light, 1930) of light receptors in Mya is of interest.

I have examined several eyes fixed in formalin, stored in alcohol, and cleared in glycerin. Although histological details were not determinable, major structures could be distinguished. Figure 6, showing only the general structure, is based on dissection of such material.

The following brief account is based largely on that of Dakin:

The eyes are situated at the end of short stalks located among the tentacles of the middle fold. The stalk is composed chiefly of connective tissue and contains muscle fibers, large blood spaces, and the optic nerve. This nerve has been supposed to come from the ganglionic circumpallial nerve, but according to Dakin (1910a) most of its fibers connect directly with the visceral ganglion. The epithelium is pigmented around the eye forming what has been termed an iris (Patten, 1886). In front of the lens it is clear and is termed cornea.

Separated from the cornea by a layer of clear connective tissue is the lens, which is composed of many transparent cells of unusual shape and arrangement. The inner face of the lens is much more convex than the outer. Back of the lens and overlying the retina is the membranous septum.

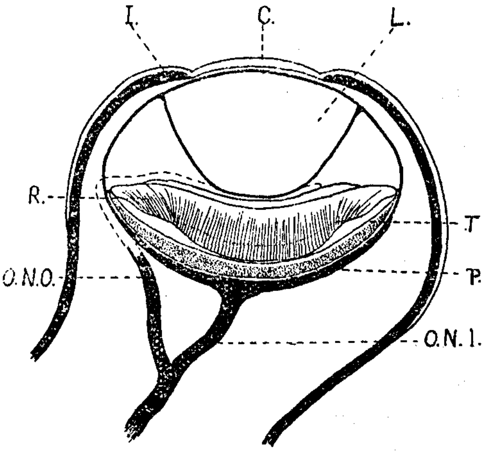

FIGURE 6.—Sketch of eye on dissection of unstained material cleared in glycerin. *C*, Cornea; *I*, iris, made up of pigmented and clear layers; *L*, lens; *O. N. I.*, inner branch of optic nerve which spreads around the base of the optic vesicle to the edge of the retina; *O. N. O.*, outer branch of optic nerve, the latter course of which, leading to the face of the retina, was not followed in these dissections; *R*, retina overlain by septum (not designated) with three noticeable layers (an outer or outer ganglionic layer, a layer of rod cells, and an inner layer of rods); *P*, pigmented layer (tapetum of Patten); *T*, tapetum (argentea of Patten)

The complex, inverted retina has been considered to consist of various numbers of layers but, according to Dakin (1910a), is best considered as of two, an outer layer of distal sense cells and an inner one of rod cells and rods. The outer layer is innervated by the outer or distal branch of the optic nerve which enters from the front through the septum, the inner layer by the inner or proximal branch which enters through the periphery.

Back of the retina are two prominent layers, each of which has been termed "tapetum." Patten (1886) referred to the inner or frontal of these, which is refractive and gives the eye its metallic glitter, as the argentea—an appropriate name. However, this layer previously had been termed "tapetum" by Krohn who discovered it (Dakin, 1910a). The outer or abfrontal of these two layers was designated "tapetum" by Patten but probably is best referred to as pigment layer (Dakin, loc. cit.). The layer of connective tissue surrounding the abfrontal half of the optic vesicle—that is, that portion back of the septum—was termed "sclerotica" by Patten, to which some authors have objected.

Although there has been so much work on the ocelli, most of it has been histological so that knowledge of their functioning still is rather unsatisfactory. From their structure they appear to be organs of vision. However, their very elaborateness and high development only add to the puzzle, for if such highly organized structures are organs of sight, their vision would be expected to be excellent and not only easily demonstrable but evident beyond a doubt. On the contrary, although scallops undoubtedly are sensitive to light, any image vision they possess is so poor or so limited as to be difficult to establish. One difficulty is in obtaining specimens that react normally (Wenrich, 1916, states that only scallops from very shallow water are satisfactory). Another is that scallops frequently cease to react after repeated stimulation.

Marine mollusks have been grouped according to their reaction to changes in light intensity into those which react to increases and decreases, those which react to increases only, and those which react to decreases only. It seems generally agreed that scallops belong with those that react to decreases only. With normally acting individuals a shadow cast on the eyes causes quick complete or partial closing. Using small objects to produce local shadows, Rawitz (1888) found that the shadow must fall on several eyes to produce a reaction. Wenrich (1916), using instead local illumination through slits or small holes in a disk, found that cutting off the light from as few as two eyes (the smallest number tested) produced definite, although sometimes local, reaction.

It has been held that, in addition to being sensitive to decrease in illumination (shadows), scallops were sensitive to movement of objects. To test this Wenrich (1916) placed individuals which had been found to react to decreases in illumination, but not to increases, in a glass dish in one end of a box at the opposite end of which was black paper. Against this black background small white cards of various sizes were moved upward to a level with the scallops. It was believed, by this means and proper precautions to prevent uncontrolled light changes, that the only change in illumination of the scallop eyes was increase (to which, as above noted, the scallops had been found not to react) and, therefore, that reactions were attributable not to changes in illumination but to perception of the movement of the object. Unfailingly the animals gave immediate and vigorous responses by closing the valves or by contraction movements of the velar folds and tentacles. The reactions occurred with both slow and rapid movements and also when downward or horizontal. The smallest effective white card was 1.5 centimeters square at a distance of 35 centimeters (the distance used throughout these experiments).

Uexküll (1912) placed a scallop in one aquarium and a starfish—its principal enemy—in an adjacent aquarium. There was no response until the starfish moved, when the scallop instead of closing extended its tentacles in the direction of the starfish.

According to my observations, movements, particularly sudden movements, of an object within a few feet of freshly caught scallops and in their line of vision (even when, as in Wenrich's experiments, an increase in illumination is involved), caused complete or partial closing. When a scallop reopens, long tentacles of the adjacent sector may or may not follow the object as it moves.

Probably there is sufficient evidence that the ocelli are organs of vision, but a better knowledge of their functioning and usefulness to the scallop is much to be desired.

The very extensible tentacles of the middle or ophthalmic fold have been supposed (Uexküll, 1912) to be endowed with both chemical and tactile sensitivity. Dakin (1910) found that the introduction of a chemically irritating substance, as one obtained from starfish, caused scallops to swim and concluded that the perception was by the "sensory tentacles." The writer does not find that this chemical sensitivity has been traced definitely to these tentacles. Tactile sensitivity is readily demonstrated.

Sections of the margin of the mantle, cut from a living scallop by the author and placed in a dish of salt water, soon relaxed with some extension of the tentacles of the middle fold. Touching one of these tentacles caused contraction not only of the tentacles but of the whole excised portion—an action not caused, in my observation, by touching the tentacles of the velar fold. However, after a portion of the mantle was so cut as to separate the middle velar folds from the tissue containing the circumpallial nerve, there appeared to be no contraction of the piece as a whole or of the parts. Touching a tentacle did not even cause contraction of that tentacle.

The third fold of the mantle margin, sometimes referred to as velum, but here termed "velar fold" or "flap," is the most prominent and distinct of the three. (Figs 3 and 4.) It is wide and well supplied with muscles, is brightly marked (as with yellow, black, and white), and, near its free margin, bears alternately large and small tentacles (the guard tentacles) in a somewhat zigzag row. The velar folds play an important part in swimming and presumably in feeding. The free margins may be brought together so that a continuous wall or curtain is formed. When the scallop lies at ease with the valves well separated, they are extended toward each other, nearly at right angles to the plane of the valves, meeting or nearly meeting close to the posterior ribs.

The so-called guard tentacles, which are not considerably extensible, are directed in a convex arc toward those of the other flap to form a screen through which the food and water is drawn. If an indrawn object, such as a large carmine grain, hits a tentacle, the tentacle makes a peculiar flicking motion, but the shell is not closed nor the object otherwise prevented from entering. Moreover, a touch with a prod, at least at times, does not cause the valves to close. While the valves remain apart, whether the opening is wide with the velar folds extending up and down, or narrow with these folds horizontal, a more or less complete screen of these "guard" tentacles is maintained. With important tactile function apparently wanting, a chemical, olfactory, or taste function is strongly suggested.

To test this a starfish was crushed in a mortar and a cloudy liquid irritating to scallops obtained. A freshly caught scallop was placed in a rectangular glass dish. When the scallop had opened wide its shell and arranged the mantle margin with the guard tentacles across the inhalent opening and well separated from the tentacles of the middle fold, the irritating cloudy liquid was gently introduced directly to the guard tentacles by a special pipette with bent tip. Repeatedly and unfailingly as the cloudy liquid came to the guard tentacles, these were sharply withdrawn and the shell violently closed. Beyond question the tentacles of the middle fold did not enter into the response and it seemed clear that the exciting substance had not entered the pallial cavity when the reaction began. Pipetting the same liquid against individual extended tentacles of the middle fold caused no reaction beyond some contraction of the tentacles touched, as when water was used—evidently a tactile response. Squirting sea water against the guard tentacles failed to induce shell closing. These experiments seem to show that the guard tentacles possess an olfactory, gustatory, or some chemical sensitivity.

Anterio-dorsally and posterio-dorsally, near the ears, the velar folds are narrowed with some abruptness and are without tentacles. When the valves are apart these folds are so extended that they touch, or nearly touch, at the ventral limit of the posterio-dorsal narrowing, bounding a well marked exhalant opening. For the young this arrangement of the folds has been termed a pseudo-syphon. The opening formed by the anterio-dorsal narrowing may be confluent with the large inhalant opening (extending from the ventral limit of the exhalant) or separated. The ciliary current through it is inhalant (and the only inhalant current when the shell is closed), but powerful exhalant currents occur during swimming and for the ejection of material rejected by the palps.

An account of the action of the mantle during swimming will be found in the description of that process.

GILLS

In the Lamellibranchiata, gills are of unusual importance. Not only do they produce the water currents which bring food and oxygen and carry away carbon dioxide and other wastes, but they also separate food organisms from the inhalent current and convey them toward the mouth. It is even claimed that they absorb food directly from the water. Presumably, in spite of recent claims to the contrary, they are important organs of respiration. In addition to being of manifold functional importance, the gills provide morphological evidence of special value for classification, as previously noted.

STRUCTURE OF THE GILLS

The minute structure of the gills, especially the filaments, has been described or figured by Kellogg (1892), Drew (1906) and Dakin (1909). The present account will not enter elaborately into the histology and will depend upon illustrations for structural details and arrangements. Studies have been largely with living or fresh material.

In the section dealing with classification it was noted that the filaments of the gills are reflected and are held one to another by spurs (not vascular connections). As now interpreted there are two gills (or ctenidia of branchiæ)—one on the right and one on the left side of the body. Each gill (see fig. 7*a*) consists of two demibranchs and a branchial or ctenidial axis from which they are outgrowths. In turn each demibranch consists of two lamellæ (direct and reflected)—one composed of the direct limbs of the filaments, the other of the reflected limbs. The demibranchs are supported only by the axis, the inner lamella of each gill being free from the visceral mass, the outer from the mantle. The lamellæ are not flat but accordion pleated or folded (plicate gills). This folding, which is steep next to the axis and relatively shallow and broad at the outer edge, is due to the arrangement of the branchial filaments, which are grouped in closely compressed folds at the axis and are united at thin plates at their tips.

Two distinct types of filaments occur (heterorhabdic gills). At the bottom of each groove is a principal filament. Making up the convex folds between are 16 ordinary filaments. (See fig. 7*b*.) As shown in Figure 3 the gills are roughly crescent shaped, being greatly curved and with the filaments shortened toward the ends of the axes. From the branchial axes and from the free edges of the reflected lamellæ, the principal filaments spread fanwise and draw the ordinary filaments (which typically are held an approximately uniform distance apart by the spurs) nearer and nearer to their level and thus broaden and flatten the lamellar folds.

The ordinary filaments are slender and relatively simple. (See figs. 7 and 8.) Around a thin-walled, flattened, chitinous tube is an epithelium which is thickest at and near the frontal face, whence arise, along its full length, the very numerous frontal cilia. Near the front on either side are the long and powerful lateral cilia. (See fig. 7*c*.) The elongate latero-frontal cilia described for Mytilus, Ostrea, and various lamellibranchs have not been found in the scallop, nor have I succeeded in demonstrating that the most lateral of the frontal cilia (in a latero-frontal position) function as would typical latero-frontal cilia. Dividing the filamentary tube into frontal and abfrontal portions is the intrafilamentary septum. The connective spurs are situated at frequent, regular intervals at the abfrontal edge. These spurs evidently are highly muscular and the filaments somewhat so, as will be discussed more fully later. The

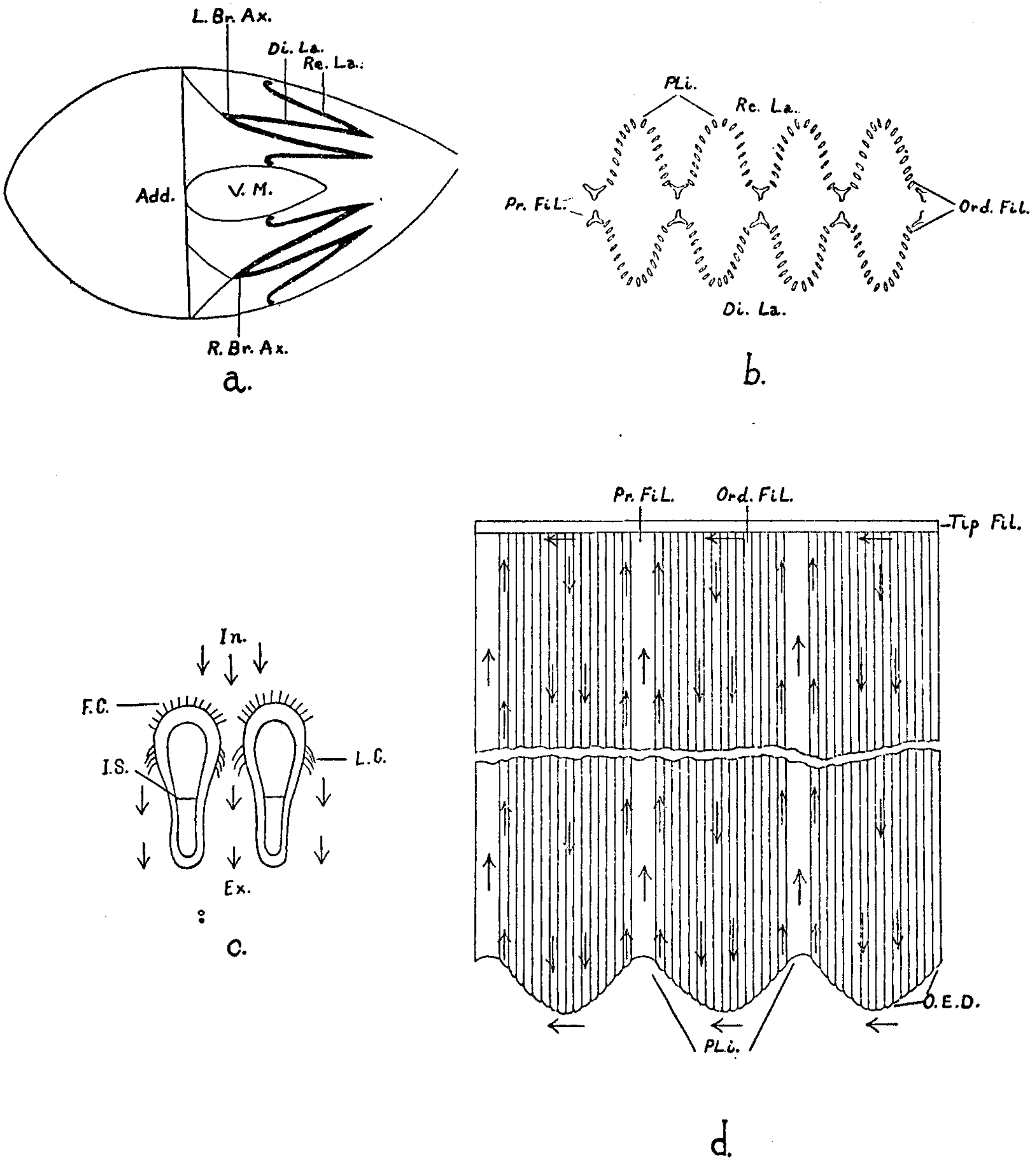

FIGURE 7.—*a*, Diagrammatic transsection of gills showing their suspension and position relative to adductor, visceral mass, and pallial lobes; *b*, longisection through portion of outer demibranch of left gill (transsection of plications and filaments of direct lamella (below) and reflected lamella (above)); *c*, transsection of adjacent ordinary filaments, showing cilia and currents produced by lateral cilia; *d*, superior view of portion of reflected lamella of outer demibranch of left gill (very diagrammatic); *Add.*, adductor muscle; *Di. La.*, direct lamella; *Ex.*, exhalant current; *F. C.*, frontal cilia; *In.*, inhalant current; *I. S.*, intrafilamentary septum; *L. Br. Ax.*, left branchial axis; *L. C.*, lateral cilia; *O. E. D.*, outer edge of demibranch; *Ord. Fil.*, ordinary filament (in "*b*" direct (below) and reflected limbs of the same filament); *Pli.*, plications; *Pr. Fil.*, principal filament (in "*b*" direct (below) and reflected limbs of the same filament); *R. Br. Ax.*, right branchial axis; *Tip. Fil.*, united tips of filaments (very diagrammatic)

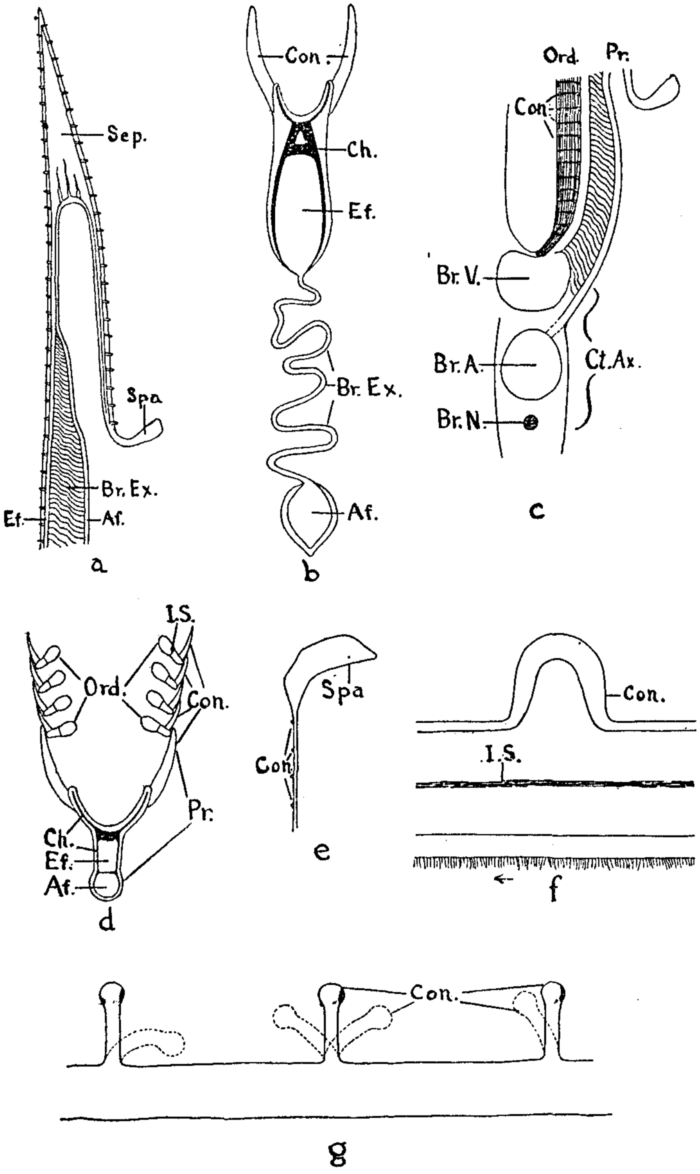

FIGURE 8.—Diagrammatic sketches of gill filaments; *a*, A principal filament; *b*, cross section of a principal filament, through branchial expansion; *c*, ctenidial or branchial axis with principal and ordinary filaments, etc.; *d*, cross section, between branchial expansion and interlamellar septum, of a principal filament and adjacent ordinary filaments; *e*, distal portion of an ordinary filament, spatulate tip drawn carefully from specimen; *f*, an ordinary filament with a contracted spur and with frontal cilia; *g*, an ordinary filament with connective spurs expanded and in various positions to show power of movement. *Af.*, afferent branchial vessel; *Br. A.*, branchial artery; *Br. Ex.*, branchial expansion; *Br. N.*, branchial nerve; *Br. V.*, branchial vein; *Ch.*, chitinous supporting structure; *Con.*, connective spurs; *Ct. Ax.*, ctenidial axis; *Ef.*, efferent branchial vessel; *I. S.*, interlamellar septum; *Ord.*, ordinary filament; *Pr.*, principal filament; *Spa.*, spatulate tip of filament

spurs bear active cilia. The ordinary filaments originate nearer the center of the face of the branchial axis than do the principal filaments, and connect only with the efferent branchial vessel.

The principal filaments are much greater in diameter than the ordinary filaments and stiffened more with chitin. (See fig. 8.) In addition they are much more complex. The connective spurs are much enlarged and frontal, rather than abfrontal, in position. The basal or *branchial expansion* and *interlamellar septum* occur on every principal filament, but on these only. The principal filaments, so numerous they lie almost one against another along the branchial axes, provide nearly all the transverse support for the gills. The interlamellar septa are important in maintaining the reflected lamellæ in position. Vascular connection is not only with the efferent but also, along the interlamellar edge and the branchial expansion, with the efferent branchial vessel. The presence of abfrontal cilia is indicated in my experiments by the movement of fine carborundum along the abfrontal edge of the branchial expansions toward the branchial axis.

Filamentary nerves of ordinary and of principal filaments are described by Dakin (1909), who figures a small nerve at the interlamellar edge of an ordinary filament. Kellogg (1892) figured no filamentary nerves, Drew only those of the principal filaments. The behavior of the filaments indicates nervous structures in both types.

