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MARINE WOOD BORERS IN BRITISH COLUMBIA

D. B. Quayle

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Contents

MOLLUSCA

CRUSTACEA (*Limnoria*)

Abstract

QUAYLE, D. B. 1992. Marine wood borers in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 115: 55 p.

In British Columbia the marine wood borer fauna is small in terms of species but large considering the damage inflicted on unprotected floating and fixed marine structures. The molluscan borers include the shipworms, *Bankia setacea* (Tyron, 1863), *Teredo navalis* Linneaus, 1758, *Lyrodus pedicellata* (Quatrefages, 1849) and the pholad *Xylophaga washingtona* Bartsch, 1921. The crustacean borers are represented by the gribbles *Limnoria lignorum* (Rathke, 1799) and *Limnoria tripunctata* Menzies, 1951.

The published knowledge of these species in British Columbia is not generally available and the purpose here is to provide a one point source of information for students and others whose activities may be affected by marine wood borers. Previous British Columbia studies are reviewed and the basic biology and ecology of the important species is given along with present control measures.

Résumé

QUAYLE, D. B. 1992. Marine wood borers in British Columbia. Can. Spec. Publ. Fish. Aquat. Sci. 115: 55 p.

La faune des xylophages marins de la Colombie-Britannique compte peu d'espèces, mais revêt une grande importance de par les dommages qu'elle cause aux structures marines flottantes ou fixes non protégées. Les mollusques xylophages y sont représentés par les tarets *Bankia setacea* (Tyron, 1863), *Teredo navalis* Linné, 1758 et *Lyrodus pedicellata* (Quatrefages, 1849) et la pholade *Xylophaga washingtona* Bartsch, 1921. Les crustacés xylophages y sont représentés par les limories *Limnoria lignorum* (Rathke, 1979) et *Limnoria tripunctata* Menzies, 1951.

Les publications traitant de ces espèces en Colombie-Britannique ne sont pas facilement disponibles et la présente communication a pour objet de regrouper en une seule source les renseignements intéressant ceux qui étudient ces organismes et ceux dont les activités peuvent être affectées par les xylophages marins. L'auteur passe en revue les études déjà réalisées en Colombie-Britannique et présente les éléments de base de la biologie et de l'écologie de ces importantes espèces de même que les mesures de lutte prises à leur endroit.

Introduction

Marine wood borers have been a problem since man began using wooden vessels and structures in the sea. The organisms responsible for the destruction are shipworms (pileworms), also known by an inclusive term "teredo" (family Teredinidae), and gribbles (family Limnoriidae).

It is difficult to assess the annual loss to the maritime industries in British Columbia, but according to Trussell (1959) losses to the logging industry alone could amount to $2,000,000 annually. In spite of considerable progress in the study and control of marine borers and fouling generally, along with expanded use of fibre glass, metals and cement for vessels in marine construction, there are still significant problems. Few areas in the world have such an extensive system of public and private wharves of wooden construction as exists along the British Columbia coast. This large amount of timber is augmented by wood from natural sources, the forest industry transport and storage of huge volumes of floating timber. Published accounts of marine borers in this province are long out of print.

Recent additions of exotic marine borers and newer knowledge warrants a review of the current situation.

Literature

The marine borer literature with special reference to British Columbia is not extensive. The more recent accounts are those of Black and Elsey (1948) on shipworm incidence at a number of sites; Quayle (1956) on the general biology of the British Columbia shipworm; Bramhall (1960) with a somewhat similar account but with emphasis on records of successes and failures of marine piling installations. The Canada Forest Products Laboratory at Vancouver held recorded symposia on marine wood borers in 1963 and 1966 (Bramhall 1964, 1966). Extensive studies of marine borers were carried out by the then British Columbia Research Council (now British Columbia Research Corporation) and these were reported in research papers and in the mimeographed publication "Tidelines" which, along with monitoring data and forecasts of marine borer activity, contain brief one- or two-page study reports in 261 numbers in 18 volumes between 1959 and 1976. These were designed for the maritime industries and were not generally available.

Some of the comprehensive publications of marine wood borers include Sigerfoos (1908), Atwood and Johnson (1924), Hill and Kofoid (1927), Ray (1959), Turner (1966), Gareth Jones and Eltringham (1968), Nair and Saraswathy (1971), Costlow and Tipper (1984) and Thompson et al. (1988)

British Columbia Marine Wood Borers

The six species of marine wood borers that occur in British Columbia waters consist of four mollusca and two crustaceans. These are:

Mollusca

Bankia setacea (Tryon, 1863)
Teredo navalis Linneaus, 1758
Lyrodus pedicellatus (Quatrefages, 1849)
Xylophaga washingtona Bartsch, 1921

Crustacea

Limnoria lignorum (Rathke, 1799)
Limnoria tripunctata Menzies, 1951

Mollusca

The molluscan wood borers (families Teredinidae and Xylophagaidae) are bivalves developed from clam-like ancestors, first living in clay or soft stone and then with further modifications to wood.

Xylophaga washingtona is the only representative of the Xylophagaidae in British Columbia and is a small, less than 5 mm long, borer most of whose body is enclosed within the shell (Fig. 1). It occurs in deep water between 15 and 2000 m. Because of small size, habitat and low abundance, it is not of economic significance in British Columbia. It is rarely seen except in biological collections.

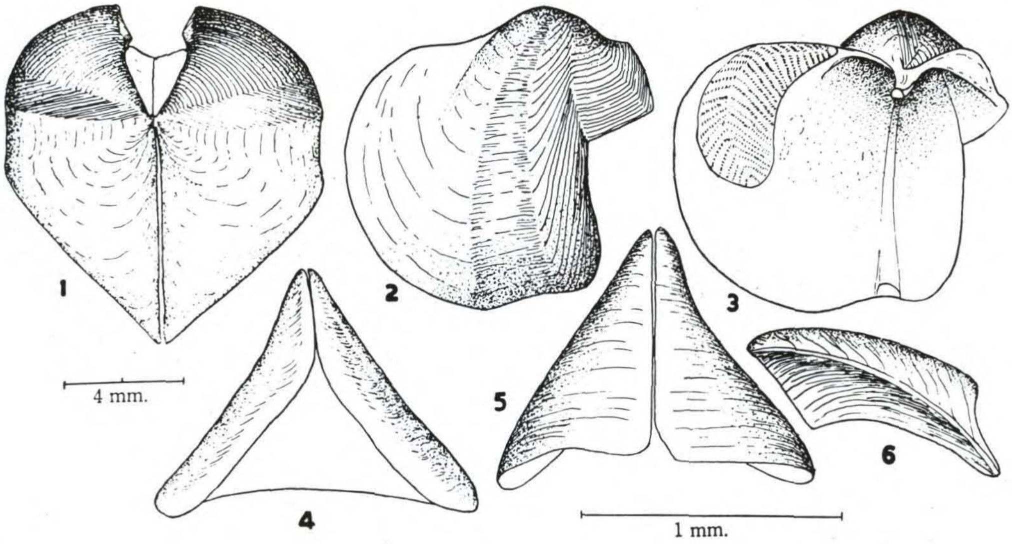

FIG. 1. *Xylophaga washingtona*. 1. Dorsal view of paratype showing the mesoplax in place. 2. External view of the right valve of the holotype showing the shallow, smooth umbo-ventral sulcus. 3. Internal view of the left valve of the holotype showing the regularly marked posterior adductor muscle scar. 4. Ventral view of the mesoplax. 5. Dorsal view of the mesoplax. 6. Side view of the mesoplax. (From Turner 1955).

In the Teredinidae, the native species is *Bankia setacea* (Fig. 2), widely distributed throughout British Columbia and of prime importance, is the main subject of this report. Another teredinid, *Teredo navalis*, an Atlantic species was introduced into British Columbia waters, but as far as known occurs only in Pendrell Sound in East Redonda Island where, for a time, it became quite abundant. The third teredinid, *Lyrodus pedicellatus*, also introduced into British Columbia, is known only by a few specimens from Ladysmith Harbour.

Crustacea

The crustacean borers are gribbles and members of the Isopoda. These are small (2–5 mm) marine versions of the common wood louse. The native species, *Limnoria lignorum*, is common throughout British Columbia waters but also occurs in the Atlantic Ocean (Fig. 3). *Limnoria tripunctata* is an introduced species and its distribution in this province is limited to the southern half of Vancouver Island. Another West American isopod wood borer, *Sphaeroma pentadon* Richardson 1904 which, although it occurs in British Columbia, does not pose a problem as it does in areas with higher water temperatures.

