Biology and Culture of the Giant Scallop, *Placopecten magellanicus:* A Review

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BIOLOGY AND CULTURE OF THE GIANT SCALLOP, PLACOPECTEN MAGELLANICUS: A REVIEW

by

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ABSTRACT

Young-Lai, W. W., and D. E. Aiken. 1986. Biology and culture of the giant scallop, Placopecten magellanicus: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1478: iv + 21 p.

Giant or sea scallops appear to be a prime candidate for aquacultural operations. The biology, life history and habitat requirements are reviewed and the culture techniques presently used in Newfoundland are described. Among the topics discussed are artificial propagation of spat, site selection, spat collection and grow-out techniques.

RÉSUMÉ

Young-Lai, W. W., and D. E. Aiken. 1986. Biology and culture of the giant scallop, Placopecten magellanicus: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1478: iv + 21 p.

Les pétoncles géants semblent être une espèce tout à fait désignée pour les opérations d'aquiculture. Le rapport décrit la biologie, le cycle évolutif et les exigences pour ce qui est de l'habitat ainsi que les techniques de culture qui sont actuellement utilisées à Terre-Neuve. Parmi les sujets traités, mentionnons: la propagation artificielle du naissain, le choix de l'emplacement, la récolte du naissain et les techniques d'élevage.

I. INTRODUCTION

Scallop culture is an established commercial enterprise in Japan and there is a reasonable possibility that comparable success can be achieved with the giant scallop (Placopecten magellanicus) in the Bay of Fundy. The giant scallop is the most important commercial species of molluscan shellfish in Canada and the growing demand has resulted in an increase in price, an increase in fishing effort, and, possibly, a decrease in scallop abundance (Fig. 1).

Scallop culture in Japan evolved in response to a marked decline in natural abundance of the Japanese scallop, Patinopecten yessoensis. The earliest record of human intervention occurred in 1935, when natural materials - cedar twigs, leaves, and baskets - were used as spat collectors. Synthetic materials developed in the 1950's provided an easier and more efficient method of spat collection and a major breakthrough occurred in 1964, when it was discovered that survival of spat increased dramatically when polyethylene mesh bags were tied around the collectors. In Japan, cultured scallops now rank with cultured oysters in value and Japan now produces about half of the world's harvest of scallops.

The potential for culture of the giant scallop in the Bay of Fundy appears good. Scallops grow rapidly in the temperature, salinity and phytoplankton conditions in Passamaquoddy Bay (MacDonald and Thompson 1985a), the scallop meats are unaffected by local dinoflagellate toxins such as PSP (paralytic shellfish poison) (White 1985), and farming activities are facilitated by the relatively ice-free conditions. If a culture industry can be developed for the giant scallop, it will enhance the wild fishery, bring culturists a stable resource with high income potential, and create employment (Taguchi 1977; Ventilla 1982).

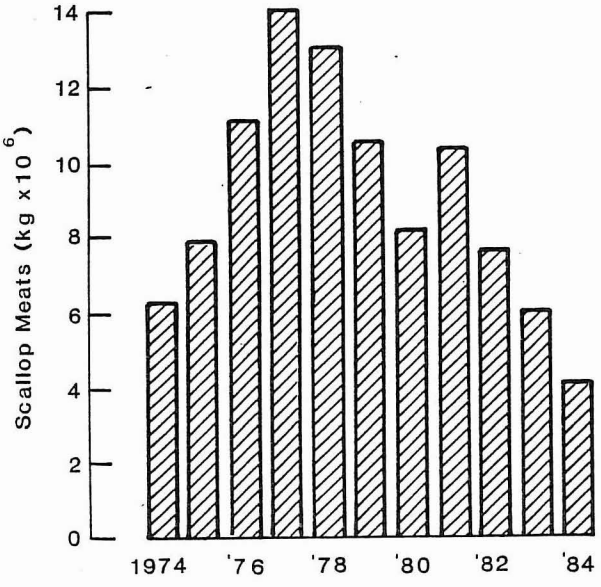

Fig. 1. Landings of the giant scallop in the Maritime Provinces from 1974 through 1984 (data from Statistics Branch, Dept. of Fisheries and Oceans, Halifax, N.S.).

The objective of this report is to synthesize the published information on the biology and culture of the giant scallop, Placopecten magellanicus. Information on culture of the giant scallop is limited to evaluations in Newfoundland. The culture techniques described in this report have been adapted and modified from Japanese technology to suit conditions found in Newfoundland.

II. BIOLOGY

TAXONOMY

Scallops belong to the phylum Mollusca, class Bivalvia and family Pectenidae. There are over 300 species in this family.

The valid scientific name for the giant scallop is Placopecten magellanicus. Synonyms are Pecten magellanicus, Pecten tenuicostatus, Placopecten grandis and Ostrea grandis. It is also referred to as the sea scallop, smooth scallop, Digby scallop and Atlantic scallop.

DISTRIBUTION AND ABUNDANCE

The giant scallop is found in the NW Atlantic from the northern edge of the Gulf of St. Lawrence south to Cape Hatteras, N. Carolina (Bourne 1964; Merrill 1960a; Posgay 1957; Squires 1962). In the northern part of their range they occur in shallow water, often less than 18 m, while in the southern end of the range they are most common in water deeper than 55 m. Under optimum conditions scallops congregate in dense local populations (beds) in sufficient quantities to support commercial fisheries (Bourne 1964; Caddy 1970, 1973). The most important fisheries occur on Georges Bank; on Brown's Bank; in the Bay of Fundy; in the Gulf of St. Lawrence, including Northumberland Strait and the Magdalen Islands; and in Port au Port Bay, Newfoundland (Bourne 1960, 1964; Bourne and McIver 1962; Dadswell and Chandler 1984; Dickie and Chiasson 1955; Doherty et al. 1963; MacKenzie 1979; MacPhail 1954; Naidu and Anderson 1984; Peters 1978; Sinclair et al. 1985). Scallop catches appear to be related to sea water temperature (Dickie 1950, 1954, 1955; Dow 1962, 1971; Posgay 1957, 1968), being greater in areas with warmer summer seawater temperatures.

EXTERNAL ANATOMY

The soft body parts of the scallop are protected by two lateral shells (valves) of calcium carbonate or calcite in an organic matrix. The convex valves are roughly circular except for the long, straight dorsal edge where the two valves are hinged (Merrill 1961). The oldest part of the valve is toward the center of the hinge, from which point fine ridges radiate. On either side of the umbo are flat protrusions which are commonly called ears or wings and are technically known as auriculas or auricles (Fig. 2).

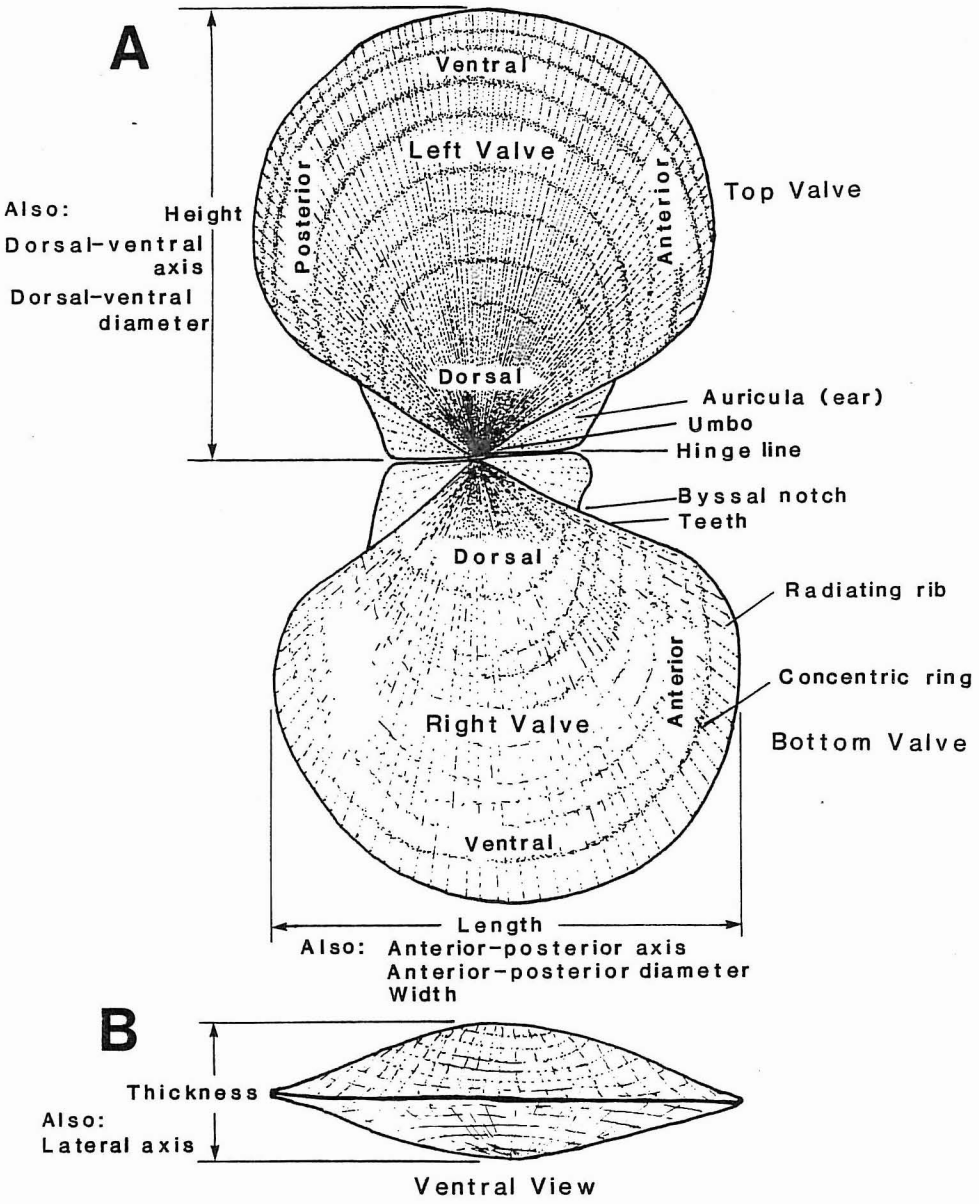

Fig. 2. Orientation and exteral anatomy of the valves of the giant scallop (from Bourne 1964).