The branchial axis is decidedly tough and firm and consists largely of connective tissue, but with a good supply of muscle fibers (Dakin, 1909). It contains the branchial nerve and afferent and efferent vessels. The epithelium is ciliated. The suspension or attachment of the axis evidently is adapted to the animal's existence with the right side down. (See fig. 7*a*.) Anteriorly each axis is attached for a very short distance to the lateral edge of the body mass (surrounding the stomach) and to the adjoining mantle. For the left axis this is over the pericardium. The next attachment is to the sheath of the adductor muscle rather close to the pallial lobe. This attachment of the left lobe continues to the posterior limit of attachment, somewhat overlapping the rectum. For the right axis conditions are more complicated. The simple direct attachment to the adductor sheath continues only a short distance, about half the length of the kidney. Ventrally and posteriorly to this, the support may be said to be twofold. On the one hand the axis is attached to the mantle lobe, on the other to the sheath of the adductor. (Fig. 7*a*.) Attachment to the adductor is by two connective tissue flaps which serve to raise the gill above the pallial lobe. The anterior and larger of these flaps is roughly triangular. Considered as an isosceles triangle, the base lies along the branchial axis, one side (attached) along the dextro-posterior margin of the kidney (or the course of the branchial nerve outside of the gill), the apex near the right urinogenital opening and the other side (free) along the course of the fourth lateral pallial nerve. At the posterior limit of attachment the second flap extends from the mantle along the adductor sheath securing the axis thereto at a considerable distance from the lobe. Each axis continues around the adductor considerably beyond the posterior limit of attachment.

FUNCTIONS AND ACTIVITY OF THE GILLS

Respiration.—The functions of the gills have been briefly alluded to in the paragraph introductory to the discussion of the gills. It was there noted that recent denial of important respiratory function has been made. Hitherto it has been almost universally held that the gills of lamellibranchs were important for respiration.

Although considerable respiratory function has been attributed to the pallial lobes, the gills are generally assumed to be the principal respiratory organs. The basis of this assumption is to be found in their typical, finely tubular structure and the fact that they are bathed as are no other suitable structure by the inhalant water current. In 1928 Pantin wrote that "A Lamellibranch mollusk feeds with 'gills,' so called, which have no respiratory function." Later, in a letter, he qualified this slightly, but admitted only a limited amount of respiratory function, as of any exposed surface. Referring to Dakin (1909) he stated that the mantle appears to be the chief organ of respiration owing to its extremely effective blood supply and probable slow metabolism, whereas the metabolism of the gill filaments is extraordinarily high, so that it is quite probable that all the oxygen absorbed by the gills is required for their own activity. He further refers to Dakin's (1909) conclusion that the heart receives completely oxygenated blood from the mantle and "*probably* [the italics are mine] only incompletely oxidized" blood from the gills. Doubtless this makes a good case for questioning, but hardly for definitely denying that gills are organs of respiration.

Considering the arguments advanced, it seems reasonable to continue to consider that the principal filaments with provisions for efficient vascular circulation and with structures so well suited for respiration as the branchial expansions, perhaps aided to an important extent by the interlamellar septa, are important respiratory structures. The extent of the branchial expansions alone are sufficient to constitute a very considerable gill. Indirectly the gills surely are important for respiration, for they produce the all-important oxygen bringing and CO_2 removing water current.

CILIARY ACTION OF THE GILLS

If there is some question as to whether or not the gills are important organs of respiration, there is none that they are important organs of feeling. The action of the lateral cilia, as shown by Wallengren in 1905 (see Yonge, 1926) and Orton (1912), create the inhalant-exhalant water current. From this current the gills filter out food organisms, often with much material that is undesirable, and pass them toward the mouth. For the filtering action the gill filaments of some mollusks are provided with long, latero-frontal cilia which interdigitate with those of adjacent filaments and beat slowly with the effective stroke toward the center of the front of the filament. As previously noted no such cilia have been found for Pecten. However, incoming organisms or other particles are entangled by the mucus secreted by the filaments and thus effectively removed from the current.

Particles caught in the mucus or otherwise brought to the frontal surface of the filaments come under the influence of the frontal cilia. Depending on whether they impinge on the filaments in the grooves (that is, on the principal filaments and those on either side) or on the tops of the folds (that is, on the filaments intermediate between the principal filaments) (see figs. 7*b* and 7*d*), they are carried by the longitudinal beat of the frontal cilia to the inner or outer edge of the lamella. At these places the frontal cilia beat transversely to the filaments in such a way as to convey the particles toward the palps. (Fig. 7*d*.) As pointed out by Kellogg (1910, see also Kellogg, 1915), this unusual condition provides a food-selective mechanism in the gills. If suspended particles are abundant, as when the water is heavily laden with silt, the material on the gills becomes imbedded in strings of mucus secreted in increased amounts, stretched across the filaments. The currents in the grooves tend to carry these strings toward the branchial axis; but the currents on the tops of the folds prove more effective and carry the material, including that in the grooves, to the outer edge of the demibranchs. It is probable that ordinarily the masses so carried, being heavy and no "food groove" being present in our scallop (although a shallow one is figured for *P. maximus* by Orton, 1912), drop off the gill. Under some circumstances, however, as I have observed experimentally, the material carried there in long strings to the outer edge is not so heavy as to drop and is carried toward the palps. When not too abundant, apparently most material falls into the grooves and, unless it is sharp or irritating so that it greatly stimulates mucus secretion or causes the gills to "writhe," is carried either to the base or tips of the filaments, where a strong ciliary current conveys it to the palps.

A few observations on the rate of travel of particles along the frontal cilia paths were made in these investigations. Most of the observations were of the speed of particles or of small mucus strings conveyed transversely to the filaments, close to their tips and toward the palps. (Fig. 7*d*, at top.) Rate of travel often could be seen to be very irregular. Sometimes a particle would hit a hump in the gill and stop or almost stop. At other times there would be obvious but less drastic slowing. However, there were many times when progression was more regular. Most of the speeds recorded fell close to 1 millimeter per second at about 21.5° C. (21.2° C.–21.8° C.). A few times notably higher speeds were noted (up to 2.3 millimeters per second) with small particles which went the distance without interference and evidently were in the most favorable current. Determination of rate of travel along the filaments was much more difficult because of conflicting currents and the "writhing" of the gills. Therefore, only a few readings were obtained. Speeds recorded were close to 0.4 millimeter per second.

It may be remarked that the ciliary motion of lamellibranchs is not reversible, nor is there evidence of nervous control of the activity of cilia (Gray, 1928). This activity is, however, affected by temperature, hydrogen-ions, and other water conditions. (See the various papers by Gray, also Galtsoff, 1928 and 1928a.)

BRANCHIAL MOVEMENT

Although muscle fibers have been found in the branchial axis, the movements of the gill and of its parts indicate much more muscular tissue than would be supposed from morphological studies. Kellogg (1910) noted the writhing and swaying of the gills when much material was deposited upon them. Touching a filament with a needle causes contortions for a considerable distance along a lamella. Examined in more detail, motion is found to consist to a large extent of elongation, contraction, and pivotal movement of the connective spurs (see fig. 8, *f* and *g*), and of the extreme transverse movement of the principal filaments. Obviously one effect of the elongation and contraction of the spurs is to vary the interlamellar space, and this may be important for filtering (as by permitting large particles to pass through or by removing more effectively abundant fine silt). The transverse movement of the principal filament is remarkable. As shown in Figure 8, *b* and *d*, the frontal surface is highly concave with widely extending lateral edges which bear the large connective spurs. In this movement these edges may be brought close together or turned abfrontally until they and the spurs lie against the sides of the axis of the filament. Excised portions of principal and ordinary filaments have been seen to bend longitudinally to a marked degree and to respond to stimuli. Presumably the principal if not the sole purpose of branchial movement is to rid the gills of irritating substances or objects.

GREENGILL

In the winter of 1927–28, the writer collected scallops in western Bogue Sound, N. C., which were found to have bluish green gills. Examination of fresh material revealed greenish pigment in the epithelial layer of the ordinary filaments. A sketch from this fresh material shows an irregular band of pigment (green granules) on the sides of the filament near the front. From the arrangement of the granules it does not seem that they were grouped in "secretion cells" as Lankaster (1886), Herdman and Boyce (1899), and others in Europe, and Mitchell and Barney (1917) in this country have reported for greengill oysters. Nevertheless there is reason to believe that the greening is of the same nature in oysters and scallops. It appears that with oysters the green granules are not always confined to the "secretion cells" (Ranson, 1927). As is generally reported for oysters with greengills, these greengilled scallops were in very good condition. The very region in which they were found had been abandoned by oystermen because the oysters became greengilled. There is much similarity in the feeding and location of scallops and oysters (both being forms which live on, rather than in, the bottom).

Although it was not learned whether *Navicula osteraria* was present, because it has been reported with such remarkable uniformity in connection with the greening of oyster gills, it may be taken as indicated that it occurs in this region of greengilled oysters. Certainly there is no reason to believe that food organisms or material which would color the gills of scallops would not affect those of oysters and vice versa. Although I have seen no other references to the greening of scallop gills, that is not surprising in this country, at least, for here the gills are removed from the market product and no economic interest attaches to their color.

LIPS

The labial palps (fig. 3) may be considered specialized, lobate prolongations of the lips. There is a pair of them on the right and left sides of the mouth, between the mouth and the end of the gills. The outer palp of each of these pairs is a continuation of the dorsal lip, the inner of the ventral. Between them is the oral groove. The adjacent surfaces of the palps of each pair are ridged and very elaborately ciliated. It is the function of the palps either to transmit to the mouth or to reject as unsuitable the material delivered by the gills. In the selection the muscular movements of the palps aid the elaborate sorting action of the complex ciliary arrangement. The ciliation of the palps of scallops has been studied and figured by Kellogg (1915). For detailed accounts of palps see Churchill and Lewis (1924) and Mathews (1928).

The lip ridges leading from the palps to the mouth (or the opening into the œsophagus) are, in the scallop, most remarkably produced into much branched, "tufted" prolongations (indicated in fig. 9*c*). In life they are active and evidently ciliated. As noted by Dakin the branched structures from the two lips interlock (or overlap) over the mouth so that there are, in effect, two oral openings, one for each groove.

ALIMENTARY TRACT

The mouth or opening into the oesophagus is wide and dorso-ventrally flattened. From this the oesophagus rapidly tapers and thereafter, bending to the left, continues in its narrowed form to join the stomach. The action of the cilia of its epithelial lining conveys food and other material to the stomach.

The stomach is of a very complex shape which is better illustrated than described. In Figure 9, *a* and *b* are from plaster casts, and *c* and *d* from dissections. The numerous, small branches are the beginnings of the diverticula. A considerable portion of the stomach walls are ridged or folded in a complex manner. Many ridges (fig. 9*d*) on the right or lower side converge toward the opening to the mid-gut. This system of ridges leads, in part, from the ducts of the diverticula.

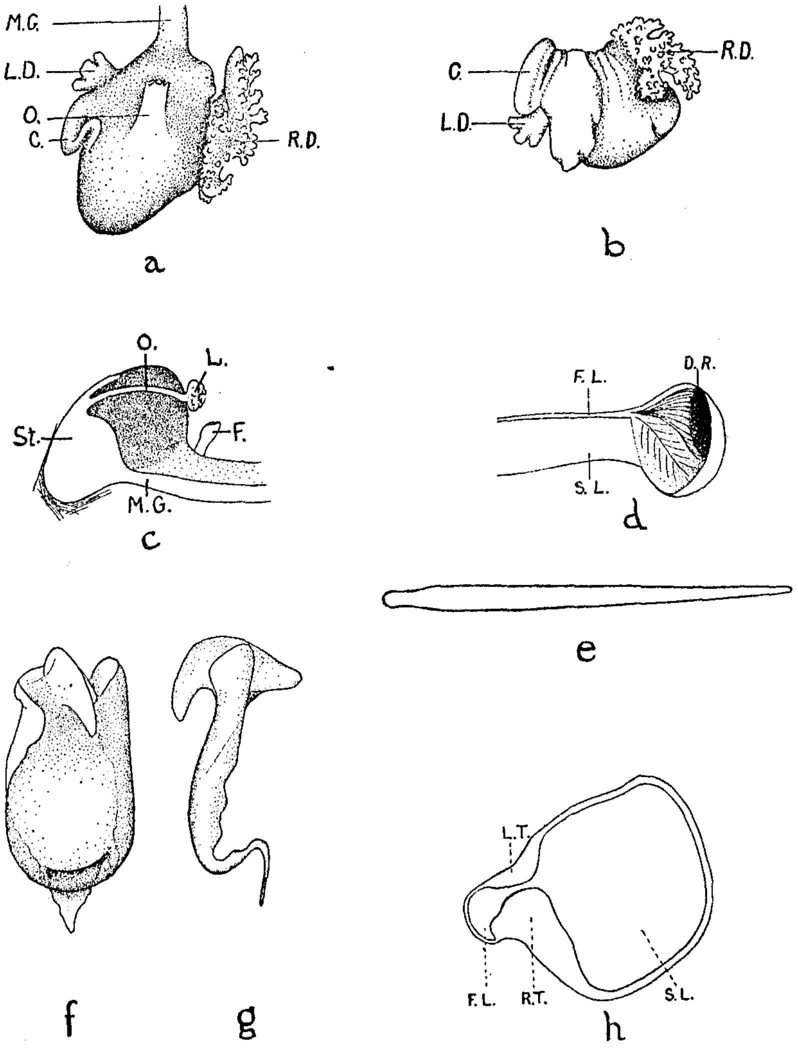

FIGURE 9.—*a*, Dorsal aspect of stomach; *b*, posterior aspect of stomach (*a* and *b* from plaster casts); *c*, dextral view of section through esophagus, stomach, and portion of mid-gut; *d*, interior view of right (lower) side of stomach; *e*, crystalline style; *f*, posterior, and *g*, lateral views of gastric shield; *h*, cross-sectional sketch of mid-gut close to stomach, antero-ventral view (looking toward stomach); *C.*, caecum; *D. R.*, duct of right diverticula; *F.*, foot; *F. L.*, food lumen; *L.*, lips; *L. D.*, duct of left diverticula; *M. G.*, mid-gut, with style lumen; *O.*, œsophagus; *R. D.*, basal portion of right diverticula

The epithelium of the stomach is possessed of very active cilia which produce a complex circulation of the stomach contents. In an opened stomach, introduced fine particles of chalk (superior to carmin in visibility in such a situation) can be seen going in and coming out of the ducts to the diverticula. Material on the ridged surface of the ducts always comes out and, at least from diverticula of the right side, follows the converging furrows to the mid-gut.

In the stomach lies the gastric shield which doubtless takes the thrust of the rotating style, as described for other lammellibranchs. The shield (fig. 9, *f* and *g*) is horny in consistency, ornately shaped, and of a somewhat greenish yellow color, with opalescence, which resembles rather strikingly the color of the lining of the mid-gut. Nelson (1918) believes the substance of the shield probably to be in the nature of chondrin, Gutheil (as noted by Yonge, 1926a) that it is secreted by the underlying epithelial cells and Yonge (1926a) that it is formed of fused cilia.

Extending into the stomach is the rodlike gelatinous crystalline style, clear greenish amber in color and sometimes spirally marked. The shape, with the stomach contents removed from the "head," is shown in the accompanying illustration. (Fig. 9e). Various workers (Barrois, 1889–90; Mitra, 1901; and Mackintosh, 1925), working with various genera have found the style to consist principally of water (about seven-eighths) and globulin (about one-eighth), and to contain digestive enzymes (Coupin, 1900; Mitra, 1901; and Dakin, 1909; Nelson, 1918; and Yonge, 1926a). The style dissolves in water but is preserved by formalin, is quite firm in a freshly opened animal, and is concentrically laminated. The head, in the stomach, is found buried in a mass of food material which must be washed or teased away before the shape of this end can be determined.

The markings to be found in or on some styles evidently are inclusions of food or some associated substance and presumably are spiral because of rotation of the style. Rotation of the style of lamellibranchs apparently was first observed by Nelson (1918) who opened the stomach for the purpose. More recently it has been observed through the shells of young mussels (Churchill and Lewis, 1924) and oysters (Yonge, 1926a), although I have not succeeded in observing it in Pecten. All observations with which I am familiar are to the effect that, viewed from the head end, the style rotates clockwise. Nelson (1918 and 1925), Allen (1921), and Orton (1924) have supposed one of the functions of the style to be the return of food from gut to stomach. If the style markings are inclusions of material being so returned, the indicated direction of rotation is clockwise, if "streamers" from the stomach, it is counterclockwise. From a consideration of the findings and opinions of recent workers it seems probable that they are the former and, therefore, that the rotation is clockwise. Moreover, in larvæ identified as *P. irradians* I have observed the stomach contents to rotate rapidly in a direction corresponding with this clockwise rotation of the style. It is supposed that the style is not only continually revolved but also pushed into the stomach (against the gastric shield) where the head is continually dissolved. Frequently, in the stomachs of scallops possessed of a firm style, mingled with the rest of the stomach contents there is to be found a sticky, yellowish substance which apparently and presumably is dissolved material of the style.

The nature and functions of the style have fascinated zoologists who have evolved many theories. Of these the following may be worthy of mention: To act mechanically upon the food, apparently as a sort of chewing organ; to prevent the food passing too quickly through the alimentary canal before digestion can take place; reserve food material; an excretion; to lubricate the undigested food material; a digestive ferment. That the style contains an enzyme which converts starch to sugar seems established, but just how important the enzyme of the style is in the economy of digestion, has yet to be determined. Nelson (1918, 1925) believes that one

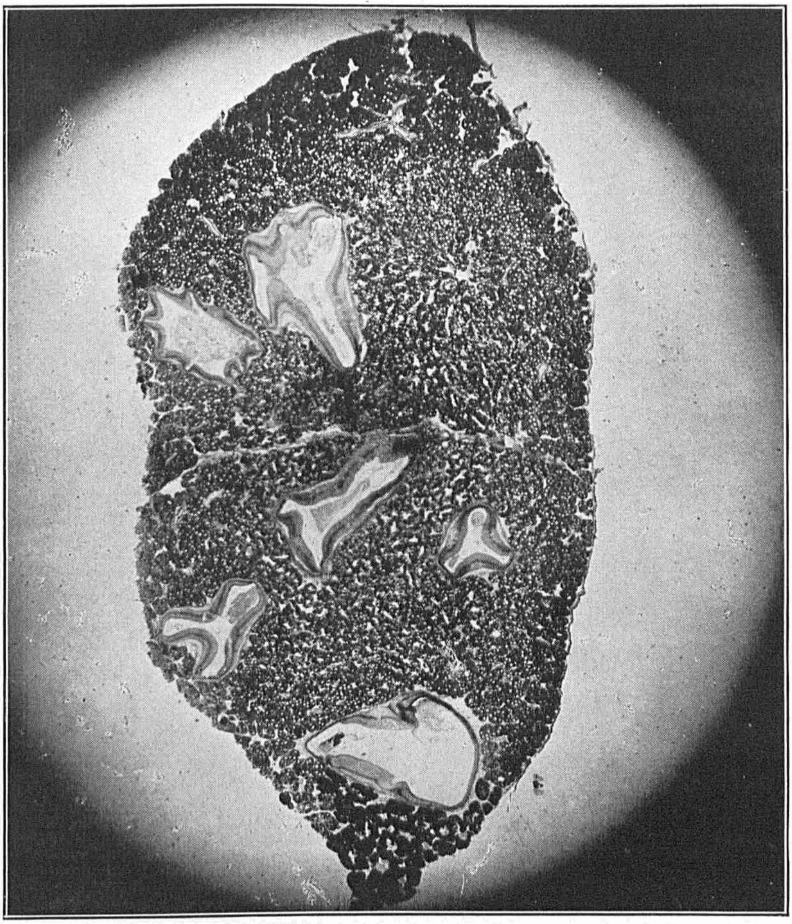

FIGURE 10.—Cross section through viscereal mass, looking away from the stomach (left and right reversed), and showing the intestine cut in six places. Close to the bottom lies the descending portion of the intestine (mid-gut), leading from the stomach; above and to the left that portion leading toward the anus. Below the lowest section lies testicular tissue; above and occupying most of this portion of the mass, ovarian tissue. Sperm and eggs abundant. Iron hæmatoxylin

of the principal functions is to rotate the food material received from the œsophagus and so aid mechanically in the sorting of food and that an important amount of food material may be caught up by the style and returned to the stomach. In addition, this stirring of the food by the style with the continual dissolving of the head of the style would seem ideal for mixing the enzyme of the style with the food material.

I have not noted a scallop freshly killed soon after removal from the water which did not possess a style. A special search of scallops in poor condition has not been made.

Nearly surrounding the stomach is a mass of tissue which in *P. irradians* is of a dark green color. Earlier writers termed this liver or hepato-pancreas. Dakin, (1909) who studied the contents of this tissue (Pecten) and found that an extract would digest proteids, starch, and fats (that is, contained amylase, protease, and lipase), naturally assumed that these substances were discharged into the stomach to prepare the food for absorption by the intestine, and gave the name digestive gland. Yonge (1926a) working with *O. edulis*, concludes that these substances are not so discharged but that the function of the organ is intracellular digestion, and employs the term "digestive diverticula," which is here adopted. "Circumstomachal organ" or "circumstomachal tissue" would be reasonably definite as to designation and noncommittal as to function.

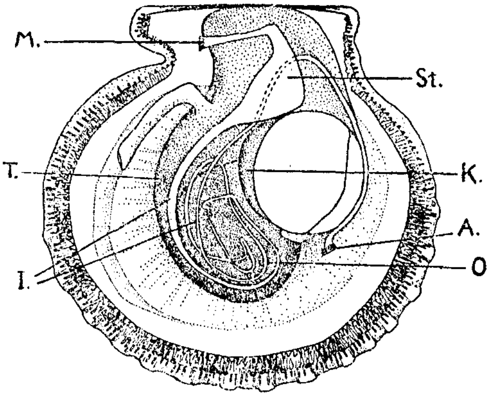

FIGURE 11.—Sketch showing alimentary canal with much convoluted intestine *in situ* with other parts. *A*, Anus; *I*, intestine; *K*, kidney; *M*, mouth; *O*, ovary; *St.*, stomach; and *T*, testis

The intestine of scallops, as figured by Drew, Dakin, and Belding, is a short affair scarcely more convoluted than that of an oyster. In local specimens, dissection and sectioning reveal a long intestine with several convolutions within the visceral mass (figs. 10 and 11), as does examination of free-hand sections of a specimen from Massachusetts. The style sack or cæcum connects by means of a narrow slit with the food passage, which it greatly exceeds in cross section. (Fig. 9*h*.) Typhlosoles are large and distinct. Ciliation, general throughout the intestine, is especially heavy in the style sack. The intestine, leaving the visceral mass, passes along the right digestive diverticula and, as the rectum, through the pericardium and ventricle, thence around the adductor muscle nearly to the tip of the visceral mass where it ends in a trumpet-shaped anus.