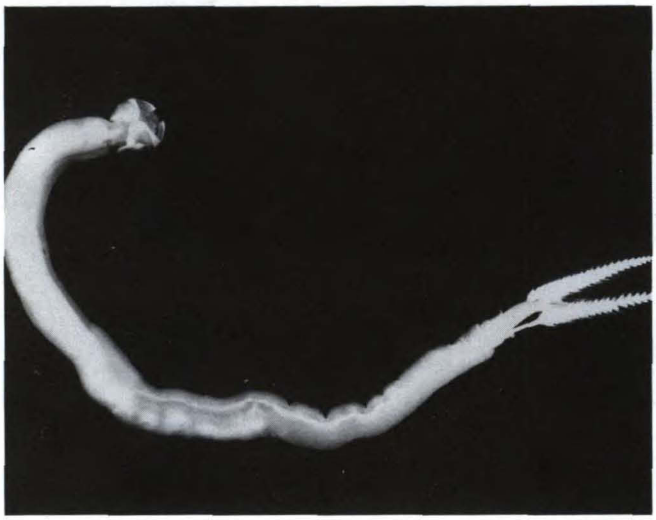

FIG. 2. Excised *Bankia setacea*. (From Quayle 1956)

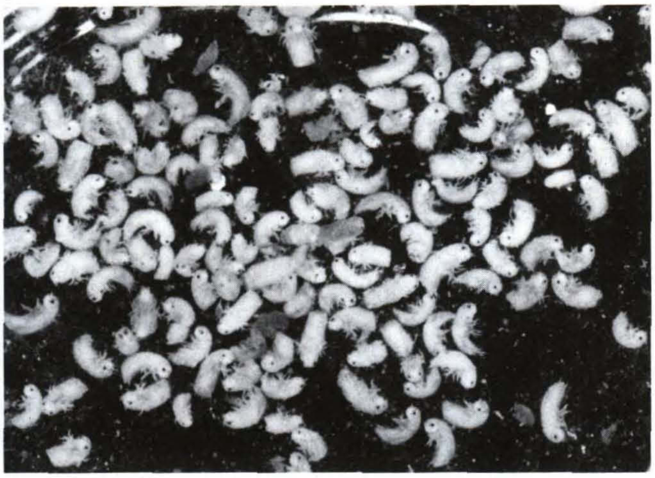

FIG. 3. Excised *Limnoria* of both species, ×1.5.

Molluscan Identification

As with most molluscan species, identification is based largely on shell characteristics and to a lesser extent on the anatomy which is quite similar in closely related shipworms. This is also true of the shell which may show some variations within a species. Tube constructions also have limited value as identification features. The remaining hard parts, the pallets, fortunately provide a suitable characteristic for distinguishing most species, although these may show some variations between individuals.

Bankia setacea

The paired pallets of *Bankia setacea* (Fig. 4) are feather-like structures consisting of a paired series of half cones more or less ''Y'' shaped fitting one within the other and cemented to a central core. Each arm (an ''awn'') of the Y ends in a fine, almost membranous point. The largest and newest cones are those closest to the body and those distal are the smallest and oldest. The pallets of *B. setacea* may consist of 30 or more cones.

Teredo navalis

Distinct from the *B. setacea* pallet, that of *T. navalis* consists of paired spade-like members (Fig. 5). The inner and outer distal margins differ slightly in the amount of concavity.

Lyrodus pedicellatus

As with *Teredo* the pallets of this species are paired and spade-like, with slightly narrower and less concave distal margins.

Xylophaga washingtona

This species may be distinguished from the teredinids by the lack of pallets and apophases, the presence of a mesoplax and with the excurrent siphon shorter than the incurrent.

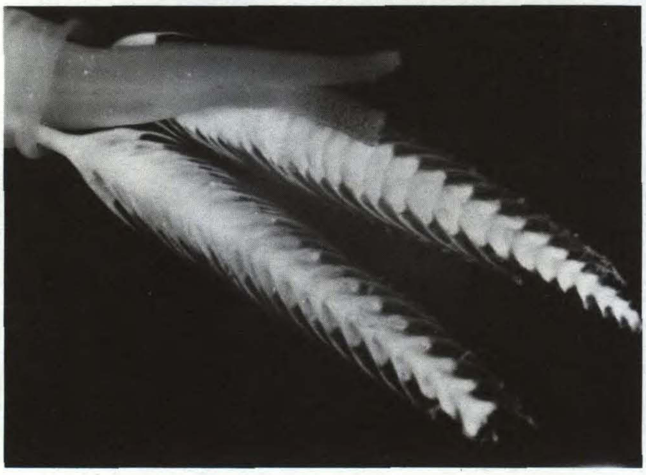

FIG. 4. Pallets and siphons of *Bankia setacea*. (From Quayle 1956)

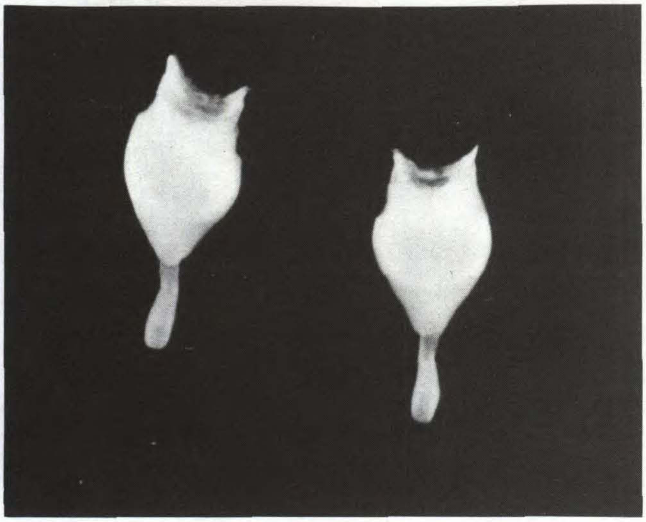

FIG. 5. Pallets of *Teredo navalis*.

Molluscan Anatomy

Shipworms have the same basic anatomy as clams and oysters (Fig. 6a,b), more familiar mollusca, but with modifications attendant to the boring habit, chiefly elongation of the body (Fig. 2,7).

Shell

Most shipworms have three calcareous components. The first is the bivalve shell, much different from but analogous to clam or oyster shells (Fig. 8a,b,c). This is located at the anterior end, and encloses only a small part of the body. Second is a pair of pallets attached at the posterior end at the base of the siphons, and the third is the tunnel lining which may be complete or partial.

The boring apparatus is the shell, composed of a right and left valve joined by two adductor muscles

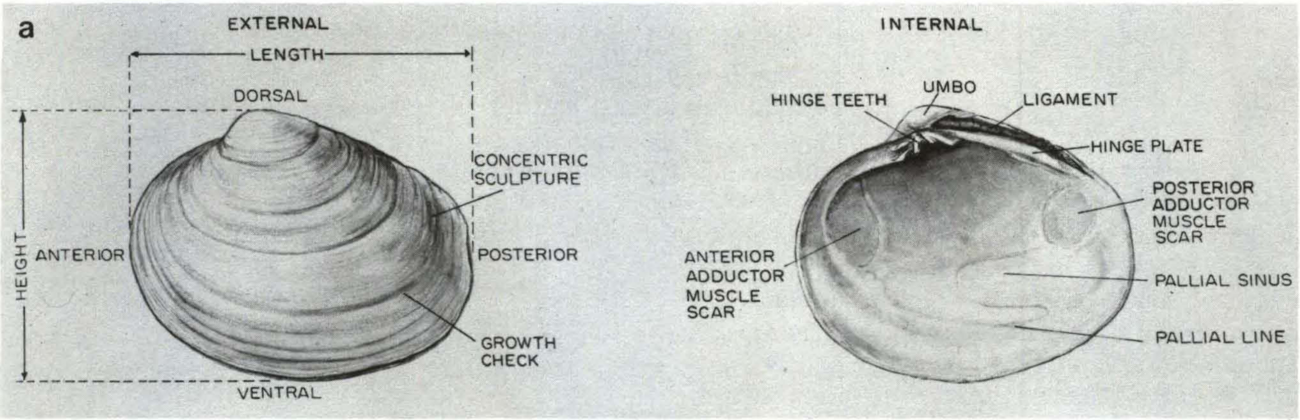

FIG. 6a. (*Left*) External view of the left valve of *Saxidomus giganteus*; (*Right*) Internal view of the right valve of *Saxidomus giganteus*.