The two valves are dissimilar in shape. The upper (left) valve is often coloured and more convex than the lower (right) valve which is usually white in colour. The right valve always rests on the bottom. It differs from the left in being smoother and having the anterior auricle modified to form a byssal notch.

For anatomical reference, the umbo region is considered dorsal and the opposite shell margin, ventral. The head region is determined by the location of the mouth and cerebral ganglion and the opposite direction, towards the anus, is posterior.

Shell length is commonly measured along the most anterior to the most posterior part of the valve. Height is defined as the linear distance between the umbo and the ventral edge (Fig. 2).

The two valves are joined along their dorsal margins by a ligament that acts as a flexible hinge. The inner layer of the ligament, the resilium (Fig. 3), lies in a socket near the umbo called the resilifer. When the valves are closed both ligaments are compressed and they work in opposition to the adductor muscle -- the valves open when the muscle relaxes. Physiological and biochemical aspects of valve closure have been described by Thompson et al. (1980) and deZwaan et al. (1980).

INTERNAL ANATOMY

Removal of the right valve reveals the soft internal anatomy that comprises 40% of the total weight of the animal (Bourne 1964).

Mantle

The outermost tissue covering the soft parts is the mantle. It is thin, almost transparent, and has a thickened, coloured margin (Fig. 4). The thickened margin of the mantle is pigmented and has three complex folds. Numerous eyes and a row of long and short tentacles occur on the middle fold. The inner fold has a row of short tentacles that form the outer fold. This is the hanging curtain part of the mantle seen when the scallop is at rest (Bourne 1964).

The mantle secretes the shell and repairs any cracks or breaks that may occur. It also controls the inflow and outflow of water in the mantle cavity. The function of the tentacles is mainly tactile and chemosensory. The function of the eyes is not completely understood. The eyes are capable of detecting direction of movement and position of shadowcasting objects (Bourne 1964), but the response of scallops to light is variable.

Adductor Muscle

Almost in the center of the valve is the large, white, circular adductor muscle (Fig. 3). This muscle is divided by a connective tissue sheet into two parts. One portion is composed of smooth muscle fibres (catch muscle), while the other consists of striated muscle fibres (quick muscle). The catch muscle contracts slowly and is responsible for keeping the valves closed. The quick muscle contracts rapidly and causes the rapid valve closures during swimming and jumping. Quick muscle comprises about 80% of the total weight of the adductor muscle.

The adductor muscle, also called the "meat" or "eye", is the only portion of the scallop that is used commercially. It is usually white, although in females it may be orange-red during the spawning season (Bourne and Bligh 1965). A grayish-brown meat color is associated with microorganisms that cause shell disease (Medcof 1949b).

The meat yield from scallops is proportionately low when they are small but it increases as the scallop increases in size (Baird 1954a; Medcof 1949a). The size and weight of the adductor muscle generally increases directly with the size of the scallops, but differences as large as 30% in meat weight for the same size scallops have been noted for different areas of Georges Bank (Bourne 1964). Food reserves are stored in the adductor muscle in the form of glycogen and glycogen stores influence flavor. Muscles which are low in glycogen content are small, stringy and watery. The content of sterol, fat and unsaponifiable compounds in the muscle varies with season (Idler et al. 1964). Proximate analysis showed that the muscle consists of 80% water, 12% protein, 0.5% lipid, and 1% ash (Naidu and Botta 1978; Hiltz and Dyer 1973). The remainder is glycogen and other organic metabolites (Matsumoto et al. 1967). The biochemical activity of the muscle was studied by O'Doherty and Feltham (1971a, b, c).

Gills

Encircling the adductor muscle are the crescent-shaped gills (ctenidia) composed of long, slender filaments folded over in a 'W' configuration (Fig. 4). The gills are covered with cilia (Drew 1906) that beat and draw water into the mantle cavity when the valves are gaping. Along with the mantle, they are used for respiration and filtering food from the water. Oxygen uptake is about 70 mL/kg/hr at 20°C (Van Dam 1954).

Labial Palps

Food particles are embedded in mucus on the gills and are carried toward the mouth by the beating of the cilia. Before being ingested the food is sorted by the gill-like labial palps which lie on both sides of the mouth (Fig. 3). Particles that are rejected by the gills and labial palps accumulate inside the mantle cavity. This waste material is called pseudofaeces and is discharged periodically from the mantle cavity by the rapid contraction of the adductor muscle.

Foot

At the anterior end is the white-coloured foot (Fig. 3). In a larval scallop it is used for turning over or locomotion but in adults it is rudimentary. At the base of the foot is the byssal gland through which the animal spins a thread-like elastic substance, called "byssus," by which it can attach itself to the substrate. Byssus function persists after metamorphosis but byssus production gradually decreases with scallop size, becoming insignificant in scallops larger than 120 mm (Caddy 1972). As the scallop grows the foot becomes relatively much smaller and loses its locomotory function.

Nervous System

The nervous system consists of three pairs of ganglia with connectives (Drew 1907). The large visceral ganglion attached to the ventral surface of the adductor muscle is connected to the mantle and branchial nerves leading into the gills and mantle.

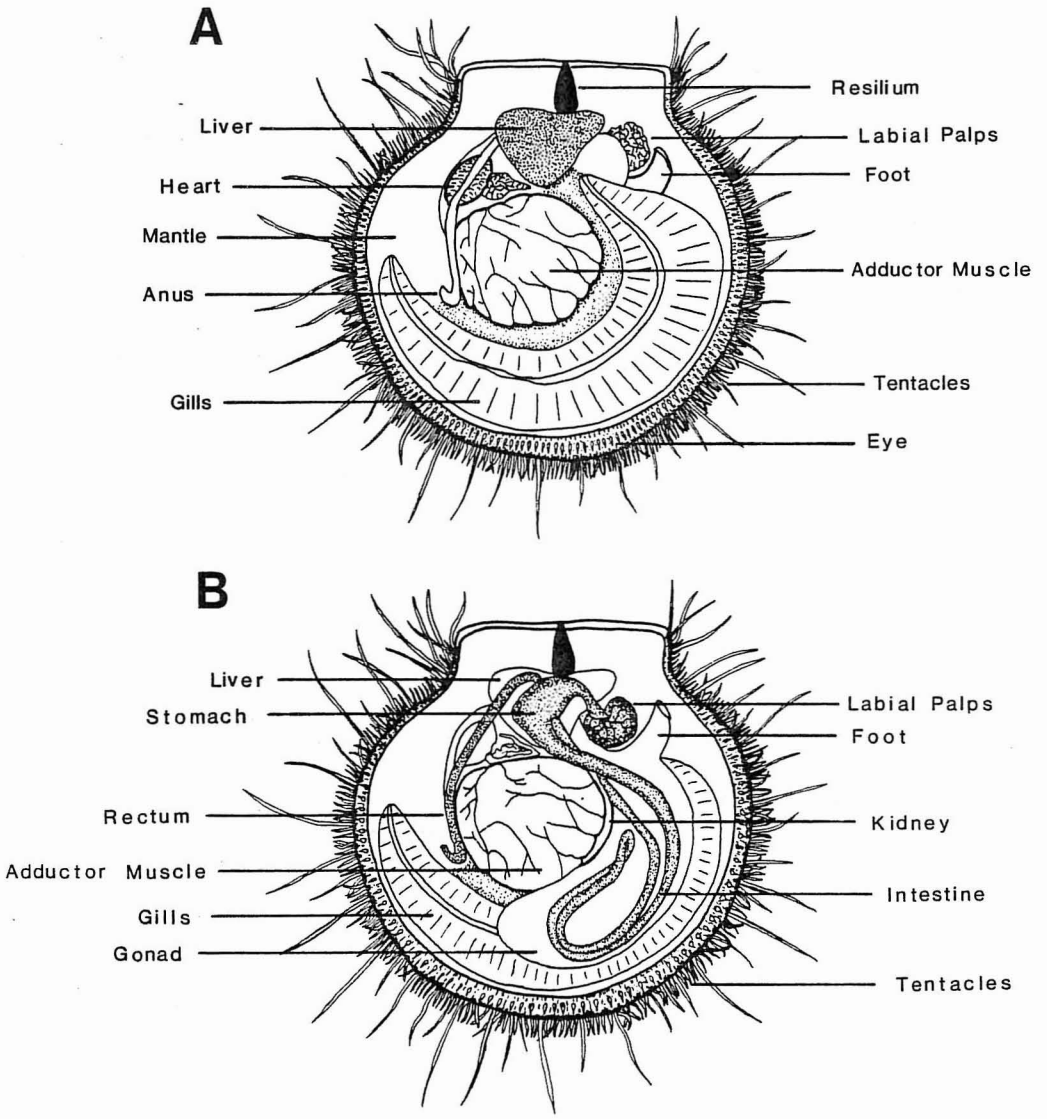

Fig. 3. Internal anatomy of the giant scallop. A - right valve and mantle lobe removed. B - with gill removed to show alimentary canal (from Bourne 1964).