FOOT

The small, roughly cylindrical foot of the adult scallop (figs. 3 and 11) is useless for locomotion. In it is located the byssal gland that secretes the byssus by which the scallop attaches itself to eelgrass or other objects. Attachment is more common with juvenile scallops but sometimes is practiced by mature or nearly mature individuals. It is interesting to note that an European species, *P. varius*, retains the practice of byssal fixation throughout life and even moves about by renewing and slightly shifting the point of byssal attachment (Fischer, 1867). It has been suggested by Dakin (1909) and claimed by Uexküll (1912), for whom a rudimentary organ can not exist, that the deeply grooved, suckerlike tip of the foot is employed in the removal of foreign material from the shell. Certainly at times the foot is rather active for an organ the only function of which is the rare spinning of a byssus. In the very young it is, of course, used for locomotion (crawling).

ADDUCTOR MUSCLE

The adductor muscle (morphologically the posterior adductor) of the scallop (see figs. 3 and 11) is of special interest. The great size of this muscle renders economically feasible the practice followed in this country of utilizing it only, of all the tissue of the scallop. It is correlated with the unusual lamellibranch habit of swimming. The adductor of a very large scallop (89 millimeters long), taken in January, was found to weigh 20 grams after draining.

The adductor muscle is composed of two very unequal parts. The larger and clearer is the motor muscle which functions to snap the valves together and provides the motive power for swimming. In the scallops it is composed of striated fibers. The smaller, milky white portion, sometimes termed "ligament" by scallopers, which lies posterior to the larger and is composed of unstriated fibers, functions to hold the shell closed or in any partially closed position. It exhibits what has been known as the "catch mechanism" and, therefore, has been termed "catch muscle." If an object be thrust between the open valves, these close sharply upon it and hold. If then the object be pulled from between them, the valves temporarily remain as they were. Pressed closer together they remain in the new position a time but resist opening. Sometimes too forceful opening tears the catch muscle in two. These phenomena have been observed by me many times and are well known. To all appearances and in effect it is as if the muscle were not pulling the valves together but instead rigidly retaining them as by a catch, or better a ratchet, which does not interfere with shell closing, but against quick opening pressure is unyielding, unless "thrown out" by the proper nervous stimulus.

Such phenomena have attracted much attention. A very interesting account is that of Uexküll (1912), who reported that certain nerves inhibited the catch mechanism and others brought it into play, but that if the nerves were cut when the mechanism was in operation, stimulation of the nerve endings could not be made to throw out the catch. The smooth muscle remained at the length it had when the nerve was cut. Important earlier investigators were Pavlov (1885), Marceau (1909), and Parnas (1910). The latter failed to find evidence, as he believed, of increased metabolism with increased strain or exhaustion after prolonged strain. This, together with the remarkable ratchetlike functioning, made a good case for the view that this portion of the adductor might be considered as a passive mechanism under nervous control, not active muscle. This is most interestingly discussed by Bayliss (1918).

Increased information and renewed consideration of the evidence have led recent investigators to doubt the validity of the catch mechanism hypothesis. Ritchie (1928) reviews the published data and some unpublished work in which he shared. From the data on metabolism, relaxation time, tension, response to stimulation, etc., he comes to the conclusion that, while there are several doubtful points, there is nothing known which is incompatible with the view that catch muscle is merely very slow muscle of great tension (but not especially great in Pecten whose muscles instead are relatively fast). See also Boylan (1928), Waele (1927), and Hopkins (1930).

Although as the expression of an acceptable hypothesis "catch mechanism" and "catch muscle" may be doomed to be discarded, merely as a descriptive name "catch muscle" is effective and useful and may be retained.

CIRCULATORY SYSTEM

The circulatory system of the giant sea scallop, *Pecten tenuicostatus* or *Pecten grandis* (see p. 571) has been studied by Drew (1906) and that of *P. maximus* by Dakin (1909), with such close agreement as to path followed, except for the quite different gills, that it may be assumed that the circulation of *P. irradians* is very much like that of these forms. This assumption receives support from such observations as are readily made, as of the vascular network of the mantle and of the veins of the visceral mass. Circulation, therefore, may be summarized as follows: Blood leaves the ventricle by the anterior and posterior aortæ. The posterior aorta supplies the adductor muscle, the rectum, and, through the large posterior pallial artery and the circumpallial artery, the mantle. The anterior aorta supplies the remainder of the body and, through the anterior pallial artery, contributes blood to the circumpallial artery. Blood from the mantle, after passing through a net work, returns directly to the heart. According to Dakin the venous system consists largely of sinuses (see fig. 12b), contrasting with the definite vessels of the arterial system. Large sinuses between the adductor and its sheath and paired veins from the visceral mass and digestive diverticula convey venus blood to the kidneys, which receive all the blood except that of the mantle. From the kidneys the blood passes to the gills and thence to the heart. Figure 12, after Dakin, shows the main arterial and venous circulation except for the mantle and gills.

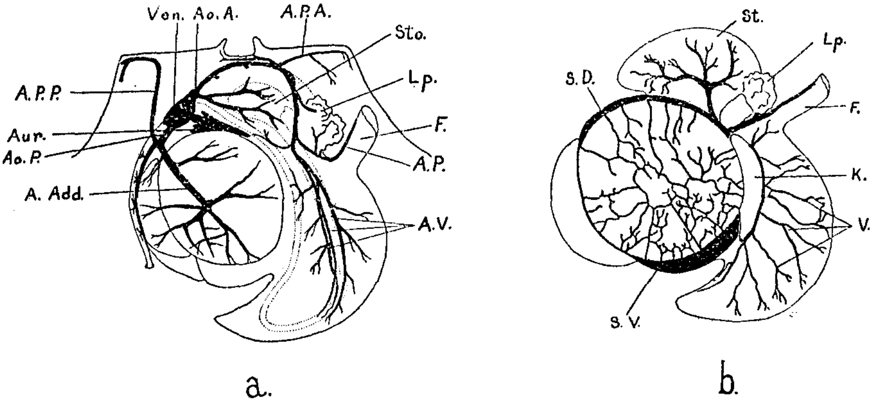

FIGURE 12.—Main vascular circulation, except for mantle and gills (after Dakin): *a*, Arterial circulation; *b*, venous luriccation; *A. P. A.*, anterior pallial artery. *A. P. P.*, posterior pallial artery; *A. Add.*, adductor; *Ao. A*, anterior aorta; *Ao. P*, posterior aorta; *A. P.*, pedal artery; *Aur.*, right auricle; *A. V.*, visceral arteries; *F*, foot; *K.*, kidney; *Lp.*, lips; *S. D.*, dorsal venous sinus; *St.*, tissue surrounding the stomach; *S. V.*, ventral venous sinus; *V. V.*, viscereal veins

The symmetrical heart consists of two auricles and one ventricle. The auricles are relatively large and very uneven of surface. The ventricle, traversed by the rectum, is greatly reduced in size when contracted and is smooth exteriorly. Drew described muscles around the openings of the auricles which he believed acted as sphincters to prevent the back flow of blood from the ventricle. The firm walled, triangular pericardium lies in the angle formed by the posterio-ventral surface of stomach and digestive diverticula, on the one hand, and the dorsal surface of the adductor muscle on the other. It extends from one pallial lobe to the other.

NERVOUS SYSTEM AND SENSE ORGANS

The nervous system (fig. 13) comprises a central nervous system of three pairs of principal ganglia with commissures and connectives and, in the ganglionic circumpallial nerve, what might be termed a peripheral nervous system. (See Boutan, 1902, and under "Mantle" in this paper.)

The three pairs of central ganglia are considerably modified in arrangement. The cerebral ganglia are closely united with the pedal ganglia, which are joined one to the other without appreciable commissure. (Fig. 14.) The visceral ganglia are so fused and developed that they form one large, complex, ganglionic mass (fig. 14) and warrant the term visceral ganglion adopted by Dakin (1910).

The elongate, slightly bilobed, cerebral ganglia are located near the surface between lips and foot. At the anterio-dorsal end of each arises the cerebral commissure which passes dorsally in a loop around the oesophagus and connects the paired ganglia. From the other end extends the large cerebro-visceral connective. Near the middle of the outer side three nerves arise together. The first, or innermost, is small and leads to the "tufted" lips and may be termed the "labial nerve." The larger, middle one, the anterior pallial nerve, sends two branches to the circumpallial nerve. The outer one supplies the palps and is here termed "palpal nerve." In some instances the anterior pallial and the palpal nerves continue as one for a short distance before separating. The fine otocystic nerve of each of these ganglia arises near the source of the cerebro-pedal connective and leads away from the surface to a small round otocyst, from which arises a threadlike structure termed the otocystic canal. For histological detail see Buddenbrock (1915) as to Pecten and Field (1922) as to Mytilus. For accounts of the importance of the otocysts as organs of balance and control of movement see Buddenbrock (1911 and 1915). They have also been considered organs of hearing. The cerebral commissure extends around the œsophagus.

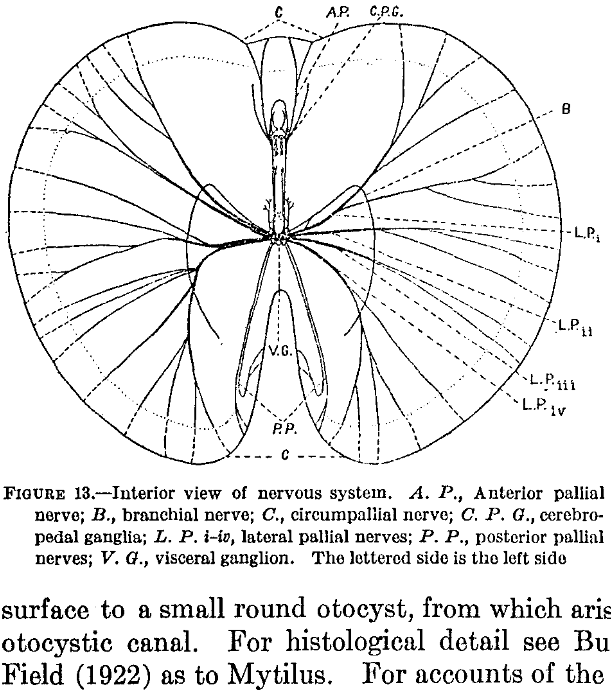

FIGURE 13.—Interior view of nervous system. *A. P.*, Anterior pallial nerve; *B.*, branchial nerve; *C.*, circumpallial nerve; *C. P. G.*, cerebropedal ganglia; *L. P. i-iv*, lateral pallial nerves; *P. P.*, posterior pallial nerves; *V. G.*, visceral ganglion. The lettered side is the left side

Between the two cerebral ganglia, and connecting them, lie the abutting pedal ganglia and the short cerebro-pedal connectives, one of which arises not far from the center of the inner side of each cerebral ganglion. From the pedal ganglia arise the pedal nerves which enter the foot, subdivide, and become much convoluted.

The large cerebro-visceral connectives lead diagonally along the stomach and midgut to the adductor muscle and thence to the visceral ganglion which lies on the anterio-ventral surface of this muscle, between it and the visceral mass, but extending chiefly to the right so that a large part may be viewed without dissecting away the visceral mass. In size, complexity of shape, and number and size of nerves which arise from it, the visceral ganglion greatly exceed any of the other central ganglia.

(See fig. 14.) The lateral pallial nerves which arise under the lateral lobes, that is, between the ganglia and the adductor muscle, pass principally ventral of the kidneys along the sheath of the adductor muscle and (on the right side) the support of the branchial axis to the mantle and spread through it (fig. 13) to the circumpallial nerves. Posterio-ventrally to the lateral, arise the posterior pallial nerves which join with the circumpallial nerve near the posterior end of the hinge. Each of the two branchial nerves has a double origin. One of these lies under the lateral lobe, anterio-dorsal of the lateral pallial nerves, the other on the surface of the central portion of the ganglionic mass between a lateral lobe and the central lobe. These roots of the branchial nerves are cross connected near the base. They pass along the ventro-lateral edges of the kidneys and thence to the branchial axes and along them to the tips. For a more detailed study of the visceral ganglion and the nerves arising therein see Dakin (1910).

Where a cerebro-visceral connective joins the visceral ganglion there arises, on each side, a small body which corresponds to the "swelling" of Drew (1906) and the accessory ganglion of Dakin (1910). Each of these bodies is connected with the branchial nerve near its base and at the tip gives off three branches. One of these parallels for a considerable distance a cerebro-visceral connective. Another, developing several obvious branches, extends somewhat dorsally toward the anterio-ventral surface of the visceral mass. The third extends into the overlying tissue of the visceral mass (ovary, etc.), and, according not only to several dissections but also to observation of material cleared in glycerin, joins its fellow from the other side. (Fig. 14.) Thus these bodies or accessory ganglia supply various portions of the visceral mass and are interconnected through a structure apparently not heretofore observed.

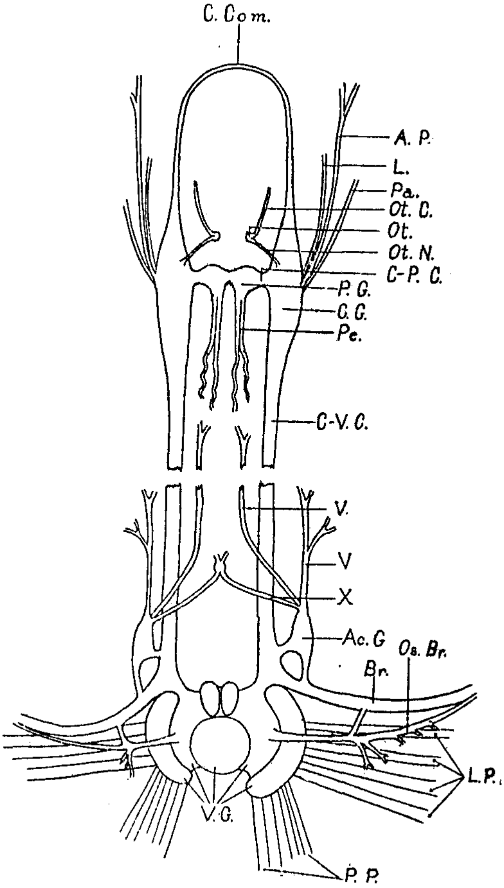

FIGURE 14.—Central nervous system. *Ac. G.*, Accessory ganglion; *A. P.*, anterior pallial nerve; *Br.*, branchial nerve; *C. Com.*, cerebral commissure; *C. G.*, cerebral ganglion; *C-P. C.*, cerebro-pedal connective; *C-V. C.*, cerebro-visceral connective; *L.*, nerve to tufted lips; *L. P.*, lateral pallial nerves; *Os. Br.*, osphradio-branchial nerve; *Ot.*, otocyst; *Ot. C.*, otocystic canal; *Ot. N.*, otocystic nerve; *Pa.*, palpal nerve; *Pe.*, pedal nerve; *P. G.*, pedal ganglion; *P. P.*, posterior pallial nerve; *V.*, nerve of the visceral mass; *V. G.*, visceral ganglion (with crescentric "lateral lobes" and central portion with large globular "ventro-central lobe" and paired "dorso-central lobes"); and *X.*, structure of unknown designation

The abdominal sense organ (Dakin, 1909 and 1910) is to be found on the edge of a connective-tissue flap near the right pallial lobe. It is small, elongate, somewhat brownish, and covered with a dense mat of fibers. Dakin (1910) was unable to find any effect made by its removal or "stimulation." Without supporting evidence, various functions, such as water testing and detection of movements in the water, have been attributed to it.

The osphradia of Pecten are very inconspicuous structures and, in these investigations, have not been positively observed. The osphradial branches of the osphradio-branchial nerves arise just ventral to the kidneys. (See fig. 14.) Dakin (1910) found no evidence of an olfactory or other sense in these organs of Pecten. On the other hand Copeland (1918) found that certain predacious gastropods responded definitely to olfactory stimuli but failed to respond after the osphradium had been removed.

The eyes and tentacles have been described with the mantle.

URINOGENITAL SYSTEM

The urinogenital system comprises ovaries, testes, pericardium, and kidneys.

The ovaries are located in the ventral or tip portion of the visceral mass and are, when eggs are present, pink or even red. The white or cream colored testes occupy that portion of the mass dorsal to the ovaries and ventral to the stomach and also extend, anterior to the mid-gut, along the outer edge of the mass well toward the tip. Occasionally "islands" of ovarian tissue are to be found within the limits of the testes, and vice versa. Rarely organs of one sex are so greatly extended as to make the individual appear unisexual. The general position of ovaries and testes is shown in Figures 10 and 11, and something of the microscopical structure of an ovary in Figure 15.

Credit for the discovery that the sexual organs of Pecten open through the kidney is given to Garner (1841). Lacaza-Duthiers (1854) figured a common duct to take both eggs and sperms to the kidney, through which they are discharged. The passages are somewhat hard to follow, but have been traced by Dakin in serial sections and demonstrated by gently pressing the ripe gonads so that masses of eggs or sperms are seen to emerge from the kidney.

The renal organs, or kidneys, are asymmetrical lozenge-shaped organs, generally light brown in color and located on the adductor muscle (figs. 4 and 11), one on each side of the visceral mass in the angle formed with the branchial axis. They are well supplied with blood vessels. The lumen is much branched. The walls are glandular (see Kellogg, 1892; Drew, 1906; Dakin, 1909) and ciliated (but see Dakin, loc. cit.). Urea is given off in solid concretions (Pelseneer, 1906) which have been figured for *P. irradians* by Kellogg (1892). An elongate, lipped urinogenital aperture is located at the ventral end of each kidney, near the visceral ganglia. Dakin states that the two kidneys communicate one with the other at their dorsal ends through a transverse duct lying between the visceral mass and the adductor muscle.

It seems to be well demonstrated that the pericardium communicates with each of the kidneys and forms part of the excretory system (Pelseneer, 1906; Drew, 1906; Dakin, 1909). I have failed to find the reno-pericardial openings in *P. irradians* or even to demonstrate them by means of red pericardial injections. In some instances a red kidney was thus obtained, but in no instance did the red fluid appear at the urinogenital aperture, which is taken to mean that in some manner the blood spaces of the kidney received the injection. Although Drew apparently found the openings without difficulty in the large sea scallop, Dakin failed to demonstrate them by injecting the kidneys and was only able to make them out by serial sectioning. In the case of the scallop the excretory function of the pericardium is stated to be carried out by the walls of the auricles, which are uneven, somewhat spongy, and of a yellow color.

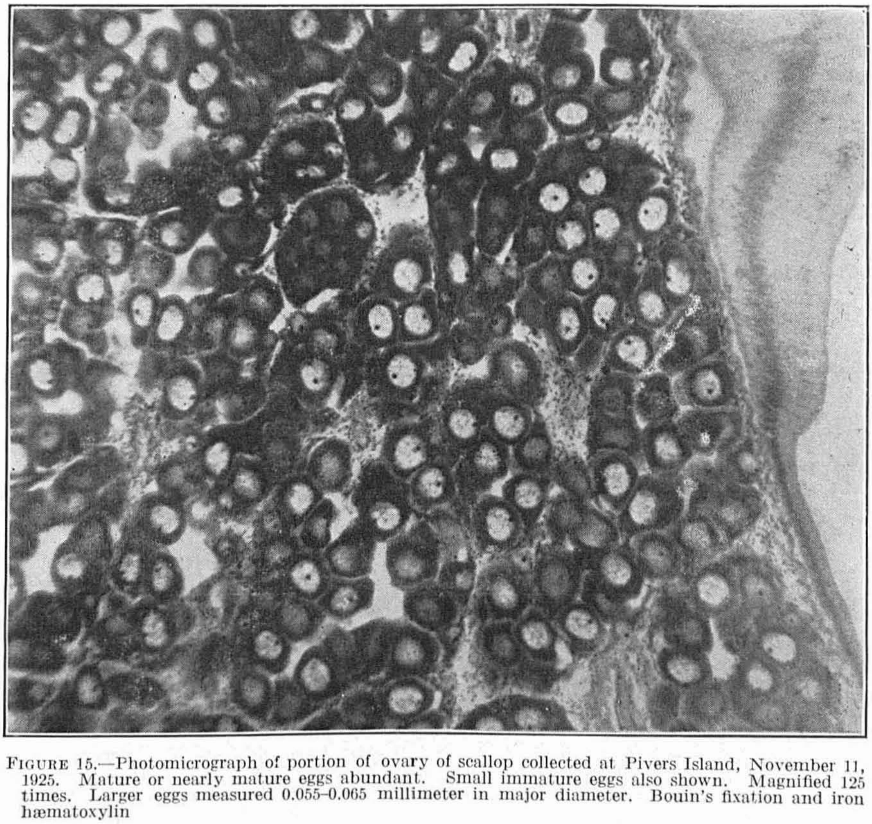

FIGURE 15.—Photomicrograph of portion of ovary of scallop collected at Pivers Island, November 11, 1925. Mature or nearly mature eggs abundant. Small immature eggs also shown. Magnified 125 times. Larger eggs measured 0.055–0.065 millimeter in major diameter. Bouin's fixation and iron hæmatoxylin

FEEDING

The principal organs for securing food, as previously noted, are the gills. For the scallop, as for some other forms, it seems clear that under certain conditions of feeding, as when much sediment is present in the water, they also enter into the process of selection (acceptance or rejection of filtered particles). For a description of the feeding currents and the location and functions of the various ciliated tracts see. under "Gills." Here it need only be noted that the gills bring in the food-laden water, separate food organisms and other particles from it, and convey these to the palps. The palps, as described by Kellogg (1910, 1915) and various workers, through the action of a complex and often puzzling arrangements of ciliary currents either pass the material to the lateral opening between the tufted lips or, if it be too coarse or in too large masses, through muscular action bring reverse currents against it and thus cast it away, near the foot, to be ejected near the byssal notch.