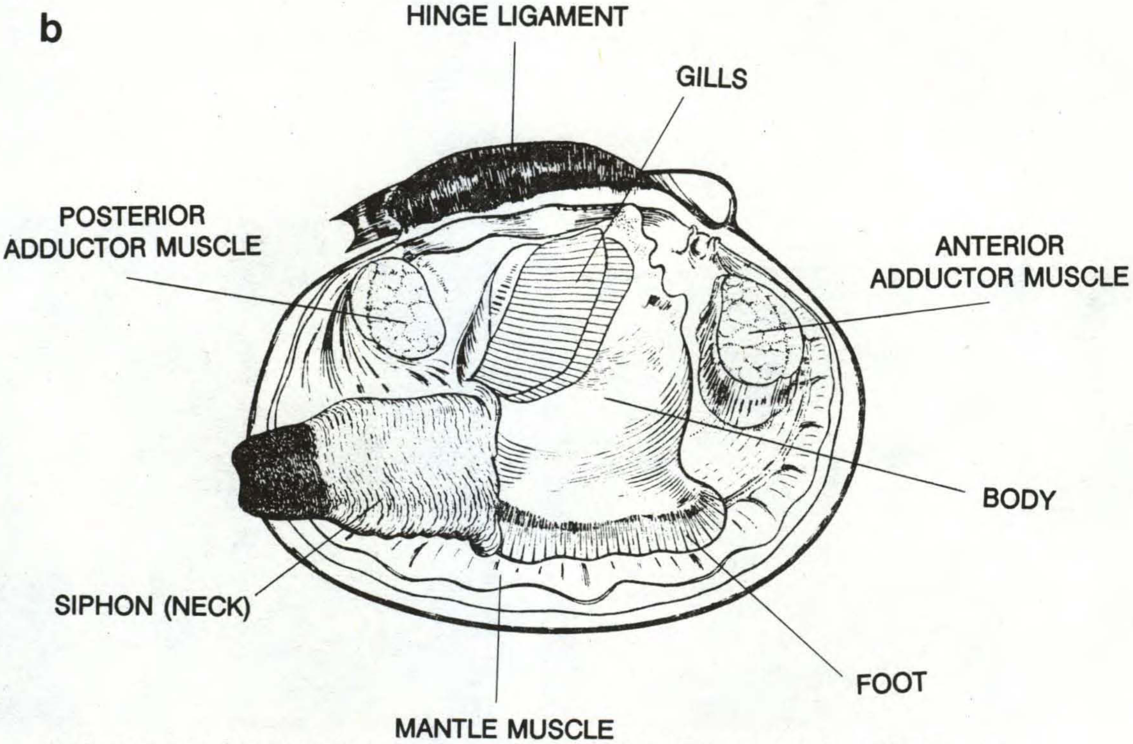

FIG. 6b. Anatomy of the butter clam, *Saxidomus giganteus*. Right valve removed. (From Quayle and Bourne 1972)

(Fig. 8b). The shell itself, largely aragonite, has the normal three layers of most mollusca: an outer periostracum, a central prismatic and an inner nacreous layer. The outer surface of each valve has three sections. The posterior area or auricle, is a smooth rounded extension to which the posterior adductor muscle is attached. Separated from the auricle by a well defined groove is the posterior section of the disc or median area, undifferentiated except for growth lines, while the anterior portion contains a nearly vertical series of denticulated ridges (Fig. 8a). At right angles, these meet the anterior lobe, also with denticulated ridges which are the cutting facets of the valves. The denticles of the vertical series of cutting ridges are triangular with the apices directed out and backwards. The denticles of the horizontal ridges of the anterior section, serrated like a fine saw, are not as well defined, (Fig. 8c).

The interior of the valves have structures quite distinct from the normal bivalve. These are shown in Fig. 8b, the interior of a right valve of a teredinid shipworm. Anterior and dorsal is a small smooth area where the

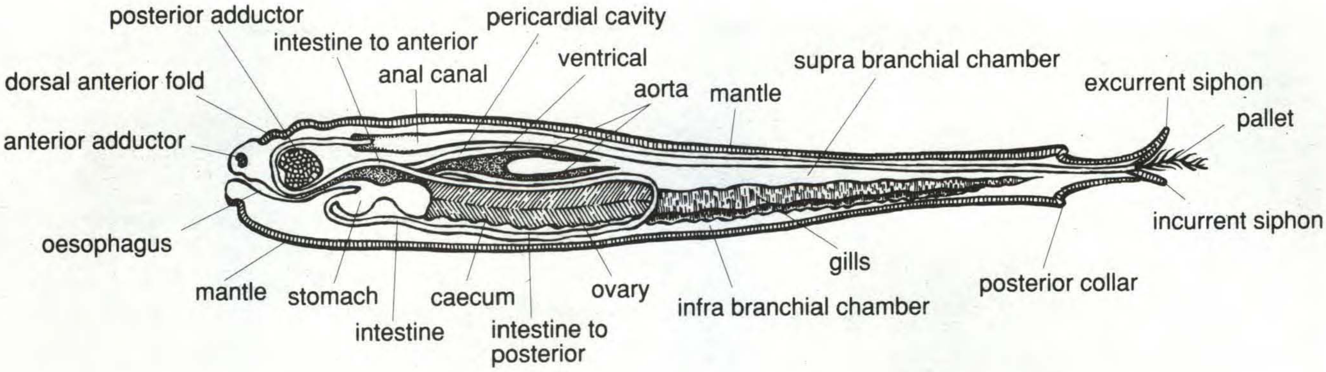

FIG. 7. Diagrammatic representation of the principal parts of anatomy of the British Columbia shipworm (*Bankia setacea*).

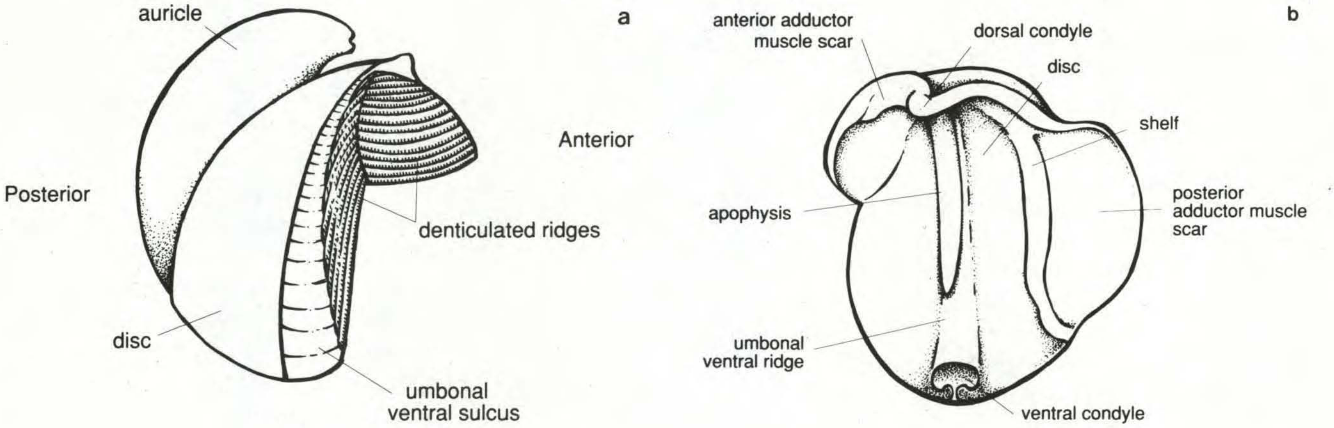

FIG. 8a, Exterior of the right valve of *Bankia setacea*; b, Interior of the right valve; c, Side view of the dorsal area of the right valve to show dentition. ×15 (B.C. Research Council photograph).

anterior adductor muscle is attached. Posterior to it is the dorsal condyle and this with the ventral condyle are the points of valve articulation, allowing them to rock freely back-and-forward. In mollusca this system occurs only in the Teredinidae and the Pholadidae. The chondrophore provides a ligamental attachment area and the apophases are for attachment of the foot muscles. One of the early formed and temporary calcareous structures is a protective feature covering the initial entry area of the tunnel. This is a fragile cone 0.3 mm in diameter and 3–4 mm high in *Bankia* with two terminal apertures about 0.1 mm wide, slightly unequal in size, one for each siphon (Fig. 9). The slightly subsurface cone is fully formed within 3 or 4 days after settlement and the outer portion persists only a short time for the small apertures cannot accommodate the growth in diameter of the siphons. Within a month the tunnel entrance has enlarged to about 1 mm and the well formed pallets can protrude above the surface.