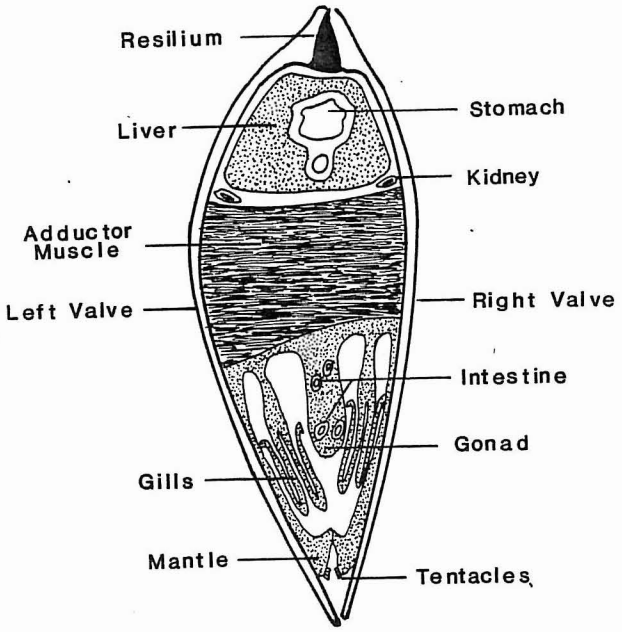

Fig. 4. Section through the valves and soft parts of the giant scallop showing orientation of internal organs (from Drew 1906).

The paired cerebral and pedal ganglia are embedded in tissues near the mouth. A pair of small statocysts are attached to the pedal ganglia.

Circulatory System

The three-chambered heart lies in a thin-walled pericardial cavity (pericardium) on the dorsal side of the adductor muscle. It has two irregular auricles and a ventricle that is traversed by the rectum (Drew 1907). An anterior and posterior aorta lead out of the ventricle and carry blood to all parts of the body. The circulatory system is a vague series of thin-walled sinuses through which blood returns to the heart.

Digestive System

Between the foot and the hinge are the leaf-like labial palps that surround the mouth and direct the sorted food material into the slit-shaped mouth. Food passes through the esophagus into the stomach where it is ground between the rotating crystalline style and the chitinized gastric shield. The crystalline style is bright amber, long, and worm-like and contains digestive enzymes in a protein matrix (Bourne 1964).

Surrounding the stomach is the dark-colored digestive gland, also called the liver (Fig. 3A). It functions in digestion and storage of food reserves. The long intestine leads out of the stomach, loops ventrally through the gonad, and passes dorsally over the adductor muscle and through the pericardium. The anus lies on the posterior side of the adductor muscle. Feces are discharged inside the mantle and are eliminated by the rapid contraction of the valves.

Urogenital System

The two excretory organs or kidneys lie flattened against the anterior part of the adductor muscle (Fig. 3B, 4). They are small, thin, sac-like bodies and are brown in colour. The kidneys empty wastes through large slits into the mantle cavity. The products of the gonads are extruded through ducts into the lumen of the kidney and then into the mantle chamber.

The large gonads wrap around the anterior and ventral side of the adductor muscle (Fig. 3B). Sexes are generally separate in sea scallops, although hermaphroditic scallops have been reported (Merrill and Burch 1960; Naidu 1970). As the gonads develop they enlarge and change from white to coral-red in females and creamy-white in males. The gonads of spawned-out and immature scallops are flacid and whitish in both sexes.

REPRODUCTION

Gonad Index

Gonad morphology was described briefly by Drew (1906) and gonad histology was detailed by Borden (n.d.), Naidu (1970) and Welch (1950). Spermatogenesis begins with the spermatogonia, and oogenesis with the oogonia, which are enlarged cells in the germinal epithelium of the follicle. The gametes (normally of one sex) move towards the center of the follicle as they mature, the follicle gradually becoming filled with gametes.

Gonadal maturity can be estimated by monitoring the changes in gonad colour, by microscopic examination of the gonads, or by measuring the gonad index. The gonad index is the ratio of gonad weight to the total soft body weight, expressed as a percent:

$$\text{Gonad Index} = \frac{\text{Gonad Wt} \times 100}{\text{Wt of Soft Parts}}$$

Gametogenesis, which is intimately related to accumulation of energy reserves during phytoplankton blooms, occurs in the scallops of SE Newfoundland in early summer (Thompson 1977) and the scallops of Boothbay Harbor, Maine, in early winter (Robinson et al. 1981). The periods of high energy demand for reproduction are synchronized with the periods of food abundance. Energy needs for reproduction seems to be met directly from food consumed rather than by use of internal stored reserves (Ehinger 1978).

Sexual Maturity and Fecundity

Sexual maturity may be attained as early as age 1, with the initial spawning occurring after deposition of the first growth ring (age 1½-2) (Naidu 1970). Size (shell length) at sexual maturity may vary from 23-35 mm (Naidu 1970; Posgay 1979), but fecundity of the younger age-groups contributes little to total egg production. By age 5 or 6, however, female scallops may produce about 2 million eggs (Posgay 1979). Fecundity has been quantified in the giant scallop and the data are being analyzed (Bruce MacDonald, Pacific Biological Station, Nanaimo, B.C., pers. comm.). In general, greater reproductive output is found in scallops from shallow water or from more favourable sites and differences in production are positively correlated with food availability and temperature (MacDonald and Thompson 1985b).

Spawning and Fertilization

The environmental factors that control spawning are not well known. Posgay (1953) estimated that spawning may occur in response to autumnal chilling of the water. Dickie (1953) believed that it was related to the tidal cycle, and Stevenson (1936) felt that spawning occurred after a spring tide. In these studies the major spawning period coincided with decreasing seawater temperatures in autumn. However, the occurrence of spawning in spring and summer indicates that factors other than temperature can be involved in the initiation of spawning. It appears that temperature cycles may also be important, and that once the gonads are mature, almost any stressful event may induce spawning (Naidu 1970). There is some indication of a relation between wave action, onshore winds and the onset of spawning. Prolonged exposure to physical shock (Naidu 1970) could be another stimulus to spawning. Posgay (1953) observed that males are stimulated first and the presence of sperm in the water induces the females to shed their eggs. Culliney (1974), Posgay and Norman (1958) and Stevenson (1936) all observed spontaneous spawning when scallops were fished from the bottom and held on board ship, indicating that changes in pressure and temperature may also play a role in spawning (Culliney 1974; Naidu 1970; Stevenson 1936). Little is known about the possible effects of periodic phenomena such as tidal and lunar rhythms, or the effects of chemical stimulants exuded by other organisms.

During spawning, muscles in the outer layer of the gonads move the eggs and sperm from the follicles into the ciliated ducts and then into the kidney. From there the gametes are discharged into the mantle cavity and expelled in a steady stream through the excurrent opening near the hinge. To assist in the expulsion of the gametes, spawning scallops periodically clap their valves. Fertilization is external.

The time of spawning varies slightly from area to area. Spawning takes place between late August and early October in Boothbay Harbor (Baird 1953): late September or early October on Georges Bank (Posgay and Norman 1958); late August to late September in Passamaquoddy Bay (Beninger 1986), early September in Digby (Dickie 1955); and late September to October in SE Newfoundland (Naidu 1970). Borden (undated) examined gonad histology and concluded there were two spawning periods in Passamaquoddy Bay - the first from June to September, and the second from December to February. Naidu (1970) also observed two spawnings in Newfoundland waters - one in June, which was minor and involved only a few individuals, and a second major spawning in autumn. The occurrence of two annual peaks of spawning activity suggests the gonads become mature at different rates and that spawning occurs over a protracted period (Naidu 1970). Naidu's conclusions contrast with the observations of Posgay and Norman (1958) that 92% of the Georges Bank scallops discharged their gametes within a brief 3-4 d period. Histological examination of Northumberland Strait scallops seems to agree with Posgay and Norman's observations (J. Worms, Dept. of Fisheries and Oceans, Gulf Region, Moncton, N.B., pers. comm.).

EMBRYOLOGY AND LARVAL DEVELOPMENT

Embryological development has been described by Drew (1906). The first external sign after fertilization is the formation of a prominent yolk-lobe which disappears as cleavage proceeds. Polar bodies are given off from the side of the egg opposite the yolk-lobe (Fig. 5A). Continued cell division results in an almost typical epibolic gastrula after approximately 12-14 hr, at which time many of the surface cells have cilia and some mobility, Fig. 5B. An hour or two later the apical cilia appear, grow rapidly, and increase in number. The embryo then elongates slightly and begins to swim freely in the water with the apical cilia pointing forward. This is the trochophore stage (Fig. 5B).