Material not rejected passes into the transverse tube formed by the interlocking tufted lips, thence into the œsophagus, and thence, still by the action of cilia, into the stomach, where it again meets complex ciliation further complicated by the action of the style.

No special study has been made of the food of the bay scallop. Apparently it does not differ greatly from that of other lamellibranchs in similar habitats and consists chiefly of the available plant and animal plankton of suitable size and shape, with nannoplankton playing an important part, and includes considerable quantities of the free moving microflora and microfauna of the bottom. In the relatively small number of stomachs examined by me, detritus sometimes bulked large, but whether it is important as food is not certain. Peterson and Jensen (1911) believed such material to be of greatest importance for the oyster. More recently Martin (1923), Hunt (1925), Savage (1925), and Yonge (1926a) have questioned the ability of lamellibranchs to digest detritus such as that formed from Zostera and believed to constitute the larger portion of the organic content of coastal waters. Hunt (loc. cit.) found that the stomach contents of *P. opercularis*, from deep water, generally reflected the nature and variation of the plankton. Peridinians were especially abundant in the stomachs during late spring and summer, diatoms (important at all times) during fall and winter.

CILIARY CURRENTS OF MANTLE, VISCERAL MASS, ETC.

The ciliation of the mantle and other surfaces within the pallial cavity has been figured by Kellogg (1915) who studied both *P. irradians* and the sea scallop, *P. grandis* Solander (*P. tenuicostatus* Mighels of Drew and Kellogg). In general my observations are in agreement with his. (Fig. 16*a*.) However, I found currents on the visceral mass of the bay scallop differing considerably from those shown by him for the sea scallop (compare 18*b* with 18*c*). These various ciliary currents convey material deposited upon them to points where it will be ejected with the feces or with material rejected by the palps.

PIGMENTATION OF THE VISCERAL MASS

If normally active scallops are opened and examined, the pendant visceral mass, tufted lips, and the outer surface of the palps are found to be more or less highly pigmented (as indicated in part by Fig. 3). This pigmentation varies greatly in intensity, but is always marked on the visceral mass except in "poor" or weak individuals or adults kept long in the aquarium, with which it is always very pale or wanting. The color varies from light green almost to black. Indeed frequently the visceral mass of juvenile scallops might fairly be termed black.

Overlying the gonads and surrounding the visceral mass is a tough transparent membrane. This may be so removed as to retain the epithelium, spread in sea water on a slide, covered with a slip, and examined under high magnification (3 millimeters water immersion). It thus appears that the coloring is due to granules of two colors grouped in the epithelial cells. Some granules are yellow, others dark. Under the microscope these darker granules sometimes appear decidedly blue but may be green. It can be seen that some cells contain only the lighter granules. Others appear to contain only the darker ones. Some cells, even in darkly colored areas, are almost devoid of colored granules.

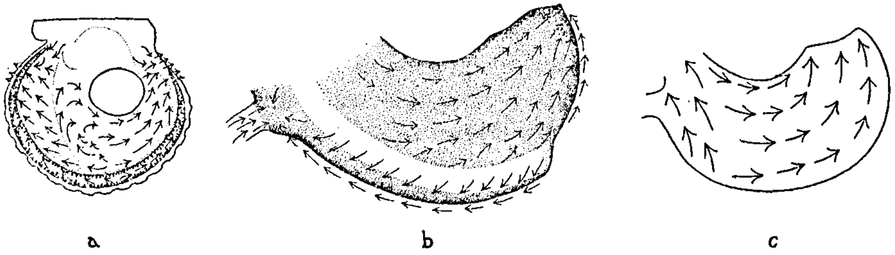

FIGURE 16.—Ciliary currents of mantle and visceral mass; *a*, right pallial lobe (after Kellogg); *b*, left side of visceral mass with base of foot shown at left and pigmentation represented by stippling (from observations on the movement of fine carborundum); *c*, ciliary currents of visceral mass of *P. tenuicostatus* (after Kellogg)

Fixed and preserved material does not retain the greenish color, appearing brown instead, but has the advantage that it may be sectioned and a different view of the epithelium obtained. In sections cut at right angles to the surface, the disto-proximal arrangement of the granules in the epithelial cells may be seen. Although distinct color difference has been lost, dark and light pigmentation may still be observed. As shown in Figure 17 the granules, particularly the dark granules, lie principally near the outer surface of the epithelium.

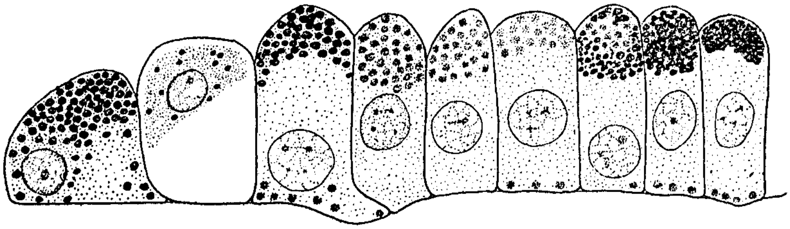

FIGURE 17.—Pigmented epithelium of the visceral mass (from material fixed in Bouin's)

Because of the evident and unfailing loss or great reduction of this bodily coloration with scallops in poor condition, the writer suggests that the pigmentation is connected in an important way with feeding or metabolism.

SWIMMING

A swimming scallop has been well likened to a bellows; the valves corresponding to the bellows boards, the velar folds or curtain to the leather sides or "bellows," and the anterior and posterior velar openings to the nozzle. The valves are opened and forcibly closed. As the closing starts the velar folds of the two mantle lobes are brought together to form a wall or curtain which prevents egress of the water except dorso-anteriorly and dorso-posteriorly through the gaps near the hinge. (See fig. 18.) The jets through these openings send the scallop in the opposite direction; that is, ventrally with the free margin of the valves in advance and tilted upward even when progression is horizontal, as along the surface, as though the animal were biting its way through the water.

Nearly all accounts agree on the means of progression. As to the manner, however, there is some difference. Jackson (1890) stated that the jets are alternately through the dorso-anterior and dorso-posterior openings, thus causing an alternate rotation through 90° or more and resulting in an extremely zigzag course. This does not agree with my observations.. As previously noted the account of Jackson seems to have been unhesitatingly followed by American writers.

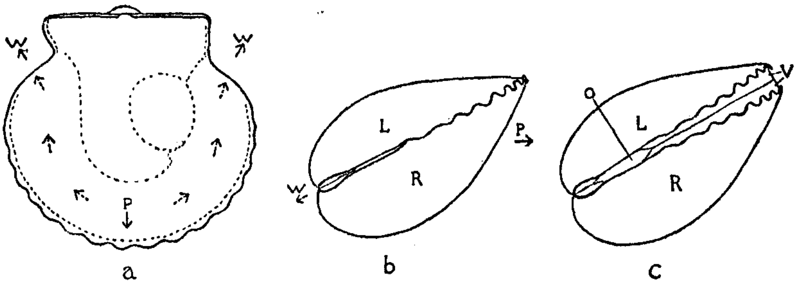

FIGURE 18.—Diagrammatic sketches of scallop swimming: *a*, As seen from above and at right angles to the plane of the valves and showing, in dotted lines and arrows, the water channels as bounded centrally by visceral mass, branchial axes, adductor muscle, etc., and peripherally by velar folds; *b*, anterior view at end of "power stroke" (shell closing), showing tilting of shell (angle not determined); *c*, anterior view, early part of "power stroke"; *L*, left valve; *O*, opening for emission of propulsive jets; *P*, direction of progression; *R*, right valve; *V*, velar folds united to form a wall or curtain which is continuous except near each end of hinge; *W*, propulsive water jet

Jackson, who worked with *P. irradians*, stated that early in the shell closing there is a ventral egress of water before the edges of the velar folds come together. Anthony (1906) and Dakin (1909), working with Eurpoean scallops, stated that the juxtaposition is timed to prevent such water movement. This is somewhat difficult to determine. Apparently at times, with our species, there is such egress, at least at the first clap or power "stroke," for which the valves may be more widely separated than for later ones.

Steering according to Dakin is effected by a partial closing of one or the other of the velar gaps, according to Buddenbrock and to Uexküll also, and more accurately, by slight local separations of the edges of the velar folds.

Besides normal swimming there have been described various sorts of scallop movement.

Under special circumstances the scallop forces out the water ventrally and darts hinge foremost along the bottom. This has been described by Anthony (1906), Dakin (1909), Belding (1910), Buddenbrock (1911), and Uexküll (1912). Belding, working with small, juvenile scallops, found that it occurred if one of these was approached ventrally with the point of a pencil and evidently was for the purpose of taking the scallop away from the pencil. Anthony, Buddenbrock, and Uexküll attributed this movement to a direct local stimulus. Dakin found the cause in sudden stimulation. I have observed this "backward" darting, especially when a scallop was touched suddenly, but, working with mature or nearly mature individuals kept in captivity, have not been able to induce it at will by mechanical stimulation. It seems to be in part a startled movement but I have induced it by repeated chemical stimulation of the midventral portion of the mantle margin.

According to Dakin and Buddenbrock this reversal in direction of progression is due to an indrawing of the velar fold during shell closing, according to Anthony and Uexküll to a local contraction of this structure which is so important for swimming. If this latter explanation is correct it is strange that the darting, according to all these accounts and in so far as I have noticed, is always hinge foremost and not sometimes hinge sidewise or diagonally.

A third type of movement described by various investigators (for example Dakin, Buddenbrock, and Uexküll) is that by which a scallop turns over after being placed wrong side up. This is performed by arranging the velar folds, along the ventral margin of the shell, so that when the valves are forcibly brought together, a stream of water is directed downward against the bottom. This lifts that edge of the shell and turns the scallop right side down. Belding (1910) states that the turning ordinarily is forward or backward. With local, adult specimens the turning is somewhat difficult to study, for scallops so placed (contrary to the experience of Grave (1909)) may remain wrong side up for hours, and indeed have been found, although rarely, in this position on the flats. It seems probable that scallops of this species lie so nearly universally in the normal position principally because they settle on the right side after swimming, which is with the left side up. As previously noted, Buddenbrock (1915) found that Pecten may also right itself around an axis perpendicular to the hinge line.

Jackson (1890) described a sort of "scuttling" movement over the bottom produced by repeatedly expelling water through one velar gap only.

Anthony (1906) noted that a scallop may rotate horizontally by a single, moderate contraction which drives the water between the velar folds at one point only.

Although scallops have been supposed to shift considerably and even to make distinct migrations, field observations indicate that during a large portion of the scallop's life shifting ordinarily, in local waters, is very slight. Not only do near-by flats yield scallops of different size or shape but, in some instances, different portions of a large flat yield scallops notably different in size. Thus, in western Bogue Sound, scallops of good size were found along the edge of the dredged channel north of Lovetts marsh. A few rods away from the channel scallops were of the dimunitive size usual in this section of the sound. Other instances have been noted. Indeed it seems probable that shifting, except as the vegetation to which the young scallops cling becomes detached and is carried away by wind or tide, is slight after the veliger stage is passed.

REPRODUCTION AND DEVELOPMENT

SPAWNING PERIOD

A knowledge of the spawning period of a species may be important for various reasons. For a commercial form it often is essential for conservation (as by legal regulations). Much of the life history and biology must remain obscure until this period is determined, at least in part. It may be of considerable theoretical interest. For the bay scallop all of these apply.

A spawning period may be determined in various ways. It may be possible to determine it, at least in part, by direct observation or by watching the animal spawn. By examination of the gonads and noting when they first show ripe sexual products, first show evidence of discharge of sexual products, and when the gonads become emptied, the beginning and end of the period may be determined. However, to learn the time of principal and effective spawning, it generally is necessary systematically to collect eggs, larvæ, or young, noting when these first appear in numbers, become abundant, decrease and disappear.

Some information was obtained by the first two methods. Seldom is it practicable to collect lamellibranch eggs. For reasons that will be discussed later, collections for larvæ gave little aid. By far the best evidence as to principal time of spawning came from collections for small scallops beyond the larval stage.

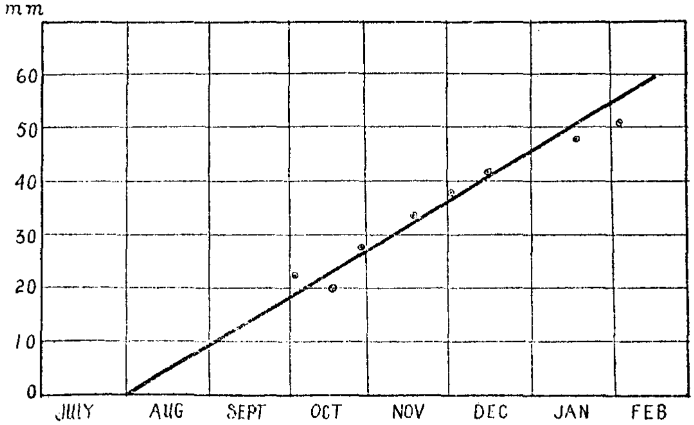

FIGURE 19.—Graph based on largest scallops of 1926 year class obtained during fall of 1926 and a portion of succeeding winter. The junction of trend with base line was taken to indicate approximately the beginning of spawning

In North Carolina very small scallops seldom, if ever, become so numerous as to be in evidence amidst the vegetation to which they attach, and it was not till the fall of 1926 that methods were developed which gave satisfactory data as to their abundance. The method consisted in collecting and drying a tub of eelgrass and other vegetation from the flats, screening the siftings from the vegetation, and examining the screenings for scallops. The material retained by the finer screen was examined under a binocular. At that time young of the year already had attained considerable size. Very small scallops continued to be found abundantly until February 2, 1927, decreased in March, and became rare in April. (See fig. 20.) Although the age of these small scallops was not definitely known, from consideration of growth rate and from observations on scallop gonads, it was concluded that important spawning continued into January. An attempt was then made to determine the beginning of spawning. From semimonthly size-frequency curves (5 millimeter groupings) the "first appearance" of scallops in succeeding size groups was noted.

These "size dates" were then plotted to represent the growth of the oldest scallops of the year's (1926) spawning and were found to lie reasonably close to a straight line. (Fig. 19.) The junction of this line (growth curve) with the base line was taken to indicate a beginning of spawning by late July or early August. Although it was realized that linear growth would scarcely be truly uniform, with such notable change of size and season, it was thought that the "indication" might be sufficiently close to be helpful.

Small scallops reappeared in the grass collections in June and continued through July, but without any evident increase and in such small numbers as to mean little. With the first August collection, however, a marked change occurred. Small scallops were present in numbers which indeed were small compared with those of the fall, but large compared with those obtained since the disappearance months before. Increased numbers were obtained later in the month and impressive numbers early in September. The spawning period evidently began in July and became rather important in August and, therefore, is an affair of late summer, fall, and early winter, but chiefly of the fall. (See Table 3 and fig. 20.) Spawning has been obtained experimentally as early as August 26.

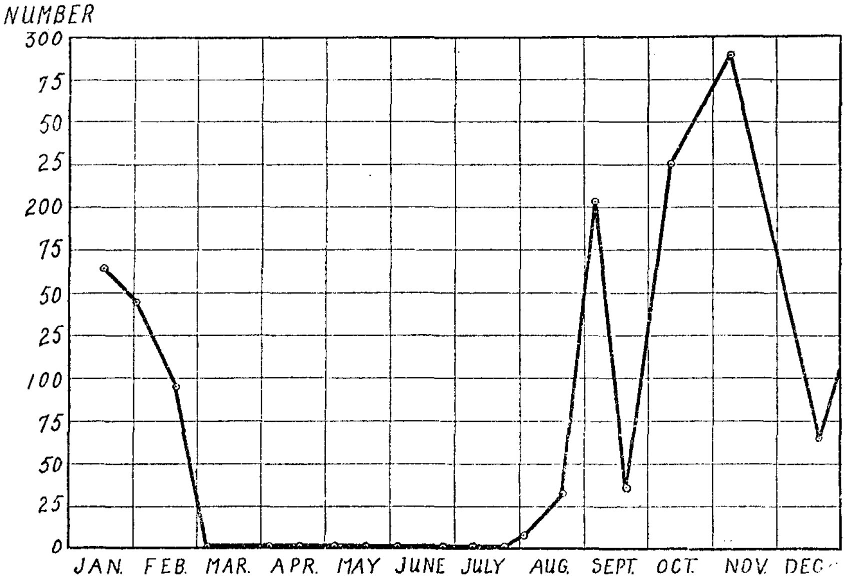

FIGURE 20.—Spawning as indicated by the abundance, through 1927 collections, of scallops 2 millimeters or less in length. (See Table 3)

This has affected the writer's recommendations for conservational regulation (Gutsell, 1928). Because various bivalves, and in the north the bay scallop, spawn during the period when water is warming, and indeed seem to depend upon a temperature rise for a spawning stimulus, the fact that scallop spawning here occurs principally while temperatures are dropping is of considerable interest.

The long-continued season explains the lack of a period of extreme abundance of very young scallops in highly productive areas.

TABLE 3.—*Numbers of scallops 2 millimeters or less in length taken in the various "grass" collections at Pivers Island from January, 1927, to January, 1928*

[When one collection was made during a period of 3 or 4 days, a central date is given. (See fig. 20.)]

Date	Number	Date	Number	Date	Number
1927		1927		1927	
Jan. 17	164	May 19	0	Sept. 20	37
Feb. 1	140	June 3	1	Oct. 11	227
Feb. 10	92	June 25	1	Nov. 9	289
Mar. 5	2	July 8	1	Dec. 23	66
Mar. 20	2	July 23	1		
Apr. 4	0	Aug. 2	8	1928	
Apr. 18	0	Aug. 22	43	Jan. 25	216
May 4	0	Sept. 6	204		

SPAWNING

As previously noted, the ovary and testis for each side open through a common duct into the kidney of that side, and thence through the urinogenital opening into the suprabranchial space, with its exhalant current. Eggs, pink or almost red in mass, and sperms, white or cream, supposedly and apparently are discharged separately to the exterior so that self-fertilization is the exception. Self-fertilization has been obtained experimentally by Risser (1901), Belding, and the writer under artificial conditions. Certain observations of Kellogg suggest that frequently a small number of eggs may be self-fertilized under natural conditions, for Kellogg (1892) frequently found a few developing eggs in the kidneys. It seems more probable that these were fertilized either in the kidney or in the common gono-duct by sperms emerging through the same passage than by entering sperms from another individual. Belding has noted in rare cases a simultaneous discharge of eggs and sperms.

Belding (1910) induced spawning by transferring scallops from relatively cool water to jars of water placed in the sun to warm. Risser (1901) and Drew (1906) confined scallops ready to spawn so that these investigators might obtain eggs and sperms, but seem not to have attempted to induce spawning. I made many attempts to apply Belding's method, but failed so frequently as to suggest that temperature rise is not a very effective stimulus to spawning, which would not be surprising in a region where scallop spawning occurs principally during a period when water temperature is declining. An alternative explanation is that the extended spawning season gives relatively small chance of finding scallops just ready to spawn.

As previously noted, spawning was obtained as early as August 26. Two scallops were placed in separate bowls of water at 25° C. Sea water heated in a flask, closed except for a condenser tube, was added to these bowls until the temperature was raised in one case first to 28.5° C., and then to 32° C., in the other case, first to 29.5° C. and then to 30.5° C. When in a few minutes the water which had stood at 32° C. dropped to 30° C., the scallop in that bowl began to spawn, casting out both sperms and eggs, many of the latter in small chunks and apparently not fully matured. "Self-fertilization" occurred and in 1 hour and 20 minutes 3-celled (or possibly 2-celled with yolk lobe) embryos were numerous.

From this experiment vast numbers of embryos were obtained. In one day most of these were in the gastrula stage, in two days either in the trochophore stage, or with shells developed. Some of the shelled larvæ remained alive six days but made little growth.

Numerous similar attempts were made (a close following of Belding's method having uniformly failed), generally with poor or no success. If eggs were obtained sperms would not be obtained or would not fertilize the eggs.

Once some success was obtained accidentally. A scallop out of water, being measured, squirted out about a quarter of a teaspoon of pink eggs. This scallop was placed in a bowl of sea water where it continued to emit vast numbers of eggs. Three other scallops were placed in separate bowls. These cast sperms. Water in which the sperms were most active was poured into that containing eggs. Larvæ from this lot lived to be 3 days old.

Although scallops sometimes, particularly late in the season, discharge a large portion of their sexual products in a brief time, from observations of the gonads it appears that in North Carolina individuals ordinarily spawn over a considerable period. This is in accord with the observations of Belding (1910).

FERTILIZATION AND EMBRYONIC DEVELOPMENT

Fertilization normally is external and consists in the union of the small, active sperm with the egg. Testicular sperms which appear mature are about 0.05 millimeter long, with heads 0.001 to 0.0012 millimeter long. These dimensions are considerably different from those shown by Belding (1910) for cast sperms (length about 0.07 millimeter, head about 0.0006). Ovarian eggs may be about 0.063 by 0.06 millimeter (sample measurement), but with shape varying. These measurements correspond well with Belding's scale drawings of cast eggs. The sperms swim until they come in contact with an egg (or perish), about one of which great numbers may cluster with heads toward the egg. Normally only one enters (see Belding, 1910), fertilization occurs, and development begins.

Scallop embryology has been studied by Fullarton (1890), Drew (1906), and Belding (loc. cit.) and is included in the general statement of Korschelt (1900). Embryonic development is of the typical lamellibranch type with unequal cleavage and without blastula. (See fig. 21.) A yolk lobe which resembles a micromere, appearing before the second micromere and later absorbed by the macromere, is described and figured by Belding and Drew. The gastrula is epibolic. At this stage the embryo is well supplied with cilia and rolls about in the water. Belding obtained this stage in about 10 hours. Next a trochophore is formed. Belding obtained this stage in 12 to 14 hours, but the writer not so quickly (from about 1 to nearly 2 days at about 25° C.). This takes the scallop through the embryonic into the larval stage.

LARVAL DEVELOPMENT

The earliest larva (fig. 21), termed the trochophore (or trochosphere) from its resemblance to the annelid larva of the same name, possesses besides shorter cilia, a flagellum which appears to be single but has been found (Belding, 1910) to be a close tuft of as many as six large cilia. A primitive digestive tract is present. At this stage the animal swims forward (flagellum in advance) and rotates.