FIG. 9. Calcareous cone formed in the entry hole in the early stage after settling by *Bankia setacea*. ×15. (From Quayle 1956)

Pallets

The pallets (Fig. 4, 5) are unique to shipworms and an adaptation to the peculiar habitat. They are used to seal off the tunnel entrance, either from intruders or unsuitable hydrographic conditions. The form of the pallets is the main feature for shipworm identification. However, care must be taken because of considerable variation, partly genetic and partly deformation, with age. The basic form of the shipworm pallet is spade-like, typical of the genus *Teredo* (Fig. 5). In *Bankia* the first formed pallet, not unlike that of the mature *Teredo*, is a single club shaped element 250 µm in length, the head 200 µm wide. The stalk is 150 µm long and 45 µm thick (Fig. 10a). Up to a length of 1 mm, the first 3 cones are closely appressed and become separated as growth continues (Fig. 10b). Additional cones are added rapidly to develop eventually into the feather-like form characteristic of the genus (Fig. 4, 10c and Table 1). Each cone in *Bankia* is somewhat oval in cross section and each side is extended into fine flexible points called "awns". Between the awns is a fine membrane termed the "web" which forms an impervious cylinder when the pallets are appressed against the tunnel wall. In British Columbia, feather-like pallets are those of *Bankia setacea* and the spadiform type is that of either *Teredo navalis* or *Lyrodus pedicellatus*. The in and out movement of the pallets is controlled by one pair of protractor and two pair of retractor muscles, along with a single adductor muscle attached to the anterior end of the pallet handle. When shipworms are feeding the siphons are extended and the pallets retracted. When disturbed the siphons are withdrawn and the pallets extended to close off the opening. It may happen that either by erosion of the wood or overgrowth of the pallets, they may protrude too far and the tips broken off. Particularly in *Teredo* with the single pallet piece, it is necessary to accommodate growth changes in its shape by adjustments to the thickness of the ends of the calcareous tube.

Yonge (1927) described external calcareous extensions of the tube in *Teredo megotara* when frass accumulates at the tunnel entrance. Extensions of the tube also occurs with *B. setacea* in similar situations. In this species the tubal extensions are formed from mucous bound frass particles.

Lining

The shipworm's contact with the tunnel wall is the mantle which in mollusca is the shell secreting organ. It fulfils that function in teredinids, although the protective role has been largely usurped by the tunnel itself. The lining of the shipworm tunnel is composed of several layers of calcium carbonate crystals secreted by the mantle. The tunnel can be completely or only partially lined except for the boring face, unless there is a complete change in direction when the old tunnel is sealed off (Fig. 11). In very young animals, the organic lining may be transparent, not readily observed but a base upon which calcification may occur later. The tunnel lining may attain a thickness of several millimetres and forms the attachment area for the developing siphons and pallets. Shipworms removed from the tunnel intact are able to construct a calcified tube if kept in seawater (Manyak et al. 1980). Trussell et al. (1968) demonstrated shipworms are able to settle and grow in substrates other than wood such as agar gel, with or without cellulose or wood flour additions.

Mantle

As with all bivalve mollusca, an important anatomical feature of shipworms is the mantle, the shell secreting organ. This is a thin semi-transparent tissue of 3 layers. The inner layer is next to the body; the central layer holds nerve and muscle fibres and the outer layer secretes shell. In most clams and oysters the mantle covers each side of the body with a lengthy ventral opening (Fig. 6). In teredinids this opening has been closed to form a long tube enclosing all the soft body with only an anterior opening for the protrusion of the foot.

TABLE 1. Relationship between pallet length, tunnel length and number of segments in *Bankia setacea*. (From Tidelines, Vol. XIV, No. 6: June 1972.)

Pallet length	Tunnel length	Number of segments
11 mm	7.5 cm	5
17	19	7
25	24	9
36	38	14
50	50	20

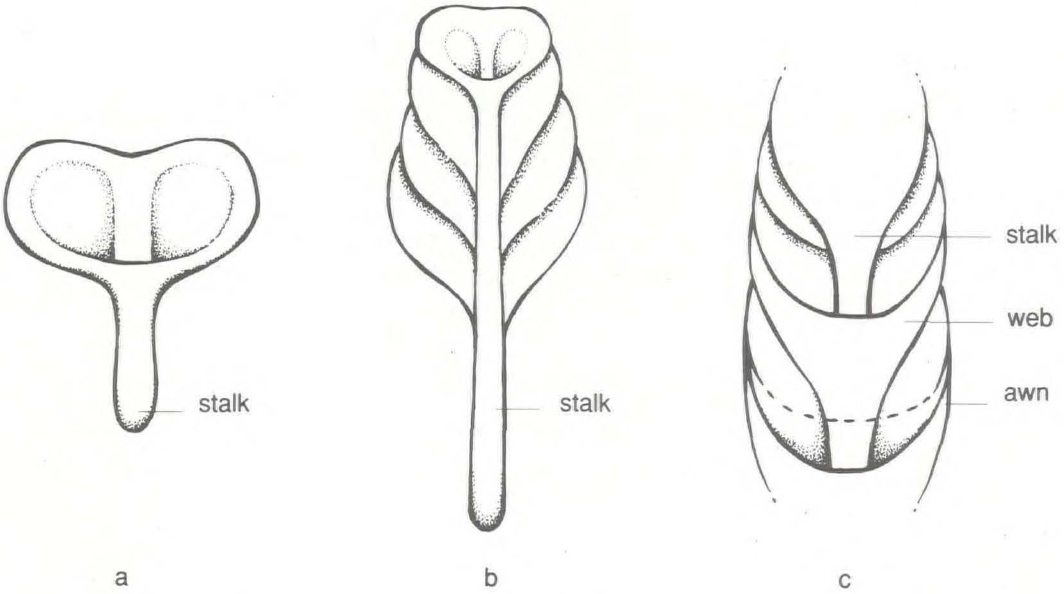

FIG. 10. Development of the pallet of *Bankia setacea*. a, Initial single spade-like form. ×50; b, Formation of additional elements. ×25; c, Final form of a pallet section. ×8.

Above the shell the mantle is thickened dorsally to form a fold (cephalic hood of Turner 1965) whose probable function is to form a seal between the area of drilling activity and the remainder of the body. In *Bankia setacea* the main fold is U-shaped with a corrugated surface and edged with a frilled apron (Fig. 12). Anterior to this is a smaller structure with similar corrugations. At the base of the siphons is another mantle thickening to form a collar which separates the main burrow from the siphon–pallet complex.

These collars prevent foreign materials entering the space between the outer mantle and the tunnel wall. The inner mantle layer is ciliated, particularly in the area opposite the free ends of the gills (the branchial groove), serving to clear and move particulate matter to the appropriate destinations in the mantle cavity. The mantle cavity is divided by the gills into a dorsal epibrachium or suprabranchial chamber and ventral infrabranchial chamber. The latter is connected to an incurrent siphon, the conduit for incoming oxygen and food laden water. The suprabranchial chamber receives the filtered and deoxygenated water which has passed through the gill ostia from the infrabranchial chamber. The suprabranchial chamber also receives true fecal material from the anal canal into which the anus enters just above the large posterior adductor muscle. Fecal

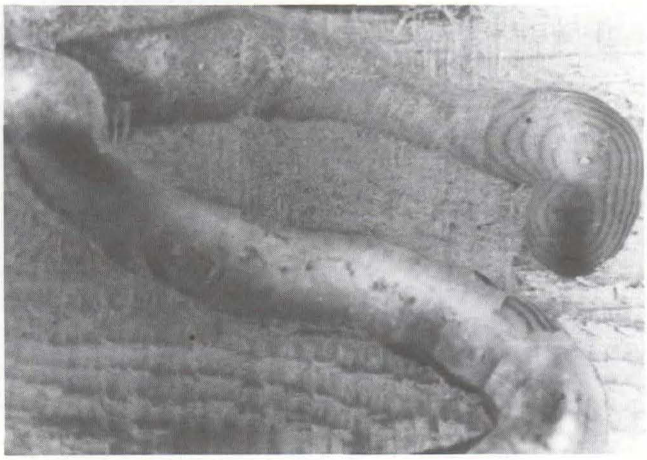

FIG. 11. *Bankia setacea* tunnel showing an abandoned section (upper right) with the calcareous seal (upper left). (From Quayle 1956)