Complete larval development has been described by Culliney (1974). Four to six days after spawning the trochophore larvae becomes a shelled, straight-hinge veliger with a very short apical flagellum (Fig. 5C). The cilia become concentrated in a swimming and feeding organ called the velum. During the late veliger stage the umbos form and the shape of the shell changes (Fig. 5D). Eyespots appear, the apical flagellum is lost, the velum is reduced, and a foot develops. At the tip of the foot is a cluster of long, active cilia and a well-formed byssal spur. During this transition period when the larva possesses both a velum and a foot, the larva begins to show adhesive tendencies. This is the pediveliger stage (Fig. 5E). The pediveliger alternates between swimming and crawling and can delay metamorphosis until a suitable substrate is found. Growth of larval scallops has been studied by Hurley and Tremblay (1986). They found that growth increments were initiated 3-4 d after fertilization and neither photoperiod nor feeding frequency had any detectable effect on growth increment count.

Borden (undated) first reported the occurrence of scallop larvae less than 0.2 mm in length from plankton tows taken in Passamaquoddy Bay. Tremblay and Sinclair (1986) have sampled scallop larvae in the Bay of Fundy, Scotian Shelf and Georges Bank and have found that there was transport of larvae within the Bay of Fundy and Georges Bank via the residual current but most larvae either remained in or were returned to the area of major spawning. Their data also indicated that there was no evidence of exchange between Georges Bank and the Scotian Shelf. Although larval ecology is still largely an enigma, the identification and distribution of larval scallops is now ongoing.

Larval development is temperature dependent. Culliney (1974) reared larvae from the ciliated gastrula to the straight-hinge veliger stage over a temperature range of 12-19°C and determined that optimum temperature for development was 15°C. Populations reared at 19°C did not complete development.

Settlement and Metamorphosis

The criteria for metamorphosis of scallop larvae are attachment by a strong byssus and complete disappearance of the velum (Culliney 1974). At this stage it is called a spat. Metamorphosis is the most critical event in the life of marine molluscs. The transition from a pelagic to a benthic existence is accompanied by drastic changes in diet, morphology, and locomotory ability to avoid predators. It is conceivable that mortality is as high during natural settlement as when spat are reared artificially (Bourne 1964; Culliney 1974; Stevenson 1936). Food seems to be the limiting factor under artificial rearing (Culliney 1974), but

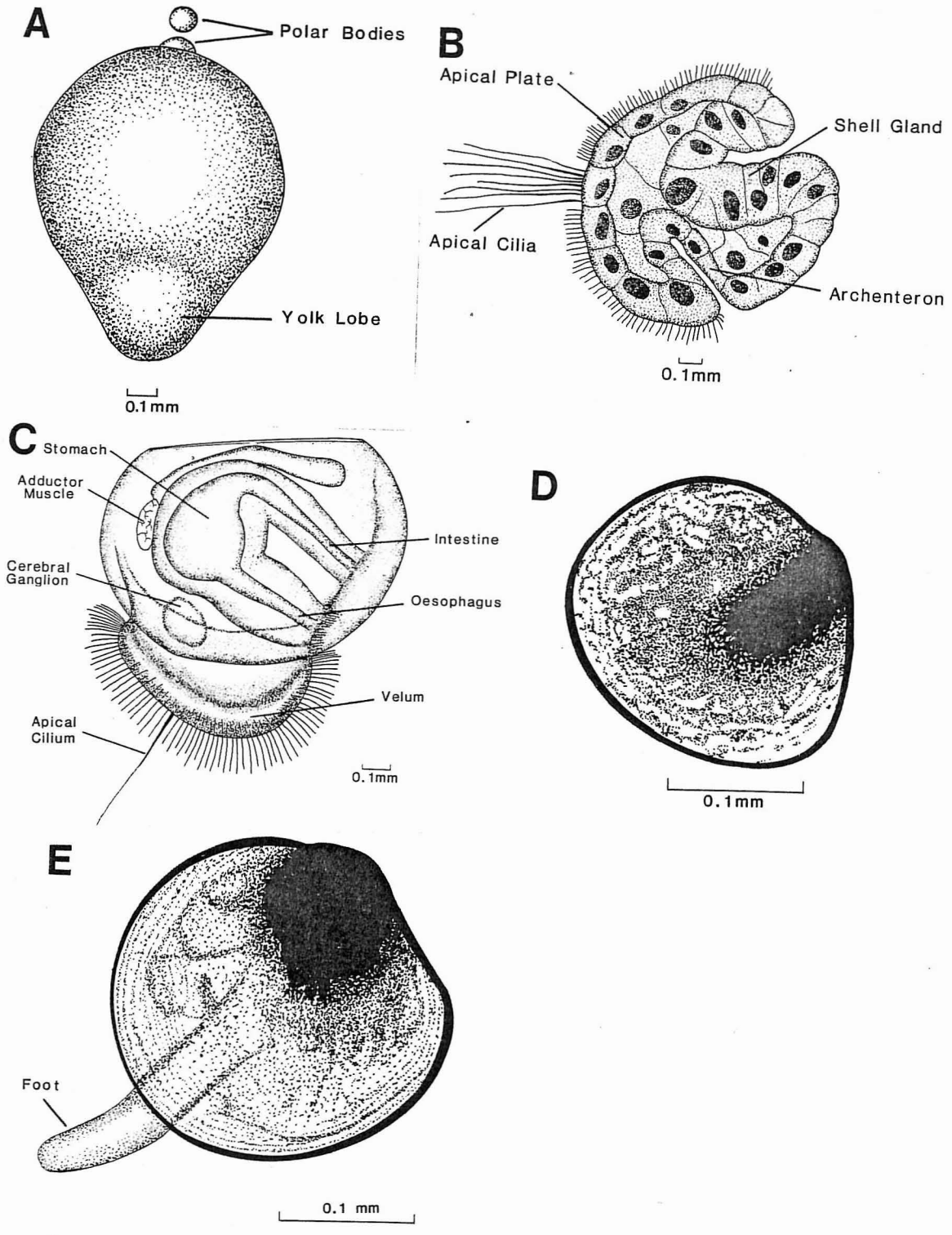

Fig. 5. Embryological and larval development of the giant scallop. A - developing embryo 2-4 hr after fertilization. B - ciliated gastrula (trochophore stage). C - straight hinge larva (veliger stage). D - umbo larva. E - pediveliger larva. (Figs. A, B, C from Drew 1906, Fig. D from Culliney 1974 and Fig. E from Bourne 1964).

wild spat are susceptible to siltation and predation (Dickie and Medcof 1956). In Passamaquoddy Bay, natural spat settlement occurs from late September to late October (Ross Chandler, pers. comm.).

Scallop larvae metamorphose into newly settled scallops, or spat, in about 35-40 d from hatching at 15°C. Settlement is a prerequisite for metamorphosis and if a suitable substrate cannot be found metamorphosis will be delayed and the larvae may die. For many bivalves any non-toxic surface will stimulate the behavioural and physiological changes of metamorphosis.

Culliney (1974) found that the giant scallop has a strong tendency to settle on the underside of pebbles, shell fragments, and glass fragments. Settling on the undersides would afford some extra measure of security from predators. In nature, spat settlement has been reported on the red alga, Rhodomela conferroides (Naidu 1970); the bryozoan, Gmellaria (Baird 1953); the hydrozoan, Hydrallmania and on the tubes made by amphipods (Larsen and Lee 1978). No substantial concentrations of spat have yet been found (Serchuk et al. 1979), and there have been no attempts to identify possible chemical agents which may induce settlement.

Spatfall is presumably influenced by prevailing surface currents during the pelagic period. Generalized sea surface circulation patterns indicate a prevailing southwesterly flow from Georges Bank, suggesting that progeny of a given bed of sea scallops are unlikely to settle in the parental area (Posgay 1979). Larvae from Georges Bank, however, may frequently remain on Georges due to a semi-persistent gyre that makes it possible for the larvae to metamorphose and settle in the region (Posgay 1979).

GROWTH

In general, sea scallops require about 4½ yr to reach 95 mm in shell length. This is the minimum size the International Commission for the Northwest Atlantic Fisheries (ICNAF) recommends for harvest if a sustainable yield is to be realized (Bourne 1964; Posgay 1950, 1953). Estimates of age and growth obtained from shell samples and tagging reveal that during the first several years of life, growth in both shell size and meat weight is rapid for Georges Bank and Mid-Atlantic populations (Merrill 1967b; Merrill et al. 1966; Posgay 1953, 1963). Merrill and Edwards (1976) reported growth of 5 mm in 6 mo on buoys and 25 mm in 18 mo on the bottom. Larsen and Lee (1978) reported growth of 0.3 mm in 11 wk.

Between ages 3 and 5 the shell height of giant scallops increases 50-80% and the meat weight quadruples (Merrill and Posgay 1964). In general, growth is slowest in the Gulf of St. Lawrence and fastest on Georges Bank (Bourne 1964; Chouinard 1984). Although there are minor differences between Georges Bank and mid-Atlantic populations, these are probably due to differing temperature regimes rather than genetic differences (Serchuk et al. 1979).

Variations in growth rate from place to place, even within one area, are probably due to variations in food, currents, and water temperature (Brannen 1940; Dickie and Medcof 1956). Naidu (1975) found differences in growth due to the composition of the bed sediment. Slower growth occurred in fine sediment, probably due to increased energy requirements for filtration.