Following the trochophore comes the veliger with its velum and with an alimentary canal in which œsophagus, stomach, and intestine have been described. Soon after the formation of the velum, a shell (the prodissoconch) appears and quickly increases to cover the animal. Swimming is by the beating of the cilia of the velum (aptly termed propeller by one waterman). The shell is of the type known as straight-hinged, although the hinge line really is concave. (Fig. 21*h*.) Belding obtained this stage in 17–40 hours, the writer in 42–48 hours at about 25° C. The anatomy of the early veliger, including early shelled larvæ, was figured in considerable detail by Belding. Besides the structures mentioned, anterior adductor and velum retractor muscles are shown.

Beyond an early "straight-hinged" stage Belding did not succeed in rearing the larvæ nor, among the forms taken in the plankton net, was he able to recognize later stages, short of the fully developed prodissoconch. This stage he figured in considerable detail, showing it as about 0.18 millimeter long and with the left valve decidedly larger.

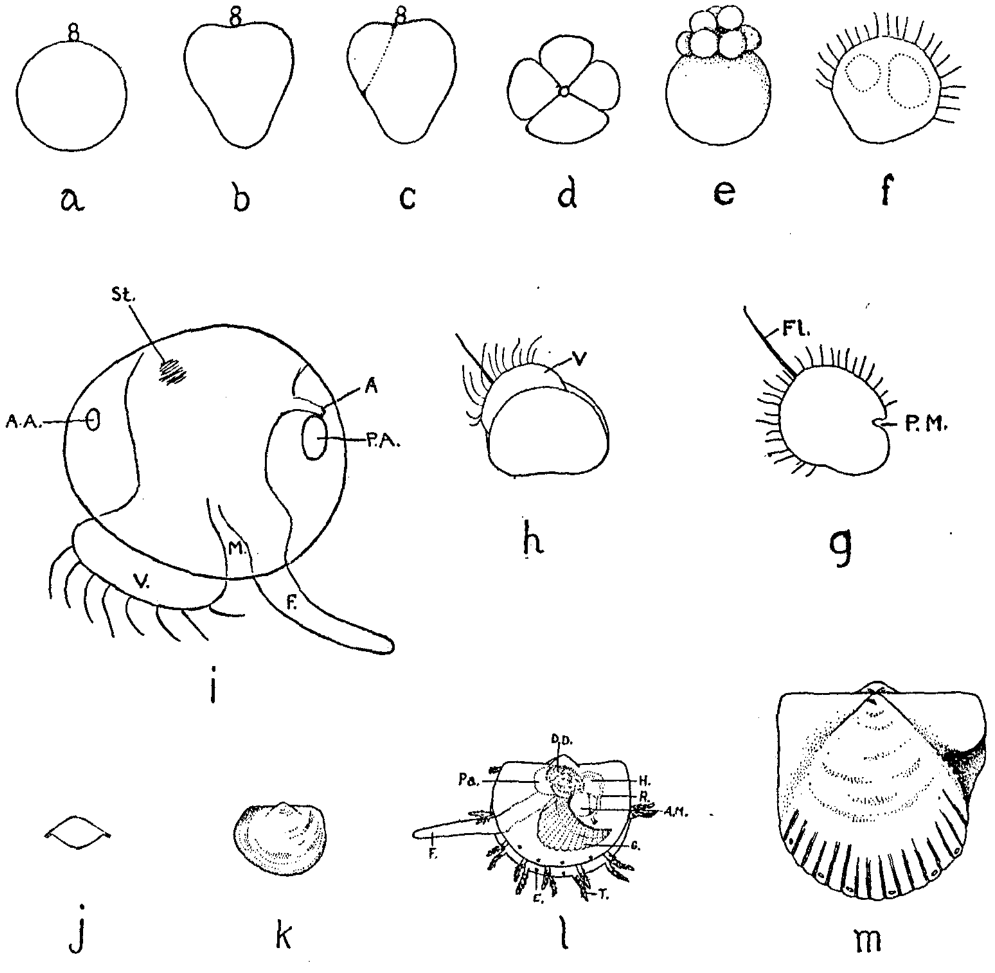

FIGURE 21.—Early development: *a*, Polar bodies formed at animal pole; *b*, yoke lobe formed at vegetative pole; *c*, first cleavage; *d*, 4-cell stage; *e*, 8-cell stage; *f*, ciliated gastrula; (*a-f*, embryonic stages); *g*, trochophore (*a-g*, after Belding); *h*, early veliger or prodissoconch, about 0.08 millimeter long; late prodissoconch, about 0.18 millimeter long (*g-i*, larval stages, see text); *j*, longisection of very early postlarva about 0.22 millimeter long, showing asymmetrical, nepionic shell growth; *k*, length 0.54 millimeter; *l*, length 1.2 millimeters (*j-l*, nepionic stages); *m*, transition stage, 1.6 millimeters long, showing byssal notch and teeth, ribs, and overhanging large umbo of left valve (drawn with right valve uppermost). Structures: *A*, Anus; *A. A.*, anterior adductor muscle; *A. M.*, adductor (posterior) muscle; *D. D.*, digestive diverticula; *E*, eye, one of six shown; *F.*, foot; *Fl.*, flagellum; *G.*, gill; *H.*, heart; *M*, mouth; *Pa.*, palps; *P. A.*, posterior adductor muscle; *P. M.*, primitive mouth; *R.*, rectum; *St.*, revolving stomach contents presumably turned by style; *T.*, tenacles; *V.*, velum

My own attempts to rear the larvæ did not take them beyond the straight-hinge stage even though they remained alive in this stage for several days. From examination of the shells of small scallops, it appeared that the fully developed prodissoconch shell was about 0.18 millimeter long and inequivalve with the left valve the larger as stated by Belding but differing from the adult, which has the right valve the larger.

Accordingly inequivalve larvæ were sought in plankton collections. Two such larvæ were found. One of these was easily recognized as that of *Ostrea virginica*, the common oyster of commerce. The other, which proved to be the larva of the interesting oyster discovered at Beaufort (Gutsell, 1926) and identified as *O. equestris*, attained a size much too large for the scallop. To this day, except for a few Anomia, only these two markedly inequivalve larvæ have been found.

Finally, late in the fall of 1927, attention was drawn to a larva with equal valves but with a shell outline suggestive of that of the prodissoconch to be seen at the umbos of postlarval scallops. This larva did not markedly exceed the size of such prodissoconch shells and, after careful comparison, was tentatively accepted as the larval scallop. Later there was received the "Report of Experimental Shellfish Station" (Wells, 1927) with two plates showing the larval development of the bay scallop. One of these plates (see fig. 22) consists of excellent photographs, one of which shows individuals with an early postlarval shell growth and beginning to assume the secondary straight hinge of the adult scallop. The photographs indicate, but do not conclusively demonstrate, an equivalve larval shell. In correspondence the author states that the larval shell is equivalve. The shell outline is that of the Beaufort form taken to be the scallop.

Mr. Wells kindly furnished some material including larvæ, like mine too poorly preserved to be helpful, and also some very early postlarvæ. Examination of these latter revealed a curious asymmetry of the postlarval growth. (Fig. 21*j*.) This tends to make the left prodissoconch valve appear the larger and probably is sufficient explanation of the semblance, with later dissoconchs, of prodissoconch asymmetry. It does not, however, explain Belding's statement, based on examination of prodissoconchs, that the left valve of the late scallop prodissoconch is the larger.

In plankton collections, the equivalve larva assumed to be that of the scallop was taken during the scallop-spawning season and in the year when the "set" failed (1928) disappeared early in the spawning season. There seems little reason to doubt that it is the scallop larva.

In a form which is to have the right valve the deeper, the temporary deepening of the left valve is a curious phenomenon. In this connection it is interesting to note that although all scallops normally rest on the right side, some, *P. opercularis* (Dakin, 1909), and our giant sea scallop of commerce have the left valve the deeper. The thought that the temporary deepening of the left valve of the postveliger shell is philogenetic therefore suggests itself.

Belding figured the fully developed prodissoconch as without velum or anterior adductor, but with large (posterior) adductor, gills, large foot, rather complex alimentary canal, and an otocyst. He supposed that the velum disappeared as the foot was developed, so that by the time the foot was "perfectly developed" the velum had disappeared.

My sketches of living specimens (see fig. 21*i*) of the larva which I consider to be Pecten show both foot and velum present in specimens 0.18 millimeter long which is nearly as large as were obtained. What was taken to be the anterior adductor was noted in specimens at least up to 0.16 millimeter long, so that it seems probable that this structure continues to the close of the larval (prodissoconch) stage. Gills were not noted.

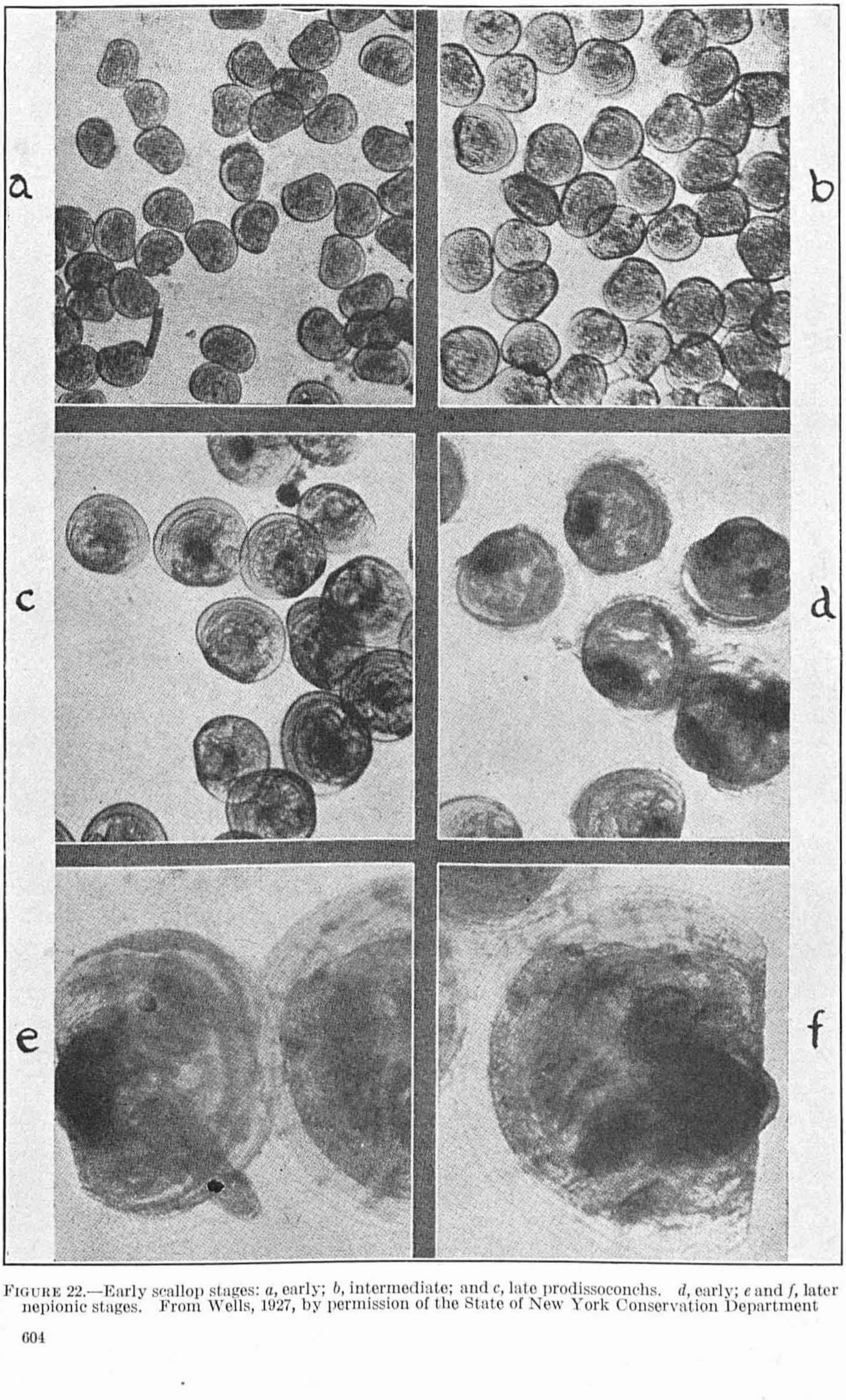

FIGURE 22.—Early scallop stages: *a*, early; *b*, intermediate; and *c*, late prodissoconchs. *d*, early; *e* and *f*, later nepionic stages. From Wells, 1927, by permission of the State of New York Conservation Department

POSTLARVAL DEVELOPMENT

It is usual to consider the late veliger or prodissoconch as ending the larval stage, and this is done here, although it is realized that the changes yet to be passed through are considerable.

The first postveliger stage is here termed the *nepionic* (after Jackson) rather than *dissoconch* [5] and begins with the appearance of the compressed, wide-spreading shell characteristic of this stage, not only in the scallop but also in the oyster. The new shell growth quickly assumes a shape resembling that of the adult, with long, straight hinge, byssal notch, and cycloid outline, but without ribs. (Figs. 21 and 22.) It begins with a length of about 0.18 millimeter and ends with one of about 1 millimeter (fig. 21), when the ribs begin to appear. During this period of growth gills attain 15 or 20 reflected filaments, heart and pericardium become plainly visible, the intestine comes to lie close to the adductor muscle which becomes large and differentiated into motor and catch portions. A few ocelli (6 in 1 specimen) and tentacles (15 in 1 specimen), together with the flap, appear around the mantle margin and palps near the mouth. The animal can attach by the byssus, crawl with the foot, swim much as in the adult, and float at the surface with the foot extended along the surface film. In the laboratory a specimen even floated for two hours at the film after the foot had been withdrawn into the shell. The foot is large, ciliated, and very active; the tentacles, papillose and sensitive. At or just after the end of the nepionic period (as indicated by shell development) the visceral mass and filaments of the outer demibranch begin to appear.

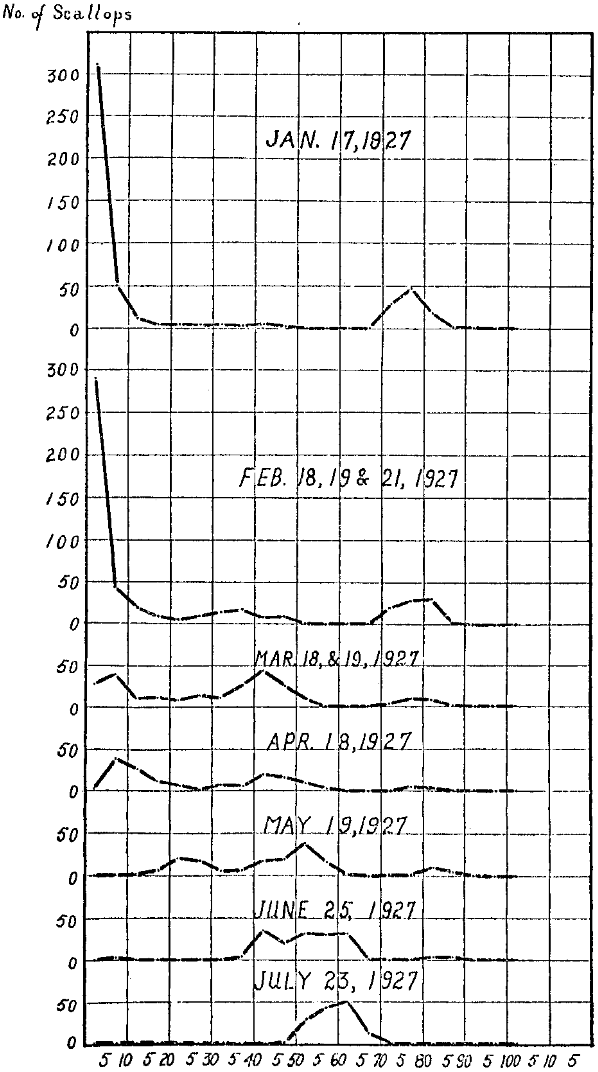

FIGURE 23.—Length-frequency curves based on one collection at Pivers Island, for each month of the first half of 1927 (5-millimeter groupings). (See Table 4)

A transition or plicate stage is recognized by Jackson. This (Fig. 21*m*) begins with the appearance of shell ribs and continues to a size of about 4 millimeters when an appearance strikingly like that of the adult is attained. During this period the "guard" tentacles appear, and lips, gills, mantle margin, visceral mass and structures, generally, attain rather closely to the condition of the adult.

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[5] Dissoconch is sometimes used specifically to designate this early stage. However, Jackson (1890, p. 281), who apparently originated the term, applies it to the shell of the adult and of all postveliger stages. See also Korschelt (1900).

GROWTH, AGE AT MATURITY, AND LENGTH OF LIFE (ANNUAL GROWTH LINE)

Although scallops from various areas have been collected and measured, the material from which was obtained the data chiefly used in the study of growth rate, age at sexual and commercial maturity, and length of life, was secured from the Pivers Island bed close to the laboratory. This was a desirable selection because of its ready accessibility and because during the first summer it offered the only known ample supply. An unfailing natural bed so close at hand has proved highly desirable, lacking only freedom from molestation by man[6] to be nearly perfect.

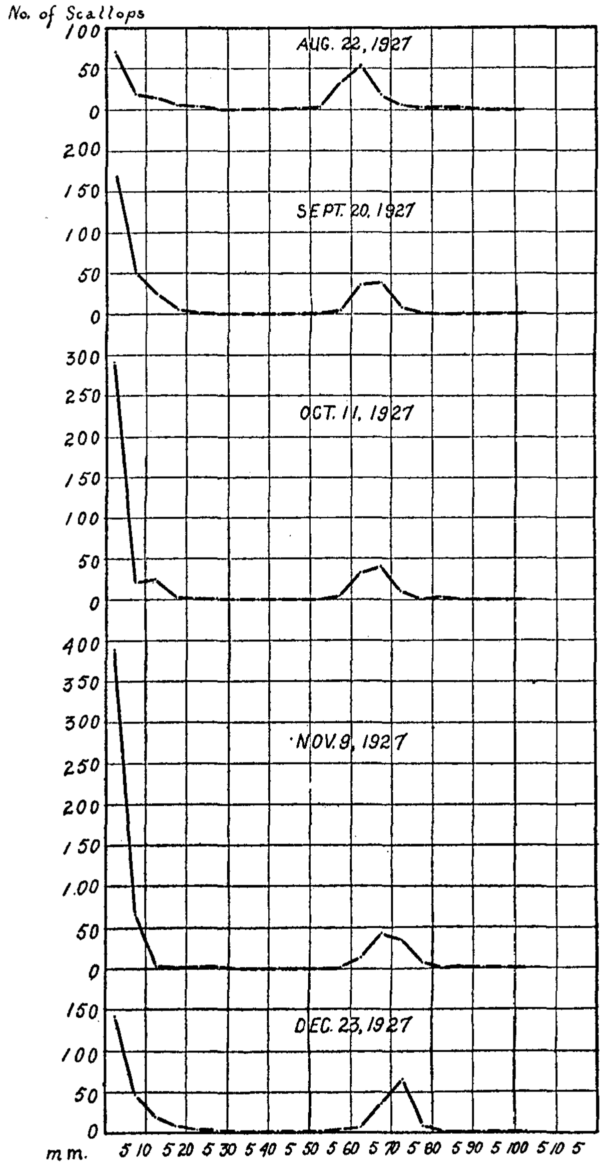

FIGURE 24.—Length-frequency curves based on one collection at Pivers Island, for each month of the second half of 1927 (5-millimeter groupings). (See Table 4)

Collections of scallops for measurement were made twice monthly over a large portion of the time. Of the scallops of considerable size, the attempt was made to secure a hundred. Therefore the number of these taken, unless markedly below that number, is not indicative of abundance. On the other hand, by the fall of 1926 collections for small scallops, which, as previously noted, not only dwell amidst vegetation but also attach themselves to it by means of the byssus, generally were made by raking a tubful of eelgrass. Numbers of these, therefore, are indicative of abundance. (See Tables 4 and 5.) One collection, as here considered, generally was made on 1 day, rarely on 2 or 3 days, and with an elapsed time of not over 4 days. In no instance is a size frequency curve a composite of two collections, as here defined.

The series of size-frequency curves (Figs. 23 and 24) show the year classes present and their appearance, growth, and disappearance. At the first of the year two classes are present in abundance, one composed of small individuals varying much as to size, the other of

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[6] In the summer of 1926 a portion of these flats was set aside by the State to be excluded from commercial scalloping. Unfortunately, it has seemed impracticable to prevent serious molestation.

large scallops of a compact size group. As the season progresses the effect of growth becomes very evident in the first class and, in time, the effect of market scalloping in the second class. By the end of the scalloping season, except for a few stray old scallops, there is present only one class. This class, because of the extended and probably irregular spawning season, for a time is lacking in compactness and may even appear divided, but by June or July becomes compact and so continues until all but eliminated by scallopers. Through the few left it may be followed (1927) into the next fall. In 1927, the first year in which suitable methods for securing very small scallops were applied throughout the year, the new class appeared in the summer. This class became prominent in late summer and through the fall and early winter increased greatly. Figure 25 shows the size frequency distribution at different seasons in different years.