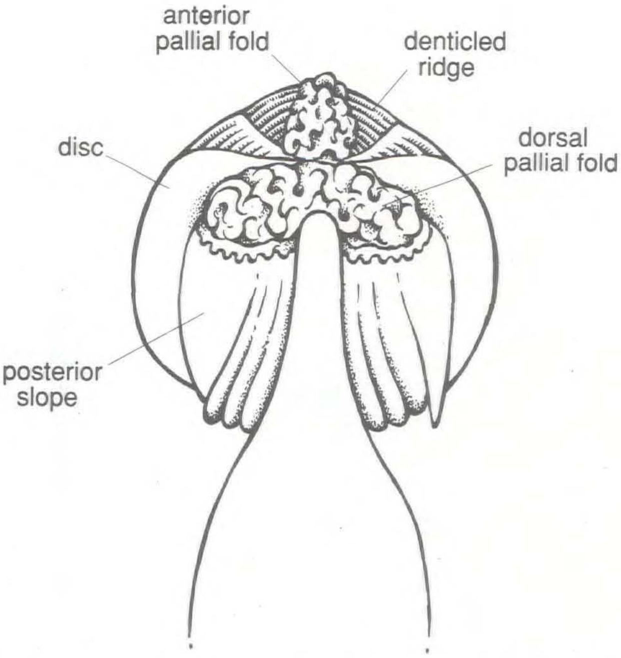

FIG. 12. Dorsal view of the valves of *Bankia setacea* showing the pallial folds (Cephalic hood of Turner). ×10.

material, known as ''frass'', in the form of white or beige strings, 2–3 cm long and 1 mm thick, is discharged through the dorsal excurrent siphon. Uningested material in the infrabranchial chamber, termed pseudofeces, is ejected externally from time to time through the incurrent siphon by a build up of hydrostatic pressures which can reach 5–17 mm of water (Lane and Tierney 1951). It is likely assisted by the contractions of muscle fibres in the central mantle layer.

Siphons

The two siphons are tubal extensions of the mantle (Fig. 13, 14). In *Bankia* they are partially separated while in *Teredo* completely so. The incurrent siphon, up to 3 cm when extended, through which water and planktonic food are brought into the mantle cavity, is slightly longer than the excurrent and the tip has a crown of small tentacles.

In *Teredo* there are 6 small and 6 large ones, while *Bankia setacea* has 6 short ones of approximately equal size. The shorter excurrent siphon tip of this species is not tentacled and tends to be rectangular in cross section in contrast to the circular incurrent. Papillae occur in 4 rows on the inner and outer corners along most of the excurrent siphons. There is considerable variation in the amount of papillation. It may be partial along the siphon or completely lacking, and occurs in both sexes, although Townsley et al. (1965) state female siphons either do not have papillae or are not as pronounced as in the male. In a 1 mm diameter siphon the inner (facing the excurrent siphon) papillae are up to 180 µm in length and tend to be more separated and flexible than the shorter (40 µm) stubbier ones on the outer corners (Fig. 13). The degree of papillation was examined in 90 specimens of *Bankia*. There were 9 specimens without papillae and 9 with partial papillation. Most were papillated along the whole length of the excurrent siphon with others only in the distal section. Of 18 papillated specimens sexed, 7 were male and 11 were female. The siphons of both specimens are variously pigmented with protoporphyrin which is a precursor to iron containing pigments (Townsley et al. 1965). The excurrent siphon has more pigment, particularly on the inner surface, than the incurrent which in *Bankia* can be quite transparent and is more prevalent in males than in females. Movement of the siphons is controlled by muscles with attachments to the shell lining near the posterior end of the tunnel.

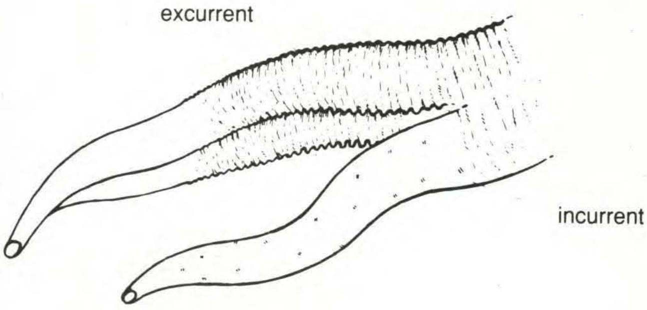

FIG. 13. Siphons of *Bankia setacea* showing the papillation of the exhalant siphon. ×15.

The extended siphons may be quite active, at times almost writhing. During these gyrations, an excurrent siphon has been observed to penetrate an incurrent one with a transfer of a translucent fluid (Clapp 1951), but whether this is an actual ''mating behaviour'' or chance contact is not definitely known. Females have been observed to discharge ova with no prior siphonal penetration.

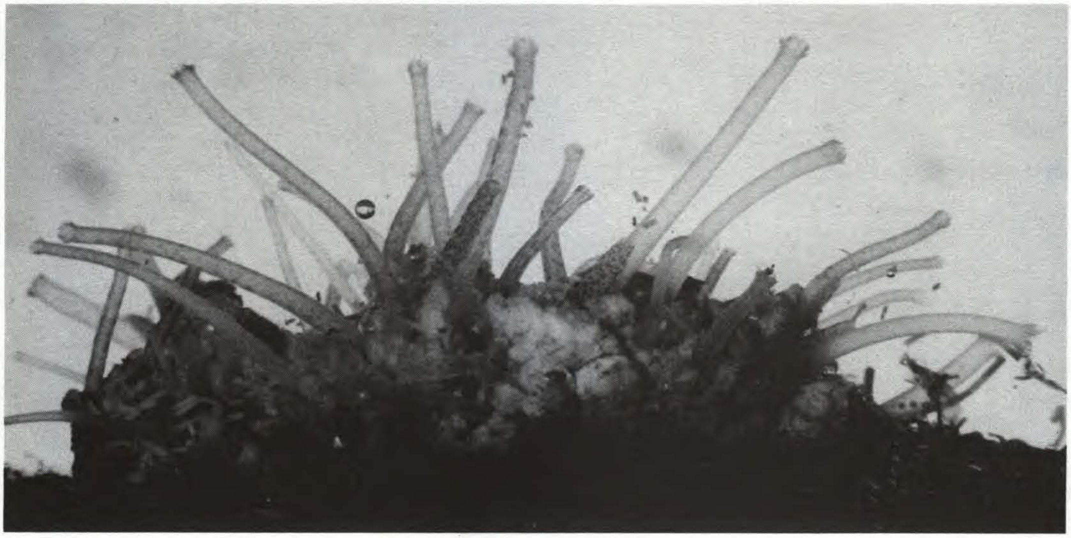

FIG. 14. Extended siphons of *Bankia setacea*. The pigmentation of the exhalant siphons is evident. ×2. (British Columbia Research Council photograph)

Gills

The gill (more properly "ctenidia" or "branchia") of shipworms, as in most other bivalve mollusca, is the organ producing the incoming water currents and filtering from it food and non-food items (Fig. 7). In most mollusca (clams and oysters), the gills are a W-shaped (2 demibranchs) arrangement of vertical, ciliated filaments on each side of the body. In shipworms these are reduced to a single V-shaped demibranch, one on each side of the body. At the base of each demibranch where the filaments of the two sides of the demibranch (each a lamella) fuse, is a ciliated branchial (or food) groove. The vertical ciliated gill filaments are connected by interfilamentar junctions, forming a net-like arrangement of the gill which functions both as a filter and an expanded area for blood oxygenation. The whole gill is highly ciliated and cilia induced water flow directs filtered particles downward to the branchial groove where they are carried forward by ciliary action toward the mouth. In the area of the visceral mass the two demibranchs have a separate attachment to the body proper, but posterior to this area, upper edges of the inner limbs (lamellae) of each demibranch are fused, forming the division between the upper and lower branchial chambers.

Gills in the region of the visceral mass region are structurally different from those forming the two branchial cavities. The gills in *Bankia* extend from the siphons to a point on the visceral mass about two thirds the distance from the anterior end. In *Teredo* the extension is about half way along the visceral mass.

Associated with the gills of some teredinid species is one phase of the organ (gland) of Deshayes (Sigerfoos 1908; Morton 1978; Waterbury et al. 1983) which is essentially a concentration of rod shaped bacteria (Popham and Dickson 1973). Other phases of this organ are located in the walls of the efferent branchial vein and, combined with a larger development of this type of tissue, beneath the umbo. This latter section has ducts leading into the oesophagus and is probably concerned with digestive processes (Sigerfoos 1908.)