Growth varies with season, and significant differences have been found in the length/weight relationships of giant scallops collected from Georges Bank in different seasons (Haynes 1966). Growth may slow, or even stop, during the winter months due to declining temperature. There is a demonstrated correlation between water temperature and growth rate (Naidu 1975; Posgay 1950, 1953; Stevenson 1936), and factors such as food quantity and quality, spawning, dredging, tagging, and stress can also affect growth rate (Dickie and Medcof 1956; Posgay 1979). In Newfoundland greater somatic growth was observed in scallops from shallow water than those in deeper water where temperature and food conditions were often less favourable (MacDonald and Thompson 1985a). However in Passamaquoddy Bay, N. B., where the water column is thoroughly mixed by tidal forces, there is no difference in either shell growth or somatic growth of scallops from various depths (MacDonald and Thompson 1985a).

Shell growth curve of scallops is typically sigmoid and growth rate increases up to an inflexion point which is reached at about 4 yr of age or 55 mm in shell length (Stevenson 1932). Thereafter, growth decreases and tends to become asymptotic between 150-160 mm (Posgay 1953; Stevenson and Dickie 1954). Male and female giant scallops grow at the same rate (Chouinard 1984; Naidu 1975) and have similar length-weight relationships (Haynes 1966).

Aging

Age of scallops has been determined from length-frequency distributions, from interpretation of growth checks or rings, from tag-recapture studies, from ligament rings (Posgay 1953), and by O^{18} measurement (Krantz et al. 1984). Present age determinations rely primarily on subjective interpretation of lines on the shell exterior. As new shell material is deposited along the circumference of the valve, fine concentric lines (circuli) are formed on the external surfaces. During periods of rapid growth, these circuli are more widely spaced. When growth slows, the circuli become crowded and collectively stand out as a growth check between the areas of faster growth and wider spacing (Merrill et al. 1966; Stevenson 1936). The prominence of such growth rings is variable and depends on the relative spacing of the circuli.

The age of each size may be determined by measurements of the annual growth rings. In general, the age of the scallop when the first annual ring is formed is approximately 0.5 yr. Generally, scallops born in August or September will deposit the first ring the following spring, in March or April. The first ring is usually laid down before 15 mm (Stevenson and Dickie 1954). However, this first ring tends to wear off as the animal grows and thus becomes difficult to see (Roddick and Mohn 1985). Subsequent rings are more discernible and, consequently, the ring laid down the following spring is often interpreted as the first ring. For example, scallops from Northumberland Strait (Chouinard 1984) and S.W. Newfoundland (Naidu 1970) have been reported to deposit the "first" ring at 30-50 mm but Georges Bank scallops deposit theirs at 40-50 mm (Merrill 1967b). These rings betwen 30-50 mm may be interpreted as the "first" ring but the actual age of the scallop is 1.5 yr old. Because of the controversy surrounding scallop ageing, there is a need to develop more accurate methods.

In addition to the annual growth rings, "shock rings" occur irregularly when growth is arrested by disturbances such as storms, scallop dredges or tagging. These shock or disturbance rings are similar in appearance to true annual rings and distinguishing between the two can be difficult. Merrill et al. (1966) have relied on clues such as color, texture, weight and curvature of the valves, ring patterns, and areas attacked by boring organisms to interpret shell growth. They have also used the calcareous part of the inner ligament (resilium), in which the annual growth rings are more distinctive.

Condition

Growth of the valves is not always proportional to growth of the soft parts. Measurements which relate the size of the shell to the weight or volume of the soft parts are referred to as condition. Generally, the soft parts of animals in good condition fill their shells while those of animals in poor condition do not. Condition, then, should give an indication of meat yield. However, there are no published reports on condition in scallops because only the meats are utilized.

Condition is highly variable and depends on season and growing conditions. Seasonal variations in condition are largely caused by the spawning cycle and food supply. Robinson et al. (1981) and Thompson (1977) monitored the buildup and decline of energy reserves in the gonads, blood, and somatic tissue during the reproductive cycle but there have been no attempts to determine seasonal variations in the condition of the adductor muscle. Experiments conducted by D. Wildish (pers. comm.) indicate seasonal differences in growth rate between the shell and soft body tissues.

SWIMMING AND MIGRATION

A unique and interesting feature of scallops is their ability to swim (Drew 1906; Posgay 1963). Swimming results from a rapid expulsion of water. The animal opens its valves, takes in water, presses the muscular edges of the mantle closely together, and then claps its valves, forcing jets of water through the incurrent and excurrent openings. By controlling the direction of the water jets, scallops can swim forward, backward or upward (Fig. 6). The rate of clapping is fairly constant and is controlled by a reflex action (Bourne 1964).

Giant scallops have never been observed swimming for longer than 15 or 20 s, or more than 0.5 m off the bottom (Bourne 1964). Observations suggest they rarely travel more than 10 m horizontally and rarely move unless disturbed by predators or unfavourable conditions. Caddy (1968) observed scallops swimming 0.4 m above the bottom for distances up to 4 m, at ground speeds of 67 cm/s. He also found that scallops over 100 mm could not be induced to swim.

Results from tag-release data suggest that giant scallops do not undertake widespread or directed seasonal migrations (Baird 1954b; Dickie 1955; Posgay 1953, 1981) and shell isotopic studies support the idea of limited movement (Krantz et al. 1984). However, it is possible that scallops less than 70 mm long utilize tides and currents to move or migrate considerable distances (Baird 1954b; Melvin et al. 1985). Recoveries from 20,086 tagged scallops released on Georges Bank indicated a clockwise circular movement around the outer perimeter of the Bank in concert with the mean direction of current flow (Melvin et al. 1985).

FOOD

Scallops are filter-feeders and feed on seston. The only data concerning the food of this species are from a study by Borden (undated), who compared the organisms found in scallop stomachs with those present in the plankton. Diatoms comprised the bulk of the food ingested and a high degree of selectivity was demonstrated. Juveniles and adults

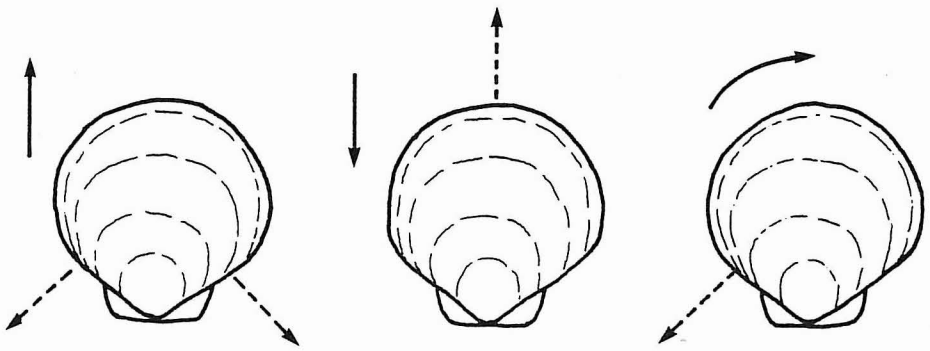

Fig. 6. Control of swimming direction by the giant scallop. Direction of scallop movement (solid arrows) is regulated by intensity and direction of water jets (broken arrows) expelled by the animal (from Bourne 1964).

utilize plankton and some organic detritus as food (Posgay 1963).

In laboratory culture, larvae have been grown on the phytoflagellate, Isochrysis galbana. Spat have been reared on mixtures of Isochrysis and Chrysomonas salina (Culliney 1974) and diatom, Phaeodactylum tricornatum has been used to keep spat alive for more than a year (Bourne 1964).

PSP AND CONTAMINANTS

Biossays for paralytic shellfish poison have shown that scallops from Georges Bank, Scotian Shelf and Northumberland Strait are essentially free of Gonyaulax toxins (Bourne 1965; Jamieson and Chandler 1983). Bay of Fundy scallop tissues other than the adductor muscles were found to be highly toxic. Bourne (1965) reported that only the liver and mantle was toxic, but Jamieson and Chandler (1983) found a high incidence of toxicity in the liver, mantle and gonad. The occurrence of toxins in the gonads renders this organ unsuitable for commercial exploitation.

Cadmium, copper, zinc and lead have been isolated from scallop tissues but the pathology and lethality of heavy metals to scallops are not known (Ray et al. 1984a, b). A comparison of the trace-metal concentrations in the various tissues indicates that generally the order in tissues for the metals is muscle < mantle < gill << viscera. Therefore, the consumption of scallop meats does not constitute a threat to human health but the viscera may.

CAUSES OF MORTALITY

Mortality in scallops is caused by biological factors such as predators, parasites, infectious agents and inadequate diet, and by environmental factors such as fishing activity and sub-optimum water quality.

Predation

Planktonic scallop larvae are likely to be eaten by large zooplankters, and during their early benthic life they are subject to predation by almost any animal large enough to ingest them. Post-larval giant scallops have been found in the stomach contents of the asteroid starfish, Astropecten americanus (Larsen and Lee 1978); cod, Gadus callarias; American plaice, Hippoglossoides platessoides; starfish, Asterias vulgaris; and the wolf fish, Anarhichas lupus (Medcof and Bourne 1964). A starfish either ingests the whole scallop or pulls the valves apart, enabling it to protrude its stomach between the valves (Welch 1950). Rock crabs, Cancer irroratus, and lobsters, Homarus americanus, are natural scallop predators (Elner and Jamieson 1979; Jamieson et al. 1982). Caddy (1968, 1973) considered rock crabs, starfish, several species of groundfish (Myxocephalus sp.) and winter flounder (Pseudopleuronectes americanus) to be probable predators of scallops that had been damaged during hauling and dragging operations. Moonsnails (Lunatia heros) can also prey on scallops weakened by temperature fluctuations (Dickie and Medcof 1963).