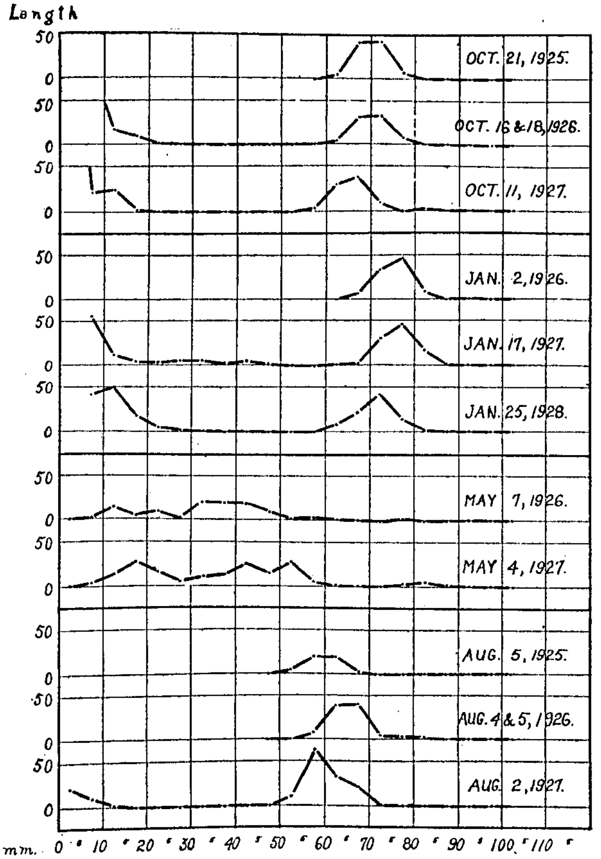

FIGURE 25.—Scallop length-frequency curves (5-millimeter groupings) for various years at various seasons. To save space and facilitate comparison, if large numbers of small scallops were found this part of the curve has been omitted. (See Table 5)

TABLE 4.—*Numbers of scallops of all sizes (in 5-millimeter groups) taken in the various collections through 1927 at Pivers Island. (See figs. 23 and 24)*

Length, millimeters	January	February		March		April		May		June		July		August		September		October	November	December
	17	1	19	5	20	4	18	4	19	3	25	8	23	2	22	6	20	11	9	23
0 to 4.5	313	256	290	40	27	13	4			4	1	4	3	22	71	243	174	290	387	142
5 to 9.5	56	36	46	21	39	53	41	4			4		1	10	19	63	51	22	56	47
10 to 14	13	19	18	6	13	21	28	14	2		1		1	3	14	12	26	26	4	19
15 to 19	5	19	8	2	12	18	13	27	7						6	3	6	3	2	8
20 to 24	4	7	6	5	9	2	8	17	20	2					4	3	2	1	3	4
25 to 29	6	7	8	10	14	5	2	6	17	13						1		1	2	1
30 to 34	6	33	14	27	12	8	7	12	5	23										1
35 to 39	3	19	17	49	27	7	7	14	7	22	5	1			1					
40 to 44	6	17	8	31	44	21	22	26	17	23	34	3		1						
45 to 49	3	7	10	20	26	15	17	16	20	21	19	25	3		1	1				
50 to 54		2	2	6	10	7	10	29	39	35	32	46	29	12	1	2				
55 to 59					1	1	4	6	16	42	30	36	43	65	32	4	5	4	1	2
60 to 64	1	1		1				2	3	6	32	19	50	35	52	45	37	32	13	7
65 to 69	2	6	2		1						3	5	12	22	18	34	39	40	43	35
70 to 74	32	22	18	12	5	1			1	1		2	3	3	5	8	8	11	35	65
75 to 79	44	44	29	41	10	5	6	4	2	3	1	1	1		2	2	1		7	8
80 to 84	18	26	31	31	9	5	4	6	10	3	2	3		1	2			2		
85 to 89	3	4	4	9	1	1	1	2	5	3	1	3	2	2	1	2	1		1	
90 to 94	1	1	1						1			1	1							

TABLE 5.—*Data as to lengths of scallops from certain seasonal collections in 1925, 1926, and 1927. Pivers Island, 5-millimeter groupings. (See fig. 25)*

Length, millimeters	Oct. 21, 1925	Oct. 16–18, 1926	Oct. 11, 1927	Jan. 12, 1926	Jan. 17, 1927	Jan. 25, 1928	May 7, 1926	May 4, 1927	Aug. 5, 1925	Aug. 4–5, 1926	Aug. 2, 1927
0 to 4.5		6	290		313	252					22
5 to 9.5		94	22		56	47	1	4			10
10 to 14		17	26		13	51	16	14			3
15 to 19		11	3		5	19	4	27			
20 to 24		3	1		4	6	9	17			
25 to 29			1		6	2	2	6			
30 to 34					6	1	21	12			
35 to 39					3		21	14			
40 to 44					6		19	26			1
45 to 49					3		10	16			
50 to 54							2	29	5	1	12
55 to 59			4				4	6	21	10	65
60 to 64	5	6	32		1	8	1	2	20	41	35
65 to 69	43	32	40	8	2	23			3	40	22
70 to 74	43	34	11	36	32	42				6	3
75 to 79	8	8		47	44	15	2	4		4	
80 to 84	1	1	2	9	18	12		6		4	1
85 to 89					3			2			2
90 to 94					1						
95 to 99											

From the data presented in these graphs it is evident that the life of a year class is as follows: It originates from summer to winter but principally in the fall, grows to sexual maturity so that its members spawn the next fall (summer to winter) when a year old. In its second winter it constitutes the market class and, as such, is nearly eliminated. Of the few not marketed some survive until the succeeding December, but neither these data nor some experiments in which scallops were confined in a pen give any close indication as to the portion which survive until then, or even to summer.

The length of life attained by the great majority of scallops reaching maturity is not over 20 months, but can not be stated with exactitude because of the extended spawning and marketing seasons. There is no evidence of any old age mortality before the close of the market season. Of those caught at the end of the season (last of April) a very few may be 21 months old, more of them 19 or 20, and a goodly proportion about 16 months. Ordinarily, comparatively few survive until the closing days of the season. By the last of February the supply is greatly reduced. At that time some of them are only about 14 months old, many not over 16 months, and the majority not over 18 months. Great numbers of scallops are caught in December when many are about 12 months old, and the majority not over 14 months. Under present conditions the length of life of the majority of scallops attaining to maturity may be taken to be from 12 to 18 months.

The normal length of life may or may not be a very different thing from the general length of life of mature scallops. Belding (1910) found that Massachusetts scallops (which spawn in June and July) suffered a heavy mortality in the spring following the market season and when lacking a few months of being 2 years old. Only a few survived to 2 years and a second spawning. This was the more remarkable because in all cases noted development of sexual products in preparation for a second spawning began and continued normally until death intervened. This suggests not death from old age but from some pathologic factor. A few survived to a second spawning and even to an age of 30 months.

Because destruction of adult scallops by man generally is so extreme in North Carolina, the problem of the normal length of life, or the length of life of scallops not destroyed by man, is difficult to determine. It is evident that some survive to 2 years of age, or somewhat more but not what portion would do so. It is not even clear that there is any general mortality following the market season and preceding a second spawning (to correspond with the spring mortality reported by Belding). With scallops of rapid growth, such as those at Pivers Island, growth becomes slower after the second winter and there is no reason to believe that the normal span of life is much over 2 years. Questions of practical importance are what proportion, if spared by man, would survive to a second spawning, and what proportion would survive to a second market season; that is, third winter. The evidence is scanty and inconclusive.

As judged by the prevalence at all times of various sized shells of recently dead scallops, there is considerable mortality at all times and ages. Because of this, any special mortality rate, among the few scallops ordinarily spared at the end of the market season, must be rapid and heavy to be definitely determined. There are no direct observations nor data to show such mortality. It is possible, however, that there is a gradual but high mortality through the second summer and the following autumn. Unless freshets or other natural agencies caused special destruction this could be determined if man did not interfere.

When the market season closed in the spring of 1929 there were still, as scallopers and dealers have stated, many adult scallops remaining in western Bogue Sound. This was because, on the one hand, these small scallops had been very abundant and, on the other, the market was poor. These small scallops bring the lowest return and in such a season are hardly desired by the dealers at any price. When I visited western Bogue Sound in November, 1929, I found among the usual small 1-year-old scallops (40–54 millimeters but principally 45–50 millimeters long) commercial quantities of scallops of large size (many of them 75 to 80 millimeters, some as small as 70 and one 65 millimeters long). These large scallops have an evident annual growth line (see succeeding paragraphs) at about 50 millimeters. There seems no reason to doubt that they were 2-year-old scallops.

Thus it is shown that in some situations scallops may survive to 2 years or more of age in considerable proportion and quantity. It is also shown that in so doing they may increase greatly in bulk and consequently in value. This leads to another question: Do the scallops of slow growth, and consequent small size at 1 year of age, live longer than those of rapid growth? In Massachusetts, Belding (1910) found this to be the case. If this is true also in North Carolina, the results found in western Bogue Sound are not indicative of what would occur in the more valuable areas which produce large scallops in one year. They do indicate, however, that failure to market the full annual crop in these areas is not all loss by any means. Indeed it is possible that it might be more profitable in such areas not to market the small yearling scallops, but to leave them to grow.

Beginning with late spring and early summer the growth of scallops which will make up the market class of the succeeding winter is well shown by the increase in average length. (Tables 6 and 7, and fig. 26*c*.) Until about this time there is extreme variation in size, and through the preceding fall and into the winter the continued addition of new stock has reduced the average so that average increase in size is considerably less than growth rate. The advance of the mode offers an even less satisfactory method of study, because of continued dominance of the very small scallops in my collections. Until late spring, growth rate of scallops less than 1 year old seems best represented by the increase in size of the largest of the year class. (Fig. 26, *b* and *d*.) These largest individuals apparently do not increase their lead over the others and may be taken to be older than more rapid-growing individuals. Typical sizes are shown by the size-frequency curves.

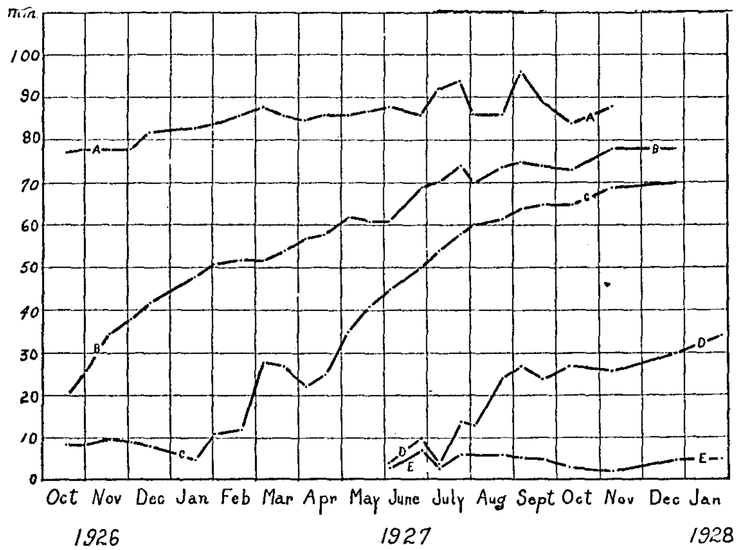

FIGURE 26.—Growth of scallops at Pivers Island, N. C. *A*, Longest of 1925 year class as determined by Table 8 (there is some uncertainty as to a few points, particularly the highest which may represent an older class); *B*, longest of 1926 year class (see Tables 7 and 8); *C*, average length of 1926 year class (see Table 6); *D*, longest of 1927 year class (Tables 7 and 8); *E*, average length of 1927 year class (see Table 6)

The sizes given in these growth and size frequency curves apply strictly only to the scallops of the Pivers Island flats. In a general way they apply to the scallops of other beds in Beaufort Harbor and in eastern Bogue Sound, some of which produce larger scallops and other smaller ones. The scallops of Core Sound and particularly of western Bogue Sound in general are much smaller.

TABLE 6.—*Average lengths (millimeters) of scallops of certain year classes according to collections made at Pivers Island. (See fig. 26)*

Date	1926 year class	Date	1926 year class	Date	1927 year class
1926		1927		1927	
Oct. 17	9	May 19	41	May 19	---
Oct. 30	9	June 3	45	June 3	3
Nov. 17	10	June 25	52	June 25	7
Dec. 1	9	July 8	54	July 8	3
Dec. 15	8	July 23	59	July 23	6
		Aug. 2	60	Aug. 2	5
1927		Aug. 22	61	Aug. 22	6
Jan. 17	5	Sept. 6	64	Sept. 6	6
Feb. 1	11	Sept. 20	65	Sept. 20	5
Feb. 19	12	Oct. 11	65	Oct. 11	3
Mar. 5	28	Nov. 9	69	Nov. 9	2
Mar. 20	27	Dec. 23	70	Dec. 23	5
Apr. 4	21				
Apr. 18	25	1928		1928	
May 4	36	Jan. 25	---	Jan. 25	---

TABLE 7.—*Length frequencies of scallops collected at Pivers Island, October 17, 1926, to January 25, 1928. (See fig. 26)*

Length millimeters	1926					1927																				1928
	October		November	December		January	February		March		April		May		June		July		August		September		October	November	December	January
	17	30	17	1	15	17	1	19	5	20	4	18	4	19	3	25	8	23	2	22	6	20	11	9	23	25
Under 2	---	---	---	12	18	119	96	13	---	---	---	---	---	---	---	1	1	---	5	24	173	20	172	244	[1] 33	176
2	---	---	---	21	42	45	44	79	2	2	---	---	---	---	1	---	---	1	3	19	31	17	55	45	[1] 33	40
2.5 to 3.5	4	7	5	45	71	122	90	138	24	12	1	2	---	---	1	---	2	2	5	22	21	78	53	67	30	18
4 to 4.5	2	21	13	23	31	27	26	60	14	13	12	2	---	---	2	---	1	---	9	6	18	59	10	31	46	18
5 to 5.5	9	13	12	24	25	20	11	16	7	13	9	7	---	---	---	1	---	---	2	5	8	12	7	30	14	7
6 to 6.5	21	12	10	22	22	11	6	14	7	9	17	8	---	---	---	---	---	---	3	4	23	20	3	16	18	18
7 to 7.5	25	5	7	13	12	10	6	6	2	7	11	6	1	---	---	---	---	---	1	4	10	6	5	4	3	7
8 to 8.5	26	16	5	9	21	8	7	5	3	8	13	8	1	---	---	1	---	---	3	5	19	7	4	6	10	8
9 to 9.5	13	13	6	14	9	7	6	5	2	2	3	12	2	---	---	2	---	1	1	1	3	6	3	---	2	7
10	11	15	1	13	16	2	4	1	1	7	5	7	1	---	---	1	---	---	---	4	1	6	7	1	7	14
11	3	6	3	11	5	5	4	2	1	1	3	5	1	---	---	---	---	---	1	4	1	2	9	1	2	10
12	2	4	5	6	21	3	5	4	1	1	5	6	4	---	---	---	---	---	---	5	5	8	3	1	6	10
13	---	5	4	6	7	---	2	4	2	2	4	3	3	---	---	---	---	---	2	1	3	3	2	---	3	8
14	1	6	4	10	3	3	4	7	1	2	4	7	5	2	---	---	---	1	---	---	2	7	5	1	1	9
15	2	3	5	3	8	---	3	2	---	1	5	4	8	---	---	---	---	---	---	---	1	4	1	---	2	5
16	4	2	3	8	12	1	3	---	---	3	3	3	7	---	---	---	---	---	---	3	1	---	1	1	---	8
17	4	---	2	2	5	2	2	1	---	3	3	1	2	1	---	---	---	---	---	---	---	2	1	1	2	2
18	2	1	1	8	1	2	7	5	1	4	6	3	5	2	---	---	---	---	---	1	---	---	---	---	2	3
19	1	---	2	3	3	---	4	---	1	1	1	2	5	4	---	---	---	---	---	2	1	---	---	---	2	1
20	3	2	1	2	1	1	2	2	---	3	---	2	2	3	---	---	---	---	---	1	---	1	1	2	---	4
21	---	---	2	1	1	3	2	---	1	2	---	1	1	2	---	---	---	---	---	---	1	---	---	---	---	1
22	---	1	---	5	5	---	1	3	1	---	1	3	7	7	---	---	---	---	---	2	1	---	---	---	3	---
23	---	1	---	2	4	---	1	---	2	2	---	2	2	4	---	---	---	---	---	---	---	---	---	---	1	---
24	---	---	---	4	5	---	1	1	1	2	1	---	5	4	2	---	---	---	---	1	1	1	---	1	---	1
25	---	1	---	---	4	3	---	1	---	2	1	---	---	2	1	---	---	---	---	---	---	---	---	1	---	1
26	---	---	---	3	3	2	3	4	---	---	1	---	1	4	2	---	---	---	---	---	---	---	---	1	---	---
27	---	1	1	---	---	---	2	1	2	4	---	1	3	3	3	---	---	---	---	---	1	---	1	---	---	1
28	---	---	---	1	---	1	---	1	4	5	2	1	2	4	2	---	---	---	---	---	---	---	---	---	1	---
29	---	---	1	---	2	---	2	1	4	3	1	---	---	4	5	---	---	---	---	---	---	---	---	---	---	---
30	---	---	---	1	1	---	5	2	4	---	2	1	4	2	6	---	---	---	---	---	---	---	---	---	1	---
31	---	---	---	1	---	1	3	3	3	2	2	---	1	---	3	---	---	---	---	---	---	---	---	---	---	---
32	---	---	---	2	---	1	9	2	5	3	1	1	2	1	4	---	---	---	---	---	---	---	---	---	---	---
33	---	---	---	---	---	2	1	1	7	3	1	3	2	2	5	---	---	---	---	---	---	---	---	---	---	1
34	---	---	1	1	---	2	15	6	8	4	2	2	3	---	5	---	---	---	---	---	---	---	---	---	---	---
35	---	---	---	---	---	---	4	3	2	2	1	1	---	1	6	---	---	---	---	---	---	---	---	---	---	---
36	---	---	---	---	2	1	4	1	12	6	1	2	1	2	6	1	---	---	---	---	---	---	---	---	---	---
37	---	---	---	1	1	---	7	1	11	7	2	---	5	1	4	1	---	---	---	---	---	---	---	---	---	---
38	---	---	---	1	2	1	3	5	15	6	2	2	3	3	1	1	---	---	---	---	---	---	---	---	---	---
39	---	---	---	---	2	1	1	7	9	6	1	2	5	---	5	2	1	---	---	1	---	---	---	---	---	---
40	---	---	---	---	1	1	3	2	8	10	7	4	1	2	3	3	1	---	---	---	---	---	---	---	---	---
41	---	---	---	---	1	1	1	---	5	8	1	2	8	---	5	6	---	---	---	---	---	---	---	---	---	---
42	---	---	---	---	1	2	4	2	7	11	6	5	6	---	4	9	---	---	---	---	---	---	---	---	---	---
43	---	---	---	---	---	---	5	2	5	6	4	4	4	3	7	8	---	---	---	---	---	---	---	---	---	---
44	---	---	---	---	---	2	4	2	6	9	3	7	7	12	4	8	2	---	1	---	---	---	---	---	---	---
45	---	---	---	---	---	1	3	3	4	4	3	5	1	2	3	5	---	---	---	---	1	---	---	---	---	---
46	---	---	---	---	---	1	2	2	3	2	3	5	2	6	5	6	5	---	---	---	---	---	---	---	---	---
47	---	---	---	---	---	---	1	1	5	4	4	3	4	2	4	2	7	2	---	---	---	---	---	---	---	---
48	---	---	---	1	---	1	---	2	6	6	3	3	6	6	5	3	9	1	---	1	---	---	---	---	---	---
49	---	---	---	---	---	---	1	2	2	10	2	1	3	4	4	3	4	---	---	---	---	---	---	---	---	---
50	---	---	---	---	---	---	1	1	1	2	1	4	7	8	9	8	7	6	2	---	---	---	---	---	---	---

[1] These data recorded as 2 millimeters or under (66) arbitrarily divided as into equal portions.

TABLE 7.—*Length frequencies of scallops collected at Pivers Island, October 17, 1926, to January 25, 1928*—Continued

Length millimeters	1926					1927																				1928
	October		November	December		January	February		March		April		May		June		July		August		September		October	November	December	January
	17	30	17	1	15	17	1	19	5	20	4	18	4	19	3	25	8	23	2	22	6	20	11	9	23	25
51							1		1	2	2	2	5	7	4	5	18	4								
52				1				1	4	1	1	3	8	10	10	6	9	5	3							
53										2		1	5	5	4	2	6	6	2	1	1					
54					1					3	3		4	9	8	11	6	8	5		1					
55													2	5	8	4	9	10	9	4						
56												1	1	6	12	7	7	9	17	3		1	2			
57											1	1	1	4	8	7	8	7	8	8	1	2			1	
58												1	2		8	9	7	9	18	6	2		2		1	
59										1		1		1	6	3	5	8	13	11	1	2		1		
60		1		1	1				1				1	2	2	10	6	12	4	11	8	5	4	2		1
61	1	1	1	1										1	4	8	4	5	8	6	8	4	5	3	1	
62		1	1	2	1								1			6	1	15	7	14	11	10	8	1	1	
63	3	3	1		1	1	1									5	4	12	10	15	4	11	6	3	3	2
64	2	7	2	2	1											3	4	6	6	5	14	7	9	4	2	5
65	8	9	2	4	1		2									2		2	10	5	11	7	7	6	5	2
66	6	4	7	3						1							2	4	7	2	12	14	11	10	6	3
67	3	2	7	3	3												2	2	5	3	7	8	10	8	4	6
68	10	15	11	8	3	1	3	2										2		3	1	5	10	13	7	8
69	5	12	8	6	5	1	1									1	1	2		5	3	5	2	6	13	4
70	6	9	11	13	14	3	2	1	2								2	1	3	3	3	5	3	13	14	9
71	8	6	11	8	7	6	1	2	1	1				1							1	1	3	5	13	11
72	6	8	4	11	8	9	5	2	2	1								1		1	2		3	6	16	11
73	8	7	9	8	12	4	3	4	5	1											1	1	2	5	12	8
74	6	1	10	5	13	10	11	9	2	2	1				1			1		1	1	1		6	9	3
75	2	6	1	8	4	9	8	6	7		1		1								1			1	5	5
76	3	1	6	5	8	13	16	2	6	3	1	1	2		1		1	1						2	1	4
77	3	1	1		7	10	8	6	10	3	1	1			1					1				3	1	4
78		1	3	11	2	7	8	10	12	4		2	1	2	1	1					1			1	2	2
79		1	1		2	5	4	5	6		2	2								1		1				
80					4	7	9	8	9	5	1	1	2	4	1	1			1	1						2
81			2			2	8	8	12	1		1		1		1										
82	1				4	4	5	7	5	2		1	2	1			1									
83						4	2	5	2		3	1		1	1		2						1			
84		1		1		1	2	3	3	1	1		2	3	1					1			1			
85		1					1	3	3		1			3	1		2					1				
86						3	2	1	5	1		1	2	1	1	1	1	2	2	1						
87				1			1							1							1					
88									1						1									1		
89																					1					
90		1			1																					
91							1																			
92						1								1			1									
93								1																		
94																		1								

Usually in the fall, rarely in the summer or as late as early winter, there is formed the only growth line which is present consistently. On the average and perhaps nearly always it represents an age of very close to 1 year and reasonably may be termed a 1-year line or annual-growth line. Its cause is not easy of determination.