Palps

An important part of the food collecting system of most filter feeding mollusca are the labial palps which lie in pairs on each side of the mouth. They are fleshy triangular shaped tissues, highly ciliated, with a presumed function of selecting only suitable food items from the material directed toward them along the food groove. In shipworms however, with filtered material as only part of the food supply, the labial palps have become less important and complex than in those mollusca depending entirely on planktonic food. It may be that the reduction of the palp systems is compensated for by the development of the caecum, also termed the appendix (see page 10), an organ unique to the teredinids. In both *T. Navalis* and *B. setacea* the palps, attached closely to the visceral mass, are small in size indicating a reduced function.

Muscular System

The teredinids are among the many bivalves with two adductor muscles, which, along with the hinge, hold the two valves together and in position. They are inserted on each valve at various sites according to species. In most clams they are located at the ends of the valves (Fig. 6). Contraction or relaxation of the adductors adjust the distance between the valve edges. In some mollusca the adductor muscles are equal in size; in others one is larger than the other, as in shipworms. Adult oysters and scallops have only a single adductor. Because of the unique habitat of shipworms there is little need for gross muscular activity and most of the muscles are of a delicate nature except for the posterior adductor muscle which, along with the foot, is mainly responsible for boring. The posterior adductor muscle insertion on the valves covers most of the inner surface of the auricle (Fig. 8a, b). The smaller anterior muscle is inserted just anterior to the dorsal condyle and umbones and is approximately one tenth the size of the posterior. Both are approximately lenticular in shape, and in life the posterior adductor is pink or reddish in colour.

The function of the foot (Fig. 15) in shipworms is adhesive in nature, rather than movement, whose limited activity is controlled by two sets of paired retractor muscles (anterior and posterior), and a pair of protractors. The action of these muscles is assisted by fluid movement within the foot to produce various levels of turgor. The siphonal and pallet muscles have already been described.

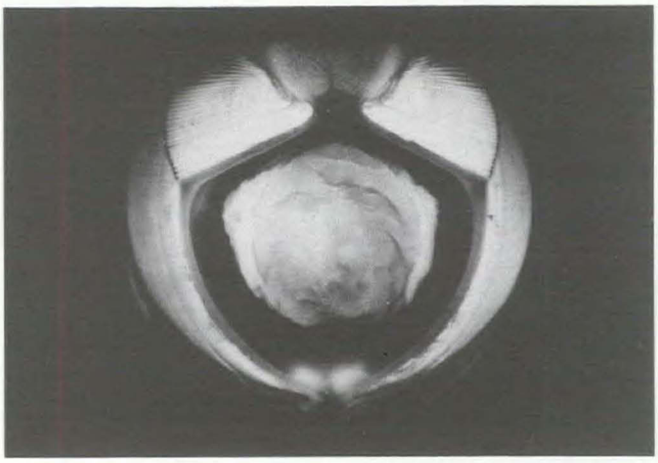

FIG. 15. Frontal view of the anterior section of *Bankia setacea*, showing the valves (left valve to the right), the foot between the valves, and the 2 cephalic hoods dorsally. x10. (British Columbia Research Council photograph)

Nervous System

Although teredinids are structurally so different from most mollusca, the main components of the molluscan nervous system are retained. These are paired concentrations of nerve cells termed ganglia, along with bundles of nerve fibres called commissures which join them. The paired ganglia are linked by nerve fibres termed connectives. In teredinids the pedal ganglion is located in the foot and is single rather than paired as in most mollusca. The cerebral ganglia are near the mouth and behind the anterior adductor muscle. The visceral ganglia are located near the posterior end of the visceral mass close to the narrowing of the auricles of the heart.

Circulatory System

The circulatory system in mollusca is relatively simple and consists of a single ventricle and two auricles contained in a pericardial cavity (Fig. 7). Except for vessels near the heart, the system is difficult to trace, consisting of vaguely defined sinuses rather than specific veins and arteries. Blood is received by the ventricle from the gills and driven into the aorta by rhythmic pulsations. The aorta divides into smaller short arteries which are connected to broad sinuses which supply slowly moving blood to various parts of the body for there are no capillaries as such. Deoxygenated blood is collected and carried either to the gills for re-oxygenation or to the organs of excretion. The blood is colourless but in *Bankia* the posterior adductor muscle, siphons and heart are red pigmented with myoglobin which stores oxygen for the adjacent tissues (Townsley et al. 1965). In some *Bankia* and *Teredo* the heart is near the anterior end of the body and in the former the ratio of heart to body length is 0.4 while 0.14 is the ratio for the latter (Turner 1966). However, in a 30 cm *Bankia setacea* the heart is located 22 cm from the head in a preserved specimen.

Digestive System

The digestive system in the Teredinidae is more complex than in most bivalves because of the need to process large quantities of ground wood from tunnelling activities. A mouth and short oesophagus leads into a stomach well described by Purchon (1960) and Morton (1978). Significant parts of the stomach are the right and left lateral caeca, digestive diverticula, crystalline style sac and the appendix (sometimes termed the caecum) which is more of an attachment than an integral part of the stomach (Fig. 7). The right and left caecum are the sites where ground wood and filtered planktonic food brought into the stomach along the food groove are directed to the digestive diverticulum. This is a gland with a series of connecting tubules of two types. One processes filtered food and the other wood fragments, both directed to appropriate sites by ciliary tracts. Most of the wood, however, is directed into the appendix where it is stored and possibly undergoes some processing for it has a very large surface called a typhlosole created by an extensive infolding of the walls. At times the caecum becomes quite large as it engorges with wood fragments, and extends posteriorly far into the infrabranchial chamber.

The crystalline style is an organ unique to mollusca. It is a gelatinous rod secreted in the crystalline style sac and in shipworms is located partly in the foot. The style is said to rotate in the sac and impinge on a gastric shield, a chitinous pad in the stomach wall opposite the sac. The style is relatively small in teredinids and likely has a minimal role in digestive processes. Another organ peculiar to shipworms is the gland of Deshayes of which there are 3 groups, one associated with the gill lamellae, one close to the umbonal area and another inside the afferent branchial vein. The glands are composed of dense concentrations of rod-shaped bacteria (Popham and Dickson 1973; Popham 1975) which Waterbury et al. (1983) have cultured. These have been termed symbionts.

From the stomach the intestine makes a small loop to the anterior before turning to the posterior to loop around and above the end of the appendix before moving to the anterior beneath the heart. In most bivalves the intestine passes through the heart but this is not so in shipworms. Moving forward it passes under and forward of the posterior adductor muscle, then dorsally over it and the anus opens into the long thin walled anal canal which is the conduit carrying faeces to the excurrent siphon.

Food

Among bivalves, shipworms are unique in possession of an ability to consume and metabolize two distinct types of food, each from a different source. Particulate planktonic food is taken in through the incurrent siphon to the infrabranchial chamber, filtered out by the gills and moved along the branchial groove to the mouth and stomach. Wood fragments from the boring activity provide the alternate food. The path from the foot to the mouth and stomach is short since the visceral mass is close to the tunnel face.

With both plankton and wood as possible nutritive sources the digestive processes of shipworms are complex and not completely understood. The relative contribution of each type of food is also unclear. The plankton is first digested extracellularly partly by enzymes from the crystalline style and then intracellularly in a specialized section of the digestive diverticula. Some wood may be treated in the stomach but most of it proceeds to the caecum where some digestion may take place probably with cellulase from the gland of Deshayes (Waterbury et al. 1983). After return to the stomach from the caecum further treatment occurs in the digestive diverticula of the stomach specialized for this form of food. Refuse from both types of diverticula is discharged through the anus into the anal canal which carries it to the excurrent siphon. A typhlosole valve presumably regulates the movement of unwanted material into the mid gut.

There is the question of the relative nutritive value of the two types of food, particularly since the nitrogen content of wood is minimal. Pechenik et al. (1979) and Gallager et al. (1981) demonstrated that *Lyrodus pedicellatus* can grow and reproduce under either phytoplankton supplied or phytoplankton deprived conditions. Recycling by-products through bacterial action was suggested as a means of supplementing the nitrogen component of the diet. Waterbury et al. (1983) isolated from the gland of Deshayes a bacterium believed to be the primary source of cellulolytic enzymes and with the ability to fix nitrogen.

Reproductive System

In *Teredo* and *Bankia* the sexes are essentially separate but there may be hermaphroditism at various times. The paired gonads are located in the infrabranchial chamber with openings (gonopores) into the suprabranchial chamber at the posterior end of the pericardial cavity, allowing sex products (gametes) to be discharged through the excurrent siphon.