Shell Boring and Fouling Organisms

The hard shell of giant scallops provides an excellent substrate for numerous fouling organisms. The species living on the valves are usually common on any suitable substrate in the vicinity of the scallop. Small scallops, because of their mobility, tend to collect fewer organisms on their shells than do large sedentary scallops, which may become heavily fouled (Merrill 1960b, 1961).

The colonial hydroid, Hydractinia echinata, can become established on the shell, overgrow the lip and interfere with the mantle, causing shell deformity (Merrill 1960b, 1967a). Boring sponges, such as Cliona vastifica, and the spionid polychaetes Polydora websteri and P. concharum, can settle on and damage the shell by their tunnelling activity (Evans 1969; Medcof 1949a; Medcof and Bourne 1964; Welch 1950). Older shells are bored by the cirratulid polychaete, Dodecaceria concharum, which usually settles in empty Polydora burrows and enlarges them as it grows (Evans 1969). The bivalve, Hiatella arctica, has also been found growing on scallop shells (Evans 1969).

These organisms do not always cause mortality but their activities may contribute indirectly to mortality. Boring organisms may make holes which weaken the shell and force the scallop to secrete new layers on the inside. This may cause dark blisters, thickening of the shell (Merrill 1960b) or meat discoloration (Medcof 1949b).

Commensals and Parasites

Post-larval and juvenile red hake, Urophysis chuss (Wigley and Theroux 1971), and species of the sea snail fish, Liparis inquilinus (Able 1973), customarily inhabit the mantle cavity of giant scallops. The fishes presumably derive some protection in this relationship but the scallop seems oblivious to the presence of the fish.

Stevenson (1936) observed two ciliate protozoans, Licophera and Trichodina sp., on scallop eggs in early stages of development, and an unidentified platyhelminth worm was found living in the alimentary tract and digestive gland of the scallop with no apparent adverse effects (Borden n.d.). A trichodinid protozoan was found on scallops near St. Andrews (Dickie and Medcof 1963; Medcof and Bourne 1964), and a flagellate, Hexamita sp., was found in moribund scallops held in aquaria (Medcof and Bourne 1964).

Conspicious colonies of a unicellular alga were observed in the mantle cavity of scallops (Naidu 1969, 1971; Naidu and South 1970). Subsequently identified as Coccomyxa parasitica (Stevenson and South 1974), this alga is believed to be parasitic but harmless during a light infection but capable of causing considerable damage in heavy infestation.

Temperature

Adverse temperatures have frequently been responsible for mass mortalities in scallops (Dickie and Medcof 1963; Johannes 1957). The dead scallops showed no abnormal pathological features, and survivors were in good condition. As most of the mortalities occurred in the summer at depths of less than 12-20 m it was believed that oscillations in the thermocline exposed the scallops to lethally high temperatures. Warm water debilitates scallops and increases their susceptibility to predation (Dickie and Medcof 1963). There is evidence that naturally occuring water temperatures above 22.5°C will cause scallop mortality (Dickie 1958).

Low summer temperatures can delay spawning and larval development (Medcof and Bourne 1964). If larval development is delayed, the period during which larvae are exposed to predators is prolonged and larval mortality increases (Dickie 1955).

Siltation and Oxygen Depletion

Oxygen depletion and bottom silt can easily cause mortality, especially among small giant scallops. High suspended sediment level can reduce the movement of cilia on the gills, causing reduced oxygen consumption and eventual suffocation (Larsen and Lee 1978).

Fishing Mortalities

When an area is dredged for scallops, many are inadvertently killed because scallops which pass under the dredges may be buried in the bottom or the mantle may be packed with mud (Medcof and Bourne 1964). Dredging causes appreciable lethal and sub-lethal damage to scallops left in the track, with incidental mortalities as high as 13-17% per tow (Caddy 1973). Survival of undersized scallops which are taken in dredges is also poor. As the dredges fill with rocks and trash, the small scallops can be smothered or crushed. Crushing, breakage, or prolonged exposure to adverse conditions can occur when the dredges are lifted out of the water and dumped on deck (Medcof and Bourne 1964).

Tagging

Mortality associated with tagging has been studied by Naidu and Cahill (1985) and they concluded that scallop deaths were more likely related to mode of capture and handling than the tagging procedure.

III. CULTURE

Scallops have several characteristics that make them attractive for marine culture: they filter their own food from the environment, they have an established market and high commercial value, the muscles are relatively unaffected by PSP, and they can be reared in water depths that minimize conflict with other uses of the marine environment.

In 1971 the Newfoundland Department of Fisheries initiated a culture project using the giant scallop. Aquaculture technicians from Japan were hired to identify suitable areas for spat collection and grow out and to transfer Japanese scallop culture techniques. The technology used in Newfoundland is therefore similar to that described for the Japanese scallop (Sanders 1973; Taguchi 1977; Ventilla 1982). A 3-phase culture technique is employed: spat collection, intermediate culture, and cage culture (Newfoundland, Dept. of Fisheries 1981).

ARTIFICIAL PROPAGATION OF SPAT

Intensive culture is necessary for the genetic improvement of scallop strains, for supplying seed scallop to areas where conditions are not conducive to natural seed collection, and for supplying seed in years when there is a poor natural set. The first recorded attempt to spawn giant scallops was by Stevenson (1936). Baird (1953), Bourne (1964), and Culliney (1974) have also spawned and reared larvae in the laboratory.

In artificial culture thermal stimulation appears to be a significant factor in inducing spawning. Culliney (1974) induced spawning by raising the temperature 3-5°C. Bourne (Pacific Biological Station, Nanaimo, B.C., pers. comm.) triggered spawning by removing the animals from the water for 1-2 h then putting them back into water 1-2 degrees above the temperature at which they had been held. Dabinett (Marine Science Center, Memorial Univ., Logy Bay, Nfld., pers. comm.) gradually increased the temperature 1 degree/day to a maximum of 10-12°C, at which temperature they spawned spontaneously. Reducing the temperature from 10°C to 4°C for 1 h, and then returning it to 10°C was also found to induce spawning (Fournier and Marsot 1985). In all these cases ripe scallops were collected from wild populations and spawning was imminent. In fact, many of the scallops spawned before they arrived at the laboratory, which indicated that many types of stress will trigger spawning. We do not know whether brood stock can be ripened in the laboratory or whether they can be induced to spawn in the same way if they are ripened in the laboratory.

Methods for artificial fertilization, egg incubation and larval rearing are summarized in the following sections as reported by Fournier and Marsot (1985).

Fertilization

Males and females were spawned separately by Fournier and Marsot. The eggs were collected and screened through a 255 µm mesh, then 100 µm mesh, and, finally, with a 20 µm mesh. The eggs were placed in filtered, sterilized seawater in a 1-L container. Sperms were introduced at a ratio of 5-10/egg, and the container was shaken occasionally to keep the eggs in suspension. Fertilization was completed in about 30 min.

Egg Incubation

Fertilized eggs were retained on a 20 µm mesh screen and then placed in a 100-L Nalgene container at a density of 700 eggs/cm^2. A mixture of antibiotics (8 mg/L chloroamphenicol and 50 mg/L streptomycine sulfate) was added to the water. Every 2 d the water was replaced and temperature maintained at 12-15°C.

Larval Rearing

Seventy-two hours after hatching, the majority of the larvae were in the veliger stage. They were sieved first through a 150-µm screen then retained on a 20-µm screen, counted, measured and placed in a tall 1-L cylinder. The weak swimmers and moribund larvae were discarded and the vigorous swimmers were transferred into 250-L tanks at a density of 7-10 larvae/mL. During this period leading to the pediveliger stage no antibiotics were used.

A mixture of phytoplankton, Pavlova lutheri, Isochrysis galbana, and Phaeodactylum tricornutum (50:40:10) were fed daily at a concentration of 45,000 cells/mL. Every 2 d the water was changed and the tanks were thoroughly disinfected with Javex. When the larvae reached the 120-µm size, they were transferred to 17-L rearing cages with 80-µm Nitex

bottom screens. These cages were then immersed in the 250-L tanks (Fig. 7). The stocking density in the cages was 2-3 larvae/mL. Gentle aeration was provided as shown in Fig. 7. As the larvae grew, they were moved into cages with successively larger bottom mesh screens, (80, 100, 153, 202, 253 µm).

Once the pediveligers appeared, indicated by the presence of a foot and bottom seeking behavior, the algal diet was reduced to 20,000 cells/mL/d and the algal mixture changed (P. lutheri and I. galbana; 50:50). Antibiotics were used during this period.

Settlement is a prerequisite for metamorphosis and if a suitable substrate cannot be located, metamorphosis can be delayed or abandoned. Pre-settlement mortality can therefore be very high in artificial culture. Even though Naidu et al. (1981b) determined that monofilament gillnetting was the best material for natural spat collecting in extensive culture, pediveligers have been reluctant to settle on the substrates provided in artificial culture (P. Dabinett, pers. comm.). There is evidence that some mollusc larvae settle gregariously in response to chemicals associated with or released by other larvae or metamorphosed adults. There is a real need for information on environmental factors which may induce settlement and metamorphosis of scallops.