This first-year line has been found, although rarely, as early as September. One old scallop was found in July with what appeared to be a second annual-growth line or 2-year line. Because the line presumably is formed by interruption of growth and because growth is continued through the winter (see fig. 27) it is evident that the growth cessation is not due to too low a temperature.

Seasonal plankton change is another conceivable explanation. Although against it may be brought not all the arguments against temperature, at present there is no direct, positive evidence in its favor and no sufficient basis for its acceptance.

In regard to spawning or spawn production the case is less indefinite. The line typically is a fall line; spawning occurs principally in the fall. Rarely a newly formed line is found in summer or early winter; the spawning season begins in the summer and extends to early winter. In individual cases, however, no close correlation between the amount of new growth—that is, growth outside the line—and the state of

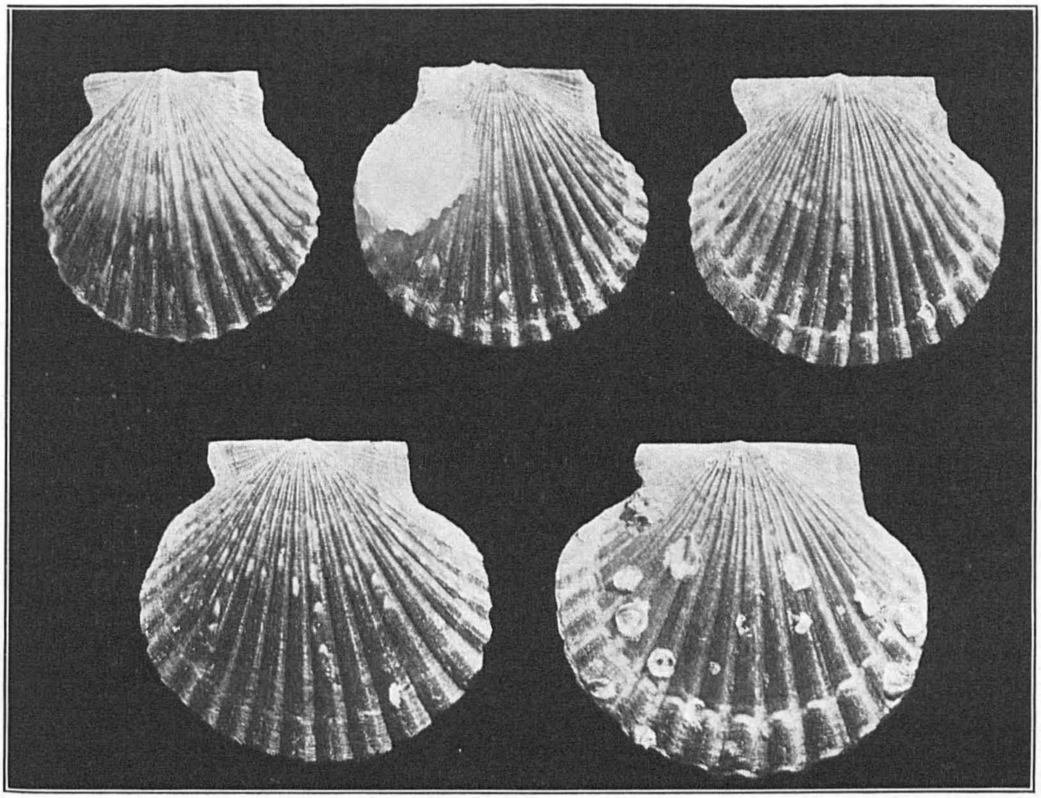

FIGURE 27.—Series of scallops with growth line illustrating the fact that this line is formed in the fall, when scallops are spawning and are about 1 year old. The scallop at the upper left-hand corner, with line just formed, was taken October 30; the second one, December 1; the third, January 31; that in the lower left corner, February 20; and that in the lower right corner, July 23. (1926 and 1927, Pivers Island, N. C.) One-half natural size

the gonads has been found consistently. A scallop might have much new growth and gonads far from empty or little new growth and gonads nearly emptied. Although such cases are extreme, it seems clear that the significant factor is not spawn emission. If growth cessation is causally connected with the spawning season (and such a hypothesis is deemed worthy of tentative acceptance) it would seem that some metabolic activity, indirectly connected with the development of eggs and sperms, must be responsible.

In this connection it is interesting to note that Risser (1901) working in Rhode Island and Belding (1910) working in Massachusetts, arrived at opposite conclusions as to the factor producing the annual-growth line. Risser found the spawning season to correspond well with the month of June and the growth line to be formed by an interruption of growth during that month. His growth curve, although it leaves such a possibility, does not show complete growth cessation during June. Neither does it definitely show growth cessation during the winter, but it indicates that if growth had ceased it was resumed by mid March. His photographs of scallop shells show no growth line by May 31 (too late, it would seem, for a winter line) but a noticeable resumed growth on shells taken July 1 to 12 and, therefore, indicate that the growth line was formed in June, the spawning month.

Belding (loc. cit.) states that the growth line is due to growth interruption not in the spawning season but rather in the winter months. In support of this assertion he gives various growth curves showing complete cessation of growth from December 1 to May 1, with a sharply marked resumption of growth on May 1. Instead of cessation of growth during the spawning season (June–July) he found a reduced growth rate (also shown in graphs). His excellent photographs of scallop shells with and without growth lines, bear no dates and, therefore, furnish no evidence pro or con. His graphs, with the sharp rise through May, the reduced inclination through June and July, and the increased inclination through August, September, and October, plainly indicate winter (and spring) cessation rather than spawning season cessation as productive of the growth line. However, it is to be considered that the time between growth resumption and spawning is short (about a month) and that not the act of spawning but rather metabolism connected with egg and sperm development may be the factor causing growth cessation. The fact that growth is shown through a period does not preclude the possibility that there has been a cessation at some interval or intervals during that period; that is, that a second growth interruption may have occurred. Moreover Belding's growth curves consist of a series of connected straight monthly lines connecting single points for each month. No collection dates nor data as to the numbers measured are given, and there is nothing to show that measurements were made at closer intervals as would be necessary to preclude the possibility of growth cessation going unrecorded.

To a degree my investigations tend to corroborate the findings of Risser and to oppose those of Belding as to the factor affecting the annual-growth line. Furthermore certain possibilities for error in Belding's conclusions are suggested (see preceding paragraph). It is, however, altogether reasonable that in northern areas the severe cold would stop growth and that the vernal resumption of growth, especially with a rapidly growing animal, would leave a well-marked growth line. Even if growth ceased for a time during the spawning season, the effect of this might be merged with the recently formed winter line.

Hopkins (1930) quotes Belding as to age and growth of Massachusetts scallops and the present writer as to Beaufort scallops.

The annual growth or first-year line has been assumed, in this discussion as elsewhere, to mark an interruption in growth. Indeed, indication of autumnal growth interruption among adults has been found. However, and especially in the upper valve, the line in question is not marked by a noticeable ridge or "terrace" but by color difference. In the lower valve the growth outside the line is unpigmented and, until discolored by growths and stains, pearly white, and is much more noticeable in this valve than in the upper. In time, however, the older part of this white growth often becomes so discolored as to make difficult the determination of the line. No such difficulty is encountered with the upper valve. In it the white (or light) growth is not long continued (ordinarily for a width of about 1 millimeter) and is followed by the usual darkly marked shell material. Obscured by extraneous growths and dirt and even darkened somewhat by stains, with a cleaned shell it stands out plainly against the dark of the upper valve and, except very rarely, is unmistakable.

ENVIRONMENTAL FACTORS

BOTTOM

Of the vast array of factors affecting a salt-water animal and constituting its environment, only temperature, salinity, current, depth, and bottom are directly considered here. The term "bottom" is used to include not only the soil but also its vegetation. As previously noted, the bay scallop is almost confined to grassy (chiefly Zostera) areas. Just why this is the case seems not to have been explained. The writer suggests that it is because early postveliger stages generally find satisfactory conditions for survival only where the vegetation affords suitable conditions for attachment above the substratum, and because subsequent migration is so slight as to leave nearly all scallops in grassy areas.

Grassy bottom, therefore, may be taken to be generally necessary for the bay scallop's existence in certain early stages of development. What its influence is on the subsequent life of the scallop, the writer is not prepared to state. Belding (1910) believed that much vegetation retarded growth. Although some of the best growing areas are very grassy, it is possible that growth in these areas would be better if the vegetation were less dense. However, it seems that locally the density of the vegetation is not very important in the growth of the scallop. This is a point of importance if scallop culture were to be developed. Possibly nongrassy areas would give better growth and prove more satisfactory for planting than grassy ones. On the other hand, scallops, which normally shift little, might dislike bare bottom and scatter badly. The type of soil influences the appearance but, within suitable limits, has little other direct effect.

DEPTH OF WATER

The depth of water is important to scallops in so far as it protects them from the effects of severe cold or from their enemies. The herring gull catches scallops only on flats exposed or nearly exposed at low water. The depth affords some protection from man in two quite opposite ways. In areas where raking is the only legal method of taking scallops, the depth of water over scallops sometimes is sufficient to be of protection from rakers. In other areas, where scallops are small and of such little value that raking them seldom is considered profitable, there is sometimes so little depth of water that even the small dredge boats can not navigate. This, of course, serves to protect the scallops from man. Sometimes in severely cold weather, as that which occurred late in December, 1925, there is considerable mortality among scallops in very shallow water or on flats which are exposed or nearly exposed at low water. Depths in productive areas are seldom over 6 feet and generally less than that. In a large proportion of the areas it is not over 3 feet. Scallops of the most rapid growth and largest size are found both on flats in shallow water and in the greater depth of channels. In some areas larger scallops are found in channels, but this may be chiefly a matter of current rather than depth.

CURRENT

Water currents are important in various ways. Undoubtedly they effect distribution of scallops, as of other oviparous bivalves, by carrying eggs, embryos, and larvæ, but to what extent and in just what way is not well understood. In addition, by carrying the loosened vegetation from scallop beds, currents doubtless transport scallops considerable distances, and may sometimes establish them in distant areas. Currents also bring food and O_2 to the scallop and so become very important.

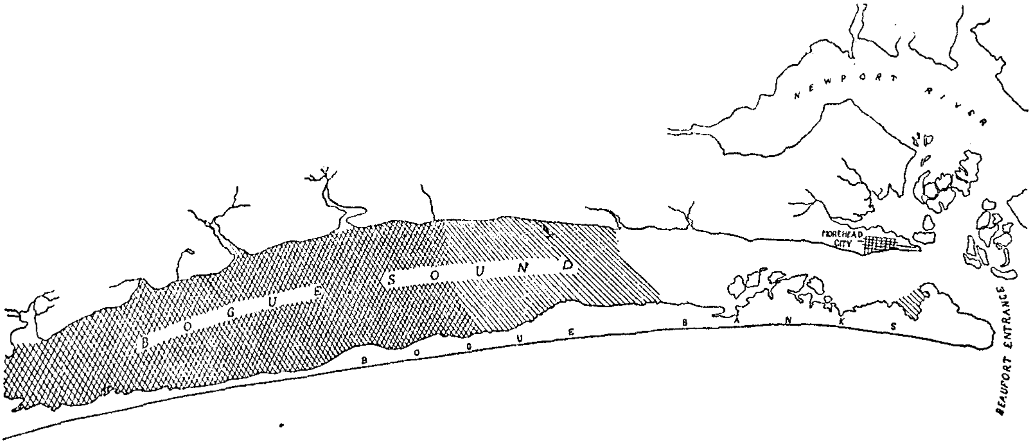

FIGURE 28.—Bogue Sound, showing areas of strong tide and rapid growth (unshaded); moderate tide and slower growth (single shaded); and little tide and poor growth (double shaded)

Because both salinity and scallop size generally decrease away from the inlets at first it seemed that salinity was the principal factor affecting the scallop growth rate. Later, as scallops became reestablished over considerable and varied areas, it became evident that the areas of rapid growth were not so much areas of saltier water as areas of greater current.

This is illustrated in Core Sound, where larger scallops are found along the west shore near the southerly end where the main current enters and leaves; in Beaufort Harbor, where scallops of moderate size are found on Town Marsh flats nearest the inlet but so situated that the tide rises over and flows off but does not traverse them; but is most easily illustrated in Bogue Sound.

Figure 28 shows Bogue Sound, from Beaufort Inlet (which furnishes much the greater tidal flow to and from the sound) nearly to the western end. It is divided into three sections. In the eastern section near the inlet, growth is rapid and produces the largest and most highly prized scallops in North Carolina. In only one productive area are the scallops of relatively inferior size (60 to 70 millimeters). This is in Tar Landing Bay, nearest the inlet but so protected by land that the tide merely rises and falls, does not sweep through. In the other productive areas the tide is very strong.

In the adjoining intermediate section the tide is reduced but still periodic. Growth is less rapid so that year-old scallops are of moderate size (60 to 70 millimeters).

The third section is that termed western Bogue Sound in this paper. Tidal flow generally is slow or, over the great expanses of scallop shoals, wanting or almost wanting and the water level greatly affected by winds. The main channel is a dredged one along the north shore. Scallop-producing areas constitute a large, perhaps the larger, portion of this section and yield great numbers of scallops. Growth is slow and the year-old scallops small but varying considerably in size over this large area (40 to 60 millimeters). Two-year-old scallops attain a much larger size.

The sound salinities normally are high, generally over 30 parts per mille and rarely as low as 27 parts per mille. Summer salinities in western Bogue Sound run as high as 37 parts per mille.

Although no quantitative data are available to show the relation between current and growth rate, it seems to me that the case is a fairly obvious one and that there is no reasonable ground for doubt that current is the chief physical factor governing growth in Bogue Sound. In other sections the case is not quite so simple and obvious but higher growth rate still is attributable to stronger current. Presumably this is in part because the current brings food, but the fact that it brings an abundance of O_2 and carries away products of vegetable decay besides CO_2, and so prevents injurious results from stagnation, may be more important. It should be considered that in the sluggish, slow-growing areas, the severity of warm-weather conditions may be a principal retarding factor.

SALINITY

Although salinity is an essential condition of the environment of the bay scallop, the limits are not easily determined. Only the lower limit is of presumable practical importance, because bay scallops are to be found in the most saline waters of their range (total salinity about 38 parts per mille). The minimum salinity may well be considered under two heads, which I term the "freshet" or temporary minimum and the distributional or continued minimum.

The distributional minimum is taken to be the lowest salinity to be found within scallop areas except during extreme freshets. This minimum has been sought particularly in Core Sound, which ordinarily contains scallops only in its southerly saltier portion but which in the winters of 1926–27 and 1927–28 contained them also in its northern portion near where it joins the less saline Pamlico Sound. The lowest salinity found in scallop areas in Core Sound or elsewhere, except during severe freshets, was 20 parts per mille, with 21.3 parts per mille or higher almost universal. (See Giral, 1926, as to the accuracy of salinity determinations.) This figure of 20 parts per mille therefore is taken as the distributional minimum.

Even in the saltier portions of the scallop-producing areas severe freshets occur which are extremely destructive. In September, 1924, a freshet occurred which almost completely destroyed the scallops (unless perhaps the very young) in all areas except those off Morehead City in lower Bogue Sound. The salinities prevailing off Morehead City during this freshet are not known, but those at Pivers Island became as low as 6 parts per mille (Table 8 and fig. 29). Because of the tidal conditions appreciably higher salinities might well have prevailed, and doubtless did prevail off Morehead City. In 1921 freshets reduced the salinities in the Harkers Island section, which includes southern Core Sound, to 13–16.6 parts per mille[7] on February 7. Scallops are reported to have been then in very poor condition. In March scallops were not being taken there commercially, but whether because they had all been caught or because of mortality in situ is not known. Tables 8 and 9 and Figures 30 and 31, show noticeably reduced salinities at Pivers Island early in 1924 and 1925. Because scallops were generally abundant in the summer of 1924 and at Pivers Island in 1925, it is evident that this low salinity caused no extreme mortality, at least among the young. In February and March, 1926, salinities as low as 20 parts per mille were attained. In January, following the severe cold of late December, there was noticeable mortality among adult scallops, but not in February or March. In October, 1928, as a result of unusual inland rains in September, observed salinity at Pivers Island became as low as about 19 parts per mille (18.6 parts per mille as calculated from routine hydrometer readings). This freshening was accompanied or followed by a considerable mortality among adult scallops at Pivers Island and other places in Beaufort Harbor. In Newport River the destruction was so great as to cause the general abandonment of its scallop grounds in the ensuing commercial season. Just how fresh the water over these grounds became is not known. However, near the mouth of the canalized connection with Neuse River and within the extreme limits of scallop extension, a salinity of 4.8 parts per mille was found. In Core Sound scallops survived salinities at least as low as 16.2 parts per mille (at Marshallberg) although in poor condition and perhaps with considerable delayed mortality.

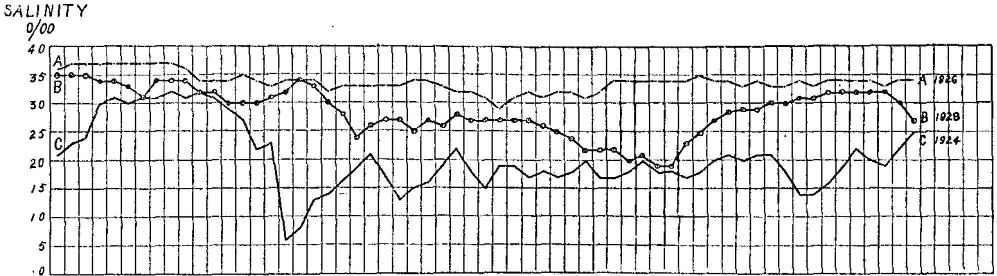

FIGURE 29.—Daily salinities at Pivers Island through autumnal periods of extreme scallop destruction (1924), moderate mortality of adults (1928), and good survival (1926). (Based on one hydrometer reading daily, corrected for temperature but instrumental error not known.) See Table 9

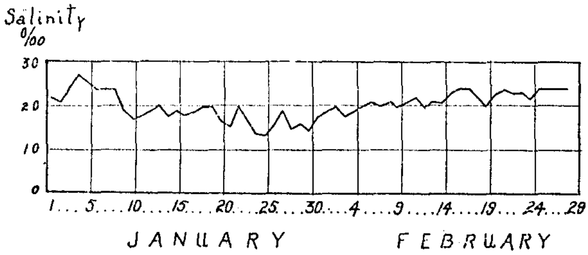

FIGURE 30.—Daily salinities through a winter period (1925) with low salinities which produced no noticeable mortality and certainly spared sufficient young scallops for a good crop the succeeding winter (based on one hydrometer reading daily corrected for temperature but instrumental error not known)

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[7] These figures for total salinity are based on data expressed as NaCl kindly furnished with other information by Dr. J. J. McManus, chief, Savannah station; Food, Drug, and Insecticide Administration; United States Department of Agriculture. The analytical work in this instance was done by James O. Clarke of the Food, Drug, and Insecticide Administration.

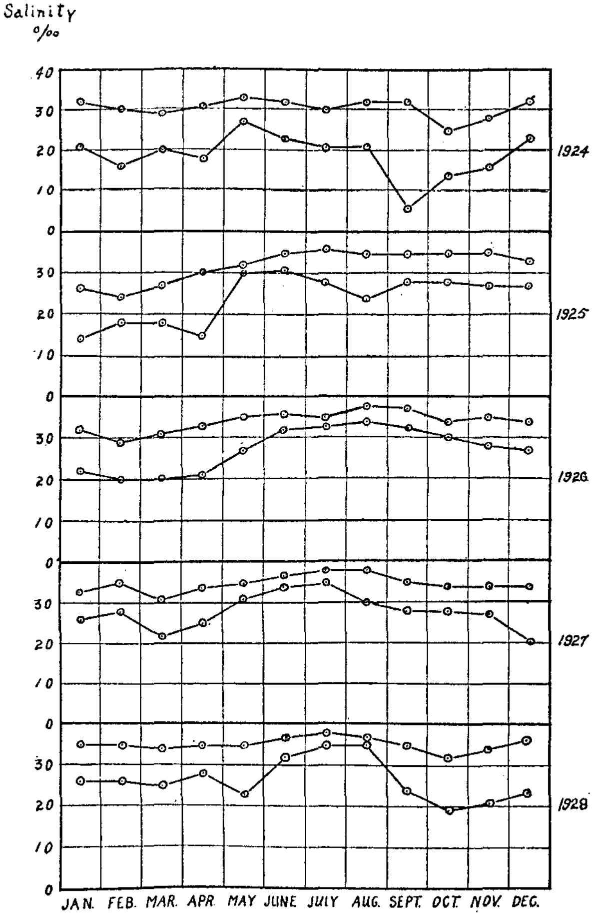

FIGURE 31.—Monthly maximum and minimum salinities at Pivers Island, 1924–1928. (Based on one daily hydrometer reading, corrected for temperature but instrumental error not known.) (See Table 10)

TABLE 8.—*Daily salinities at Pivers Island through autumnal periods of extreme destruction, moderate mortality, and good survival*

[Fractions of parts per thousand are omitted]

AUTUMN SALINITIES

Date	Day of month																														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
September, 1924	21	23	24	30	31	30	31	31	32	31	32	31	29	27	22	23	6	8	13	14	---	---	21	17	12	15	16	19	22	8	---
September, 1926	36	37	37	37	37	37	37	37	37	36	34	34	34	35	34	33	34	34	34	32	33	33	33	33	33	34	34	33	32	32	---
September, 1928	35	35	35	34	34	33	31	34	34	34	32	32	30	30	30	31	32	34	33	30	28	24	26	27	27	25	27	26	28	27	---
October, 1924	15	19	19	17	18	17	18	20	17	17	18	20	18	18	17	18	20	21	20	21	21	18	14	14	16	19	22	20	19	22	25
October, 1926	31	29	31	32	31	32	32	31	32	34	34	34	34	34	34	35	34	34	33	34	33	33	34	33	34	34	34	34	33	34	34
October, 1928	27	27	27	27	26	25	24	22	22	22	20	21	19	19	23	25	27	28	29	29	30	30	31	31	32	32	32	32	32	30	27

WINTER SALINITIES

January, 1925	22	21	24	27	26	24	24	24	19	17	18	19	20	18	19	18	19	20	20	17	16	20	17	14	14	16	19	15	16	15	18
February, 1925	---	20	18	19	20	21	20	21	20	21	22	20	21	21	23	24	24	24	20	23	24	23	23	22	24	24	24	24	---	---	---

TABLE 9.—*Extreme monthly maximum and minimum salinities at Pivers Island, 1924–1928*

[Fractions of parts per thousand are omitted]

Year	Month											
	January	February	March	April	May	June	July	August	September	October	November	December
MAXIMUM												
1924	32	30	29	31	33	32	30	32	32	25	28	32
1925	27	24	27	30	32	35	36	35	35	35	35	33
1926	32	29	31	33	35	36	35	38	37	34	35	34
1927	33	35	31	34	35	37	38	38	35	34	34	34
1928	35	35	34	35	35	37	38	38	35	32	34	37
MINIMUM												
1924	21	16	20	18	27	23	21	21	6	14	16	23
1925	14	18	18	15	30	31	28	24	28	28	27	27
1926	22	20	20	21	27	22	33	34	32	30	28	27
1927	26	28	22	25	31	34	35	30	28	28	27	20
1928	26	26	25	27	23	32	35	35	24	19	21	23

When fall towings were begun at Pivers Island in 1928, larvæ believed to be those of the scallop were taken regularly. They soon disappeared, however. This might have been one of the vagaries of distribution or collecting but, in view of the failure of the "set" or crop of young it seems probable that it was due to death from the freshets which were responsible for a destruction vastly more serious than that of adults.