As in most bivalves the gonad consists of a series of branching tubules called follicles on whose walls the germ cells are developed. Between spawnings the follicles become filled with nutritive Leydig tissue which is utilized and replaced by developing gametes. When ripe, the follicles are distended with either eggs or sperms (Fig. 16a, b, c) and in shipworms come to occupy a large part of the infrabranchial chamber to the point of dislodging other organs such as the caecum (appendix), which, according to Turner (1966), may be emptied at this time. This may imply dependence on planktonic food rather than wood during the breeding cycle. After spawning the follicles collapse and contain only a few generally isolated unspawned gametes termed ''relict''. These usually disappear by resorption and for a time sex determination is difficult or impossible. Soon, however, the sex celles (ovocytes or spermatocytes) appear on the follicle walls and the cycle is repeated. When ripe, the ova of *B. setacea* are 50 µm (0.05 mm) in diameter and the sperm heads about 5 µm (0.06 mm) in length. The ova of *T. navalis* are slightly larger. Egg production of most teredinids is in terms of millions.

Sexuality

In many species of bivalves and gastropods (snails) sex determination may be quite labile depending on either internal or external factors, or both. In *Teredo navalis* the initial gender is male (protandry = male first) which after initial spawning is followed by a female phase with possibility of further alternations (Coe 1941). However, some may retain the male phase indefinitely. *Bankia setacea* is also protandric with a

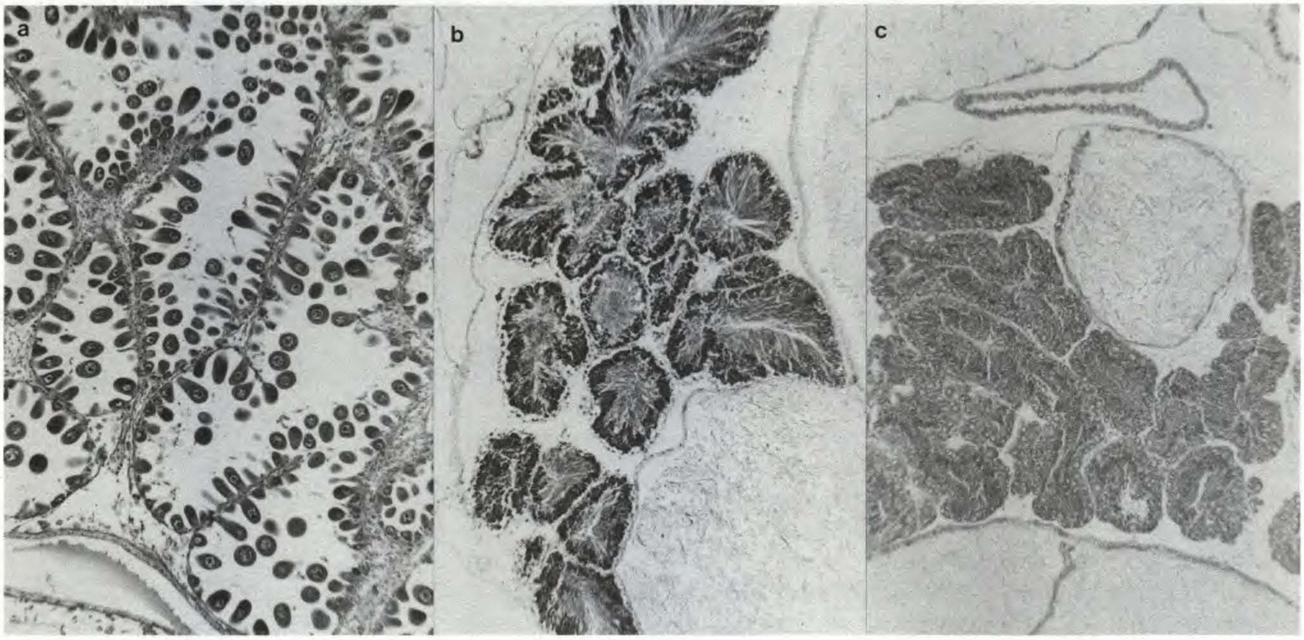

FIG. 16. Microscopic sections of the gonad of *Bankia setacea*. ×100. a, Female with ova on the follicle walls. b, Male with sperm in the centre of the follicles with darkly staining spermatogonia on the walls. c, Hermaphrodite with both ova and sperm.

similar rhythmic alternation of sexual phases, but hermaphroditism (Fig. 16c) may occur during the primary sexual phase. However, judging from the high level of breeding success the flexible sexuality is able to sort itself out satisfactorily to provide approximate equality in the sex ratio.

Breeding Process

Larval Development

Bankia setacea

In *B. setacea* both eggs and sperms are discharged freely through the excurrent siphon into open water where fertilization takes place. To ensure fertilization males and females must spawn at approximately the same time and mass spawning is typical of bivalves with external fertilization. The initial stimulus to spawn, providing the gametes are mature, is often a rapid change in temperature or salinity. Once an individual has spawned, adjacent animals are stimulated by chemicals in the sexual products as they are drawn into the body with other planktonic organisms. In hatchery situations, temperature change, sex products and various chemicals are used to stimulate spawning in bivalves.

After fertilization the embryo develops into a ciliated trochophore, succeeded by the formation of two forms of larval shells. The first is Prodissoconch I and from its shape is sometimes, not necessarily accurately, called the ''D'' or straight hinged stage, nearly indistinguishable from other bivalve larvae at this time (Fig. 17a–f). Typically, the granular surfaced Prod. I (120–130 μm long) is normally clearly marked off from the succeeding Prodissoconch II shell, which is concentrically marked and laid down by the mantle edge. During the early stages of this development the larva acquires a velum, a protrusile ciliated circular lobe used for food acquisition and swimming. Because of this organ the larva is called a veliger. The term veliconcha is also used to designate the larva after the deposition of Prod. II shell. The adult shell deposited after settlement and metamorphosis is termed dissoconch and is distinctly marked off from the prodissoconch. Soon after the formation of Prod. II a characteristic dark rim appears around the perimeter of the larval shell. At a length of about 150 μm (0.15 mm) nipple-like umbones appear, the larva, begins to assume a yellow colour, and is nearly circular in outline (Fig. 17c). Viewed through the shell valves, internal organs soon become defined but never as clear as in thinner shelled veligers of most other bivalves. At a length of about 200 μm (0.2 mm) the larva is still spherical in shape, a foot and an otocyst (sense organ) are visible as well as indications of the future gills. As growth proceeds the larva becomes thicker and can no longer lie flat on its side and the valve surfaces show fine concentric lines. The provinculum is now well developed and conforms to Rees's (1950) type *b* for the Adesmacea, with two strong teeth on the left valve and three on the right (Fig. 18). At a length of 245 μm (0.245 mm), height of 256 μm and 200 μm wide, the now walnut shaped larva must contact a suitable wood surface into which it can burrow (Fig. 17c). The free swimming planktonic period for *B. setacea* is estimated to be about 3 weeks at a temperature of 12–15°C (Quayle 1953, 1959a; Townsley et al. 1966).

Teredo navalis

Females of this species discharge ova from the gonad into the epibranchial chamber where they are retained and fertilized by sperm from adjacent spawning males brought in via the incurrent siphon and through the gill ostia. Early development takes place within this chamber, closely associated with the interlamellar spaces of the gills. This type of breeding is said to be ''larviparous''. The larvae are retained here until the straight hinged stage with a length of less than 100 μm when they are simultaneously released in a process called ''swarming''. The size of *T. navalis* larvae at settlement is approximately 250 × 220 μm (Sullivan 1948), but can vary with locality, as does the length of larval life which approximates that of *B. setacea.* As with most teredinid species, the larvae of these two species are quite similar in appearance throughout most of the larval period.

Larval Culture

In recent years there have been significant developments in the culture of marine bivalves with commercial hatcheries producing large quantities of oyster and clam seed. With similar techniques it is possible to culture shipworm larvae as demonstrated by Loosanoff and Davis (1963) and Townsley et al. (1966). Knowledge of this phase of shipworm biology may assist in the search for control measures.