Mortality between settlement and 5 mm is also extremely high under intensive culture (Bourne, pers. comm.). Nutrition seems to be important during this period, and the problem cannot be overcome by simply feeding excessive quantities of food. In fact, Dabinett (pers. comm.) observed reduced mortality with reduced feeding.

SITE SELECTION CRITERIA

The location of the culture facility is very important and the necessity for selecting a suitable site cannot be overemphasized. Every potential location will have its own unique site-specific problems that are due to local conditions.

A rule of thumb to follow in choosing a site is to locate the facility where scallops occur naturally. If conditions are suitable for a natural population, they should be suitable for culture (Naidu and Cahill 1986). The facility should not interfere with other fishing activities, recreational interests, or navigation. It should be located where it can be overseen so that vandalism and theft will be discourgaged. If at all possible, the grow-out facility should be in close proximity to the spat collecting site so that transportation stresses are minimized.

Small bays, inlets and baylets with a narrow sill entrance are ideal, providing there is no massive influx of fresh water and the occurrence of ice is minimal or non-existent. The area should be sheltered or protected from storm damage and it should not be located where strong tidal currents can damage gear.

The giant scallop is a stenohaline species that requires a salinity of at least 30 ppt. It also requires cool temperatures and grows best within a temperature range of 10-15°C. Upper lethal temperature is about 22.5°C. Below 8°C, growth is slowed and below 4°C, growth ceases. Wide fluctuations in either temperature or salinity are detrimental to survival.

COLLECTION OF WILD SPAT

Spat collection is based on the natural tendency of larvae to settle before metamorphosis. Artificial substrates such as nylon netting, burlap, fiberglass, and polyethylene film have been tested (Naidu and Scalpen 1976), but monofilament gillnetting has proved to be the best for collecting spat (Naidu et al. 1981a, b).

A single spat collecting line consists of 20 onion bags, each filled with about 540 g of 15-cm mesh monofilament gillnet and tied to a 26-m length of 1-cm polyproylene rope which is anchored by 20 x 20 x 40 cm concrete blocks and supported 2 m off the bottom by six trap floats (Fig. 8).

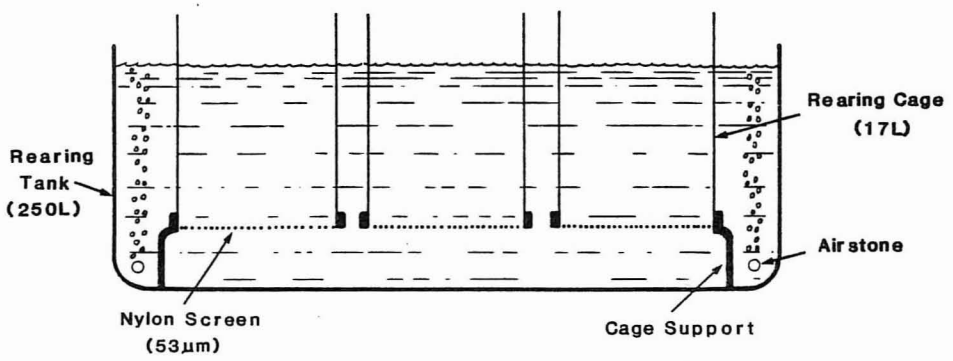

Fig. 7. Tank used for rearing larval giant scallops (from Fournier and Marsot 1985).

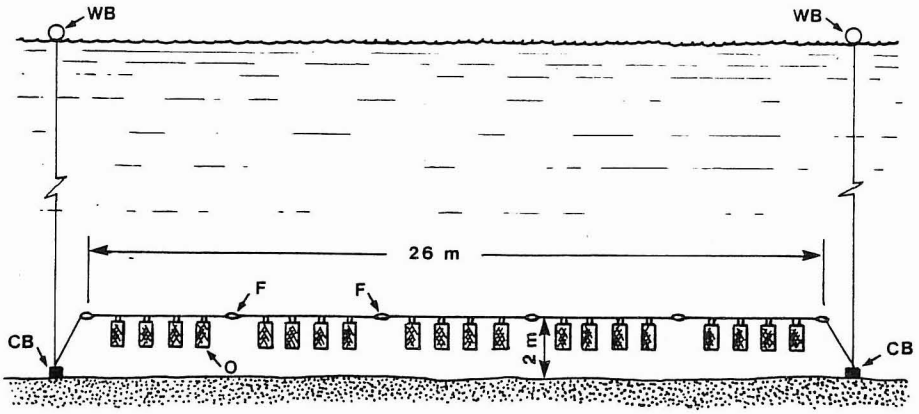

Fig. 8. Spat collection system (from Naidu and Cahill 1986).

The collectors must be set early enough to take advantage of the peak settlement, but not so early as to expose the collectors to excessive fouling or starfish settlement. Collecting lines are set out in the fall, after scallops have spawned in late September to early October (Naidu 1986).

The number of spat collectors to be set will depend on the number of spat required and the expected spatfall densities in the local area. In Newfoundland, spat collection has been variable from year to year. In a given area the number of spat per collector may vary from 10 to several thousand from one year to the next (Bob Haynes, Scallop Co-ordinator, Nfld. Dept. of Fisheries, St. John's, Nfld., pers. comm.).

When the spat reach about 10-12 mm in length (approximately 1 yr), they are moved to pearl nets for intermediate culture. Cool, calm days are best for spat removal and the time spent out of water during transfer must be minimized. The onion bags are removed from the lines, one by one, and opened while submerged in a 70-80 L tub of fresh seawater. The bag is turned inside out and the gillnetting shaken until all the spat drop off. When all the spat are removed, the gilnetting is replaced in the bag for reuse and the contents of the tub are strained through a 3-4 mm sieve. The good spat are then placed in pearl nets and the unwanted material discarded. Spat removal is delayed until they reach this size in order to maximize retention in the pearl nets (Naidu and Cahill 1978).

INTERMEDIATE CULTURE

Normally 50 spat are stocked in a pearl net, and 20 pearl nets are attached to form one array. Twenty arrays (400 pearl nets) are attached to a 50-m length of 18-mm leaded-polypropylene rope. This is supported by eleven 1-m polyfoam single-eye buoys and secured by a 90-kg anchor at each end (Fig. 9). The number of pearl nets and the length of the headline depend upon the local conditions and the number of spat available.

At the onset of winter, the pearl nets are weighted and lowered beneath the surface for protection from ice and storms. The following spring, the nets and floats are returned to the surface. Spat remain in the pearl nets until they are 40-60 mm in length (about a year) and they are then transferred to the grow-out phase. During 1 yr, giant scallops grew from 13.2 mm to 48.3 mm with a survival of 86.1% (Naidu et al. 1981a).

THE GROW-OUT PHASE

Net Culture

Scallops 40-60 mm in length are transferred from the pearl nets to lantern (accordian) nets (Fig. 10) and suspended from a head rope. Each lantern net has 10 compartments and the initial holding density is usually 20 scallops per compartment. Stocking density appears to have a greater effect on growth rate than does the depth at which the animals are held (Naidu and Cahill 1978). Lantern nets are attached in pairs by a 2-m length of rope to a 50-m headline which is secured at each end by a 90-kg anchor. The headline is supported by 11 1-m polyfoam single eye buoys along its length (Fig. 11).

The headlines are submerged in the fall and refloated the following spring. At this time fouling organisms are removed and stocking densities reduced to 10 scallops per compartment. Harvesting would normally occur the following year.

Longlines should be set parallel to local currents and tidal flow and the distance between

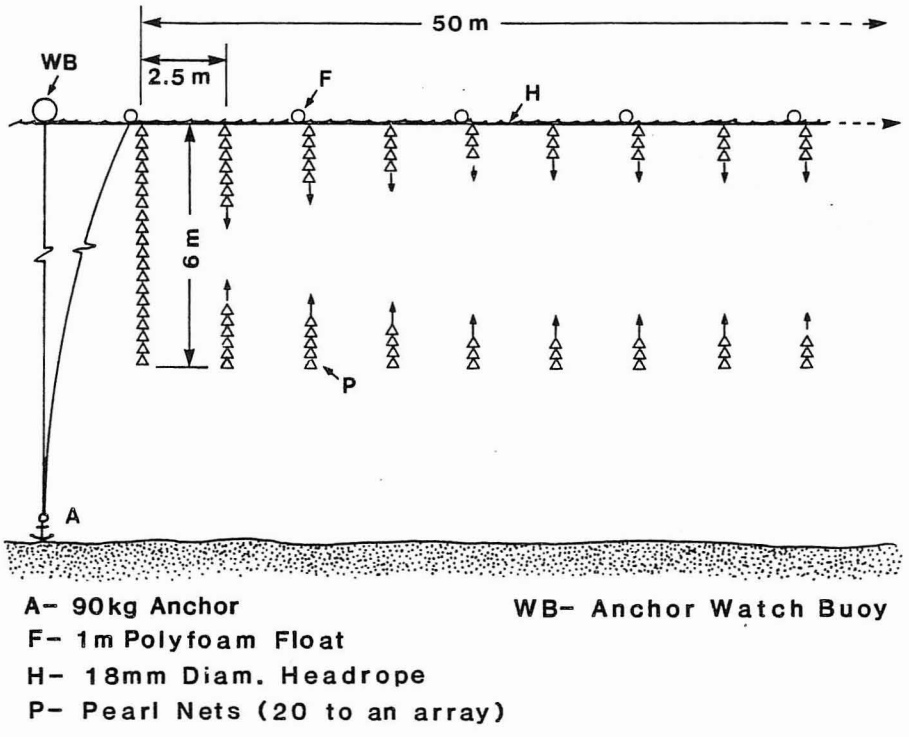

Fig. 9. Intermediate culture system using suspended pearl nets (from Naidu and Cahill 1986).