At Pivers Island, routine daily hydrometer readings are taken. Although these might readily miss the extreme reduction during a brief freshet, they would be expected to yield satisfactory data for a long-continued saline reduction such as occurred in the fall of 1928. However, although there was definite mortality, presumably due to the freshet, not only at Pivers Island but also nearer the inlet, the lowest reading corresponds to a salinity of about 19 parts per mille. (Fig. 30.) If the figures obtained really represent the lowest salinity occurring over the Beaufort Harbor scallop beds, it is indicated that salinity reductions below 20 parts per mille are dangerous. On the other hand the fact that the salinity in Newport River at a point where salinities of 25 to 35 parts per mille were found before the freshet, went as low as 4.8 parts per mille would make it appear not improbable that salinities at its mouth (that is, in Beaufort Harbor) went considerably below such a figure as 19 parts per mille.

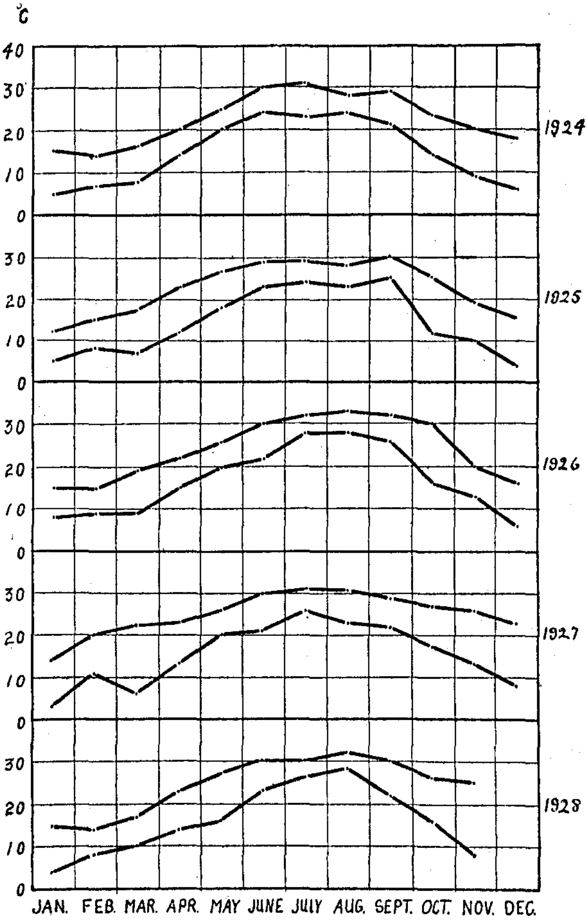

FIGURE 32.—Monthly maximum and minimum water temperatures at Pivers Island, 1924–1928, based on one reading daily. (See Table 12)

From the foregoing evidence it is difficult to determine the lowest salinity which the bay scallop will temporarily survive. A salinity as low as 6 parts per mille evidently is destructive. In various instances salinity reductions to 13–14 parts per mille have not proved quickly fatal to adults and there is evidence of ample survival by young during a period of salinity reduction which on two succeeding days was as low as 14 parts per mille. (See table 8 and fig. 31). In contrast we find in 1928 scallops at Pivers Island dying in appreciable numbers and apparently because of a freshet which was not found to go below 18.6 parts per mille. In the case of adults, at least, the delay between undue freshening (unless it is extreme, as in 1924) and death seems to be extraordinary (weeks or even months). Death from freshets may occur considerably after an improvement in salinity.

One of the possibilities suggested by the inconsistent results of water freshening is that not NaCl reduction but some change in minor constituents is the major factor in the destructiveness of freshets.

With a more hardy form, definite experimental information as to permissible salinities would have been sought. The great uncertainity of scallop survival in aquaria was taken to indicate as unwise efforts in this direction.

Although a distributional as distinguished from a temporary minimum salinity is here considered, it is possible that the prevailing or so-called distributional minimum is merely incidental, and that the only functional minimum—where considerable fluctuations occur—is the temporary, and that it depends on the length of time involved and even on the prevailing salinity.

The evidence was at first taken to point to a correlation between growth and salinity. Later investigations, however, pointed to current as the principal factor, and no clear relationship between salinity and growth was found.

A temporary reduction in salinity "fattens" or "swells" scallops by lowering the osmotic pressure of the surrounding medium so that the tissues of the scallop absorb water and become distended. Thus in Core Sound, where the tidal effect of wind is pronounced, a cold snap with its northerly wind and consequent influx of less salty water from Pamlico Sound, results in plump scallops and has led to the belief that sudden cold fattens scallops.

TEMPERATURE

Upon the feeding and growth of various lamellibranchs, water temperature has been found to exert a profound direct effect. At a temperature approaching 0° C., the activity of gill cilia nearly ceases so that syphoning (and consequently feeding) becomes negligible. Up to a limiting temperature (in certain instances in the neighborhood of 30° C.) the ciliary activity and rate of syphoning increases with the temperature. Thus Round (1914), studying the rate of bacterial elimination in oysters, found that above 9° C. there was evidence of pronounced gill currents, but that at 5° C. only after five days was there reduction; Nelson (1921) found that from 0° to 5° C. the feeding current of the oyster was extremely minute; Gray (1923) states that the ciliary speed (*Mytilus edulis*) increases from 0° to 33° C.; and Galtsoff (1926) found that the optimum (for the oyster) lies between 25° and 30° C. with no current produced at or below 5° C.

Examination of the temperature graph (fig. 32) and Table 10 shows that water temperature at Pivers Island varies from a minimum of 3° to 6° C. generally in January, to a maximum of 30° to 33° C. in July, August, or September. This, and the generally even character of the maximum and minimum curves, would suggest a cycle of growth beginning with zero or nearly that (and a growth line) in January and culminating in mid or late summer. However, it is to be noted that January temperatures fluctuate from a minimum of 3° to 5° C. to a maximum of 12° to 15° C. so that there is opportunity for growth at this season even if feeding does not occur at or below 5° C. or some temperature close to this. A further complicating factor is the early maturing, with short life. Thus growth rate for one year is complicated by all the physiological changes involved in the transformation from minute larva or early postlarva to large mature adult. The "annual" (about 1 year old) growth line generally is formed in the fall when it could be explained as directly due to temperature only on the assumption that the sudden autumnal temperature drop, or the loss of summer warmth, temporarily inhibits growth.

TABLE 10.—*Monthly maximum and minimum water temperatures (° C.) at Pivers Island, 1924–1928, based on one reading daily*

Year	Month											
	January	February	March	April	May	June	July	August	September	October	November	December
MAXIMUM												
1924	15	14	16	20	25	30	31	28	29	23	20	18
1925	12	15	17	23	27	29	29	28	30	25	19	15
1926	15	15	19	22	26	30	32	33	32	30	20	16
1927	14	20	22	23	26	30	31	31	29	27	26	23
1928	15	14	17	23	27	30	30	32	30	36	25	18
MINIMUM												
1924	5	7	8	14	20	24	23	24	21	14	9	6
1925	5	8	7	12	18	23	24	23	25	12	10	4
1926	8	9	9	15	20	22	28	28	26	16	13	6
1927	3	11	6	13	20	21	26	23	22	17	13	8
1928	4	8	10	14	16	23	26	28	22	16	8	5

A noticeable direct effect of temperature comes with extreme cold. Thus late in December, 1928, unusually cold weather was accompanied by extreme ebb tides that left the scallop flats exposed (but not quite free of water which, as usual, was impounded by vegetation, etc.) for considerable intervals. As previously stated, it is believed that the considerable scallop mortality which followed was due to unusual chilling. Extreme water temperatures on the flats under such conditions doubtless exceed those recorded, as do also those under similar tidal but reverse temperature conditions in summer. Thus in the instance cited, with an air temperature (at night) of about −10° C., it is not impossible that the little water left on the flats at low water became colder than 0° C. Some few scallops may have been directly exposed to the air temperature. The recorded minimum water temperature (4° C.) is extreme for December.

ENEMIES AND PARASITES

Of the animals which prey upon postlarval scallops, the best known are the starfish, the oyster drill, and the herring gull. Of these the herring gull is much the most conspicuous. From fall to spring at Pivers Island the gulls are daily to be seen, as the tide drops, floating over the scallop flats and—when the flats become sufficiently exposed—catching the scallops, dropping them on the beach to crack the shells, and eating them. This happens also at other beds about Beaufort and Morehead City where the scallops are especially valuable. Obviously many marketable scallops are thus destroyed. However, it is to be considered that the greater portion of the scallop-producing areas are not sufficiently exposed by the tide to enable herring gulls, which are poor divers, to get the scallops. Furthermore these gulls, notable scavengers, are abundant principally about harbors.

Ducks, and possibly other water birds, occasionally feed extensively on young scallops. In the winter of 1921–22 the white-winged scoter was found to be decidedly destructive to scallops in Massachusetts (Nelson, 1922).

The oyster drill, listed by Belding (1910) as a principal enemy of the scallop, does not seem to be destructive here, for almost no drilled scallop shells have been noticed. It is thought that ordinarily the drill, which moves slowly, is not an important enemy of the scallop,which is active and quick moving.

The starfish is considered by Uexküll (1912) to be the principal enemy. Possibly it is, except for man, the principal predatory enemy of adult and juvenile scallops. Locally, starfish occasionally are found eating scallops. Of the recently emptied scallop shells generally to be found on scallop beds, it is impossible to say what portion are the work of the starfish, for, unlike the drill, it leaves no identifying mark. It has not been found in great abundance on North Carolina scallop grounds. In some regions the starfish may be extremely destructive. In North Carolina it probably is considerably destructive but not a menace. The experiments of Dakin (1910) and Uexküll (1912) indicate that the scallop particularly avoids starfish.

Possibly predatory planktonic forms and larger animals which feed upon plankton are much more destructive of scallops (larvæ) than any forms which prey upon juveniles or adults.

As previously noted, examination of tables and graphs of scallop collections, shows tremendous reduction in abundance of scallops above the smallest sizes. (See Tables 4 and 7 and figs. 23 and 24.) During times of abundance the largest collections of scallops under 5 millimeters is about eight times as great as that of any group over 5 millimeters at any time of the year. Moreover the smaller sizes are much more apt to escape notice than larger ones. Thus an average mortality of perhaps 85 per cent between some size under 5 millimeters and one between 5 and 10 millimeters is indicated. More specifically, from Table 9, it appears that mortality is most severe from 3.5 to 10 millimeters. There is no evidence as to whether or not this is due to predatory animals.

Comparatively few scallop parasites seem to be known. Dakin (1909) found *Lichomolgus maximus*, an ectoparasitic copepod, on the gills and mantle of *Pecten maximus*, but no internal parasites in that species or in *P. opercularis*. At Beaufort I have found trematodes and a nematode.

According to the investigation of Dr. N. A. Cobb (1930) only one nematode (a larva) previously has been found in a scallop (Vadel, 1855). The one (*Paranisakis pectinis* Cobb, 1930) I found in the visceral mass thus appears to be the second ever found in a scallop.

It has been reported (private correspondence) that trematodes are not found in *P. irradians* at Woods Hole. At Beaufort I have found them on the gills, in the gills, and in the walls of the stomach.

On a few occasions I have found scallops the gills of which bore large numbers of trematode sporocysts. When these were examined fresh, each sporocyst was found to contain several rediæ and each redia hundreds of cercariæ which were released when a cover glass was placed over a redia (so that the cercariæ were released prematurely and may have differed considerably from mature cercariæ). Some few cercariæ were surrounded by a membrane, presumably the original covering of the germ ball.

In the spring of 1928 I found a scallop of the market class of the preceding winter with a parasite present in the interlamellar septa of the gills and abundant in the wall of the stomach. Thereafter, every scallop of this class examined was found with this parasite in the walls of the stomach, generally in abundance. In the winter of 1928–29 it was again found prevalent. The appearance suggested a recently encysted miracidium, or a very young sporocyst. Later examination of Tennent's (1906) account and illustrations (see his fig. 12) of *Bucephalus haimeanus*, and reexamination of material, led me, as Tennent had been led, to doubt this. The particular stage in the life of the parasite, which is assumed to be a Gasterostome, therefore, is not clear. Neither is its effect upon the scallop. With the oyster and some other lamellibranchs, Gasterostome infections render the host sterile, but there was no indication that the scallop was so affected by this parasite. In addition Tennent found evidence indicating that heavy infection rendered the oyster unable to resist unfavorable conditions. It is possible that the puzzling mortality which followed the apparently moderate freshening of the water over certain areas in the fall of 1928 was due in part to lowered resistance from these parasites.

Parasitic infection is worthy of consideration in connection with certain aspects of the life history of the scallop. The length of life of the scallop is unusually short. Moreover (as previously noted) Belding, working in Massachusetts, found that, although scallops generally died in the spring before they were 2 years old, gonadal development began as for a second spawning and continued to this end if the individual survived to the spawning season. This would suggest that some specific disease caused the mortality, and not old age. The intensity and the apparent universality of the parasitic infection just described seemed a reasonable explanation. However, examination of scallops from Massachusetts stated to be 22 months old did not reveal the parasite. The decided natural mortality reported by Belding has not been observed by me (although it might be evident were it not for the extreme destruction wrought by man) either in the time of year or at the age when he found it.

As a higher vertebrate which feeds on the adult scallop in areas where parasitism is prevalent, the herring gull is suggested as a probable host of later stages of parasites of the scallop.

Besides these definitely parasitic forms, a supposedly commensal crab, *Pinnotheres maculatus* Say, is to be found frequently in scallops in North Carolina. Although Hay and Shore (1918) state that only the female is common, three of four specimens sent to the National Museum and identified by Dr. Mary J. Rathbun proved to be males. As to the actual relationship between mollusk and crab the writer has no evidence to offer.

IMPORTANCE OF A KNOWLEDGE OF SCALLOP BIOLOGY FOR CONSERVATION

Scallop conservation at present is almost entirely[8] a matter of legal regulation. In order that regulation may be intelligently applied or the possibilities understood of supplementing it by more active means, such as scallop farming, a considerable knowledge of scallop biology is essential. Points of special importance for conservational regulation are: Time of spawning, age at sexual maturity, age at marketing, and length of life. Thus the knowledge that in North Carolina the bay scallop

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[8] Planting small scallops on private beds seems to have been practiced on a small scale at Wareham, Mass., for some time and may become an important industry on Cape Cod. At Wareham the town also pays for the transplanting of seed scallops from flats to deep water to prevent winter killing. At Nantucket transplanting has been tried experimentally.

spawns in the fall, is sexually mature in a year, and suitable for marketing the succeeding winter, when a little over a year old, greatly simplifies the problem of regulation. It makes a winter market season ideal, for at that time the only scallops large enough to be profitably marketable are mature and have spawned. With spring spawning many, if not most, of the immature scallops would be large enough to market and might make up the bulk of the catch. The problem of conservational regulation with a winter market season would then be different and much more difficult. Extreme destruction by man of mature scallops makes it difficult to determine the normal length of life. However, the knowledge that nearly all the scallops are immature in the summer makes it plain that scalloping at this time is wrong in principal and dangerous if carried on to an important extent or during a critical year.

For scallop farming it is important to know that scallops ordinarily shift little, increase rapidly in bulk, and are ready to market when a little over a year old. It is also important to know that they die quickly out of the water and that transplanting, therefore, would be much more apt to kill them than it would oysters or clams.

For a more detailed consideration of scallop conservation and of industrial scallop problems, generally, see Gutsell (1928).

SUMMARY

The bay scallop is of considerable economic importance. In value ($874,306 per annum according to statistics quoted) it ranks third among the edible bivalves of the Nation, after the oyster and the hard clam Venus. It is an article of commerce intermittently from Massachusetts to North Carolina where these studies were made and where it is of great local importance. Recently a small commercial catch in Florida has been reported.

Because of the types of interfilamentary connections to be found in certain European scallops, in the American bay scallop (*Pecten irradians*), and in the sea scallop (*Pecten grandis*) with vascular connections, it is considered that if classification into large groups is to be based on gill structure the scallops belong at the end of the group of bivalve mollusks the gills of which typically are without vascular connections (Filibranchia) and adjacent to (and connecting with) the group typified by interfilamentary vascular connections (Eulamellibranchia). This agrees with the arrangement of Ridewood (1903) but not with his terminology.

As stated by various writers, the range of the bay scallop is from Massachusetts to Florida or the Gulf of Mexico. It occurs principally in inclosed grassy waters of a depth varying from about a foot at ordinary low water to as much as 60 feet (Belding). In North Carolina it occurs principally in water less than 6 feet deep and of a normal salinity range of 38 parts per mille to 20 parts per mille.

Structure and function are considered at some length and in considerable detail. Studies were principally of living and fresh material.

Evidence from the examination of gonads and from periodic collections for young points to a spawning season beginning in mid or late summer, attaining its height in the fall, and continuing into January.

The form believed to be the late veliger or prodissoconch is equivalve, whereas Belding described and figured the late prodissoconch as inequivalve.

Sexual maturity and a large size are attained typically in the fall at an age of 1 year. In the vast majority of cases death comes at the hand of man before the next spring. So extreme is this destruction that the normal length of life has not been determined. A few individuals live to be about 2 years old and to spawn a

second season, but what portion normally would do so, or the extreme age attained, is not known. Slow-growing scallops that are small when 1 year old may be large when 2 years old.

A prominent line, reasonably termed a 1-year line or annual-growth line is formed in the fall and followed by notable winter growth. It is tentatively assumed to be due to some metabolic activity connected with egg and sperm development. On the upper valve it is a light line on a dark ground.

Scallops seldom are found far from grassy bottom. It is here suggested that this is because eelgrass and associated vegetation comprise the most favorable objects of attachment for the young and because thereafter scallops usually shift but little.

Depth is not found to be very important except as shallow water exposes the scallops to the attacks of enemies and the effect of unusual cold.

No close correlation is found between growth and salinity. Scallops taken in water of a winter salinity of 20 parts per mille to 21.6 parts per mille were larger than those from some areas where much higher salinities prevail. Although scallops have been found, in poor condition but alive, in water of a salinity as low as 13 parts per mille and although there is evidence of plentiful survival at least by the young of reductions nearly to this figure, considerable mortality presumably attributable to low salinity in certain instances has followed reductions to about this concentration. The delay between water freshening and scallop death may be great. A reduction to 6 parts per mille at Pivers Island was almost if not quite completely destructive, at least of adults. Moderate mortality in Beaufort Harbor followed a reduction in the fall of 1928 not known to have gone below 18.5 parts per mille. The lowest concentration observed over scallop beds except in time of extreme freshets was 20 parts per mille, the highest observed 38 parts per mille.

From field observations it is concluded that among the physical factors affecting scallop growth, current is most important; the faster the current the more rapid the growth and the larger the market scallops.

Perhaps because of the rapid growth and early maturity and the absence of any prolonged period of water temperature sufficiently low to inhibit feeding no direct correlation between temperature and growth is found. The only consistent growth line appears typically in the fall, occasionally in the summer, and always by early winter. It can be accounted for on a temperature basis only on the supposition that temperature drop or loss of summer warmth temporarily causes growth cessation. This does not seem probable.

Enemies possibly are most destructive during larval and prelarval stages, but there is indication of very heavy mortality of scallops less than 10 millimeters long. Of the forms which prey upon adults and juvenile the best known are the starfish, the oyster drill, and the herring gull. Of these the herring gull is much the most conspicuous. In the limited but valuable areas subject to exposure at ordinary ebb tides it is considerably destructive. No evidence was found of serious destruction of scallops by oyster drills, and it is believed that the slow-moving drill ordinarily is not an important scallop enemy. The starfish, a destructive form, is not found to be a menace in North Carolina.

An account of two parasites, believed to be trematodes and apparently not previously found in scallops, is given. One of these, rarely found, occurred on the gills as a sporocyst, containing rediæ which contained very numerous, peculiar cercariæ. The other, found abundantly in the walls of the stomach, resembled the figure of a parasite found by Tennent in oysters at Beaufort and believed by him to be a stage of *Bucephalus haimeanus*. Largely because of this resemblance, the scallop parasite is considered a Gasterostome. The herring gull is suggested as a probable higher host species.

For conservation, which is by legal regulation of the fishery, it is important to know that the spawning season, beginning in the summer, and largely autumnal, extends into early winter, and that sexual maturity and marketable size are attained in a year. A closed season should begin in the spring before the young become marketable and extend to early winter. If restrictive measures are to be supplemented by active measures, as in some form of scallop culture, it is important to know that scallops ordinarily shift little and that certain areas produce larger and more valuable scallops, and that, therefore, such areas if depleted might well be stocked from areas which produce inferior scallops. The quickness with which scallops die out of water offers special difficulties to the planter. On the other hand rapid growth, early maturity, and high value offer special inducement.

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