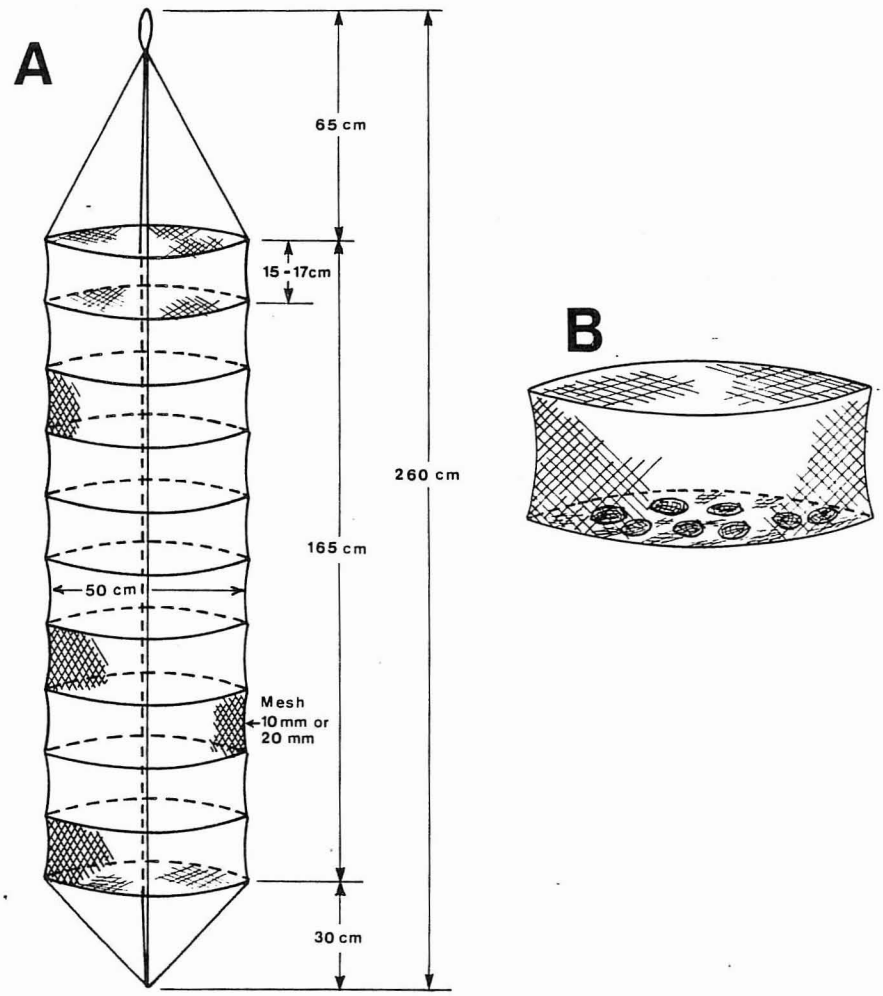

Fig. 10. Lantern net for growing giant scallops in suspended culture. A - entire lantern net (from Naidu and Cahill 1986). B - detail of one compartment.

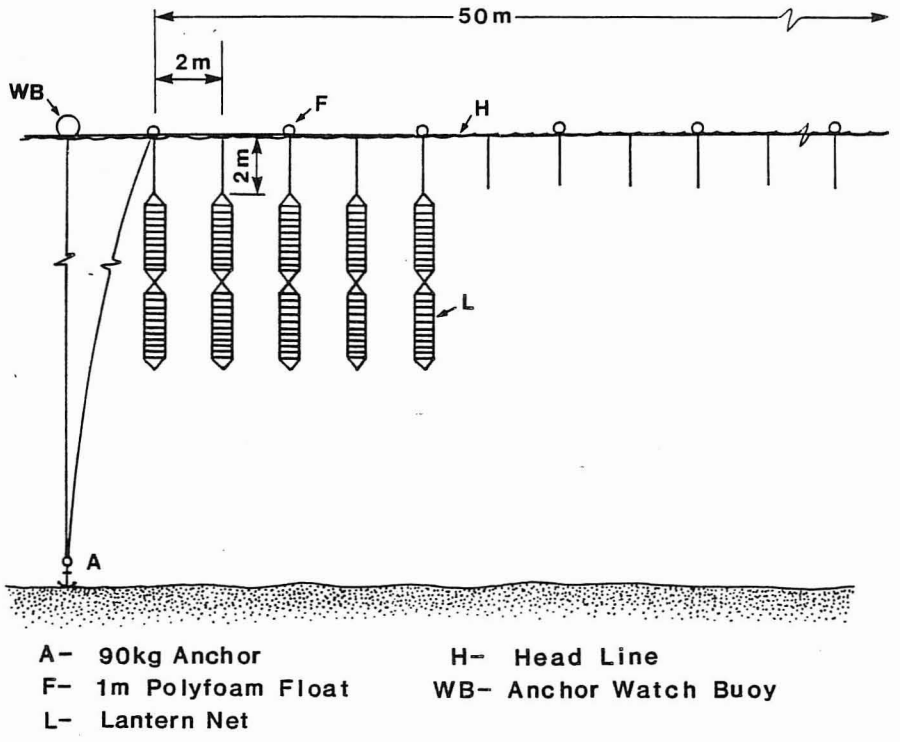

Fig. 11. Grow out line using lantern nets for scallop culture (from Naidu and Cahill 1986).

parallel lines should be 20-30 m.

Bottom Culture

Bottom or relaying culture is an alternative to net culture for grow-out. In this method scallops from the pearl nets of intermediate culture are broadcast over the sea bottom in a suitable area and left to grow. A suitable bottom grow-out site should be relatively devoid of predators, about 25-50 m deep, and with a flat, predominantly sandy bottom suitable for dragging (Naidu and Cahill 1986). Releasing spat directly from spat collectors is not recommended because of the catastrophic mortalities in the young. Harvesting is normally 1 yr later than with cage culture (i.e. the fifth summer) and is accomplished with a scallop drag.

Bottom culture reduces capital expenditure, labor costs, navigational conflicts and vandalism but these advantages are offset by slower growth and increased mortality.

ECONOMICS

While the biological feasibility of scallop culture is assured, the economic feasibility remains to be estabished. A general dynamic bioeconomic model based on spat population, mortality, recovery, and price functions to simulate and forecast return on investment was conducted by Frishman et al. (1980). Cost estimates for materials, supplies and labor were obtained from various local suppliers as well as potential participants in the project (Naidu et al. 1980). Expenditures and revenues were reported in 1979 Canadian dollars. Computer runs forecasting annual compounded rates of return from bottom culture under various assumptions for recovery rates, spatfall, mortality and price options indicated that best economic return was achieved with bottom culture.

IV. CONCLUSIONS

This report has reviewed published information pertaining to the biology and culture of the sea scallop. From this, it is evident that gaps exist in our understanding of scallop biology and that further research is necessary. For example, the factors affecting spawning are not well understood, and there is limited information on the biochemical and biophysical stimuli for larval settlement, the nutritional requirements of larval scallops before and after settlement and the effect of temperature on larval growth rate. Post-larval growth, behavior and ecology is largely an enigma and almost nothing is known about the nutritional requirements of scallops at different life stages or diseases in scallops.

It is possible that commercial production of cultured scallops will become established in Canada in the future. The present technology for scallop culture is fairly simple and the capital and operating costs relatively modest, depending on the techniques used. Scallops can be grown with maximum utilization of the water column and minimum interference with other marine activities.

Sea scallops have been grown successfully in suspended cages and in bottom relay culture. Best growth has been achieved in suspension culture but bottom culture has proved to be more economical. Fluctuations in the availability of wild seed could

represent a severe size limitation to a developing scallop culture industry but seed supply could be stabilized by systems and techniques for large-scale hatchery production of seedstock. Artificial propagation will also allow development of superior strains of scallops.

In shellfish cultivation, the enclosures inevitably become fouled and a great deal of time and labor is involved in changing and cleaning the cages. Fouling restricts the water flow through the cage meshes and reduces the food available to the animals. Fouling also increases the buoyancy requirements. The main group of fouling organisms are algae, mussels, starfish, barnacles and hydroids. Biofouling is very specific with respect to site, depth and season; wide variation in intensity being common, even within relatively small geographic areas. Therefore, the prevention and control of fouling organisms will play a critical role in the economics of scallop culture.

With the optimum environmental conditions that exist in the Bay of Fundy, the sea scallop appears to be a good candidate for local culture. In the early stages of local culture, the technology developed in Japan and adapted for Newfoundland will probably be used. However, local conditions will necessitate modifications to this basic technology so evaluations and experimentation should be incorporated into local scallop culture development plans.

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V. LITERATURE CITED

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