Settlement

Isham and Tierney (1953) have described the swimming and crawling activities of *Lyrodus* larvae and those of *Bankia* are similar. Foot activity and shell placement resemble the sequence of digging movements of sand dwelling lamellibranchs Quayle (1949). Immediately after settlement the larval valves become

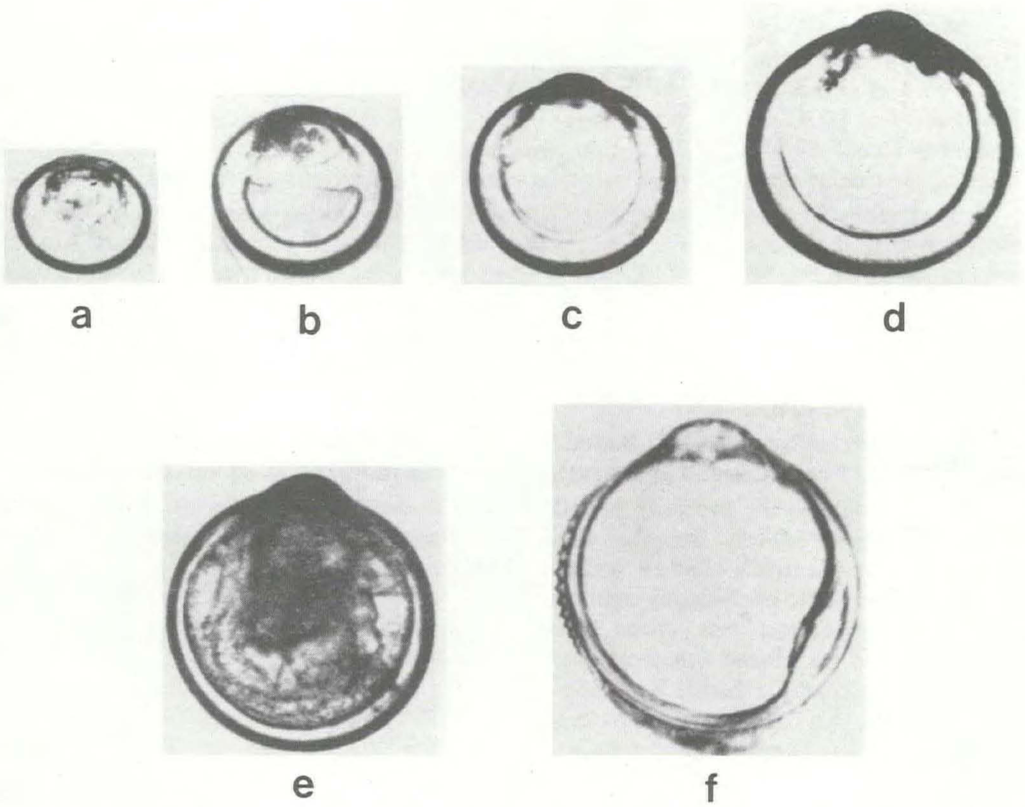

FIG. 17. a, *Bankia setacea*. Early veliger; length 100 µm; b, Larvae showing the development of the inner line; length 145 µm; c, Single valve, external view; length 175 µm; d, Single valve, external view; length 220 µm; e, Whole larva; length 220 µm; f, External (left) view of left valve of a newly settled spat with cutting teeth on the anterior edge and articular area on the ventral edge; length 245 µm (From Quayle 1953)

asymmetrical, as the posterior rim of the right valve atrophies to become little more than half the size of the left. The first cutting teeth develop on each anterior edge of the valves and 48 h after setting, there is a single row of 14 teeth, 14 µm in length. At a shell length of 20 mm there are 7 or 8 rows of teeth.

A newly settled and attached *Bankia* can bury itself completely in about 24 h and formation of the calcareous cone (Fig. 9) begins almost immediately. The 2 siphonal apertures separated by a bridge are fully formed in about 4 days and the whole cone completed within 7 days. The diameter of the incurrent and excurrent apertures are approximately 80 and 50 µm, respectively. The bridge between the apertures disappears in about a month.

After reaching settlement size the larvae of most bivalves, with few exceptions, must soon chance on an acceptable substrate or perish. On wood, in the case of shipworms, the larva is able to crawl about for short distances with the aid of a ciliated foot until a suitable site is located. Many larvae tend to seek slight depressions or crevices. Initially *Bankia* larvae attach with a byssus, a fine elastic thread originating from a gland in the foot, and which holds the larvae in place. Within 48 h after settlement, the first row of 14 cutting teeth, 12–14 µm in length, are formed on the anterior edge of the shell (Fig. 17f). The byssus probably holds the shell in place as it rocks back and forth to create the burrow. More rows of teeth are developed as tunnelling proceeds until deep enough for the formation of the calcareous cone. As this is going on, the internal structures are rearranged, particularly the formation of siphons and modification of the position and size of the adductor muscles, with the posterior enlarging greatly relative to the anterior, and assuming a dorsal position.

Settting Behaviour

A number of factors, operating alone or in combination with others, affect the settlement behaviour of shipworms larvae.

Current

Since lamellibranch larvae have limited swimming ability, and shipworms are not excepted, currents play a large role in distribution and ability to hold to a settlement substrate once striking it. During larval life, as demonstrated by Elsey and Quayle (1939) for Pacific oyster larvae (*Crassostrea gigas*) with approximately the same length of larval life as *Bankia setacea* currents can carry larvae as far as 80 km from the

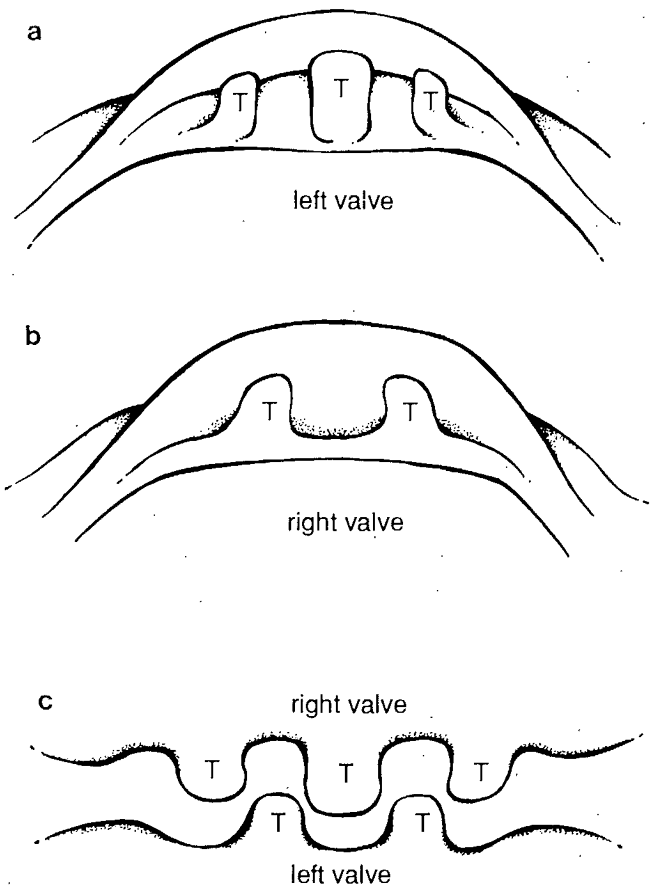

FIG. 18. a, Provinculum of left larval valve. (T-teeth); b, Provinculum of right larval valve; c, Interior view of provinculum. ×300.

spawning site. Scheltema (1971) found shipworm larvae in the open ocean, far from land. While water currents are mainly responsible for carrying larvae to a setting site (wood substrate) too rapid a current can prevent settlement. The normal tidal cycle presents a range of current speeds (or none at slack water, the time when the tide changes its direction). Doochin and Smith (1951) studied the effect of current speed on settlement of the larvae of the shipworm *Lyrodus pedicellata* and concluded current speeds above 1.4–1.8 knots (approximately 2 miles per hour) prevented settlement of this species.

Light

It is known that on submerged shorelines shipworm attack on wooden structures is greatest at depth near the mud line. This indicates there is an inducement for larvae to move to lower levels. Oceanographic factors such as temperature and salinity have an effect in certain situations, but as a reason, are not uniformly applicable. Light has been suggested as a probable cause. The larvae of a number of bivalve species undergo diurnal migrations, deep during daylight hours and near the surface at night. This has been shown for several species by Yasuda (1952) and Quayle (1953, 1969) and for shipworms by Isham et al. (1951) and Quayle 1959a (Fig. 19a, b). Owen (1953) observed settlement of *Teredo norvegica* to be concentrated in shaded areas of subsurface structures. Yet it is also indicated by various other studies (British Columbia Research Council. 1963, Tidelines, Vol. 5, No. 6.) that shipworm settlement occurs with greater frequency on the upper surface of test panels where light is more intense than on the underside. However, studies at the Biological Station in Departure Bay over 2 years showed attack to be approximately equal on both sides of the panels at 9 depths. The deepest 3 panels had 30% more attacks on the upper surface than on the lower (Quayle, unpublished data). The local situation, the type of panels, their arrangement and intensity of settlement may influence the selection of setting surfaces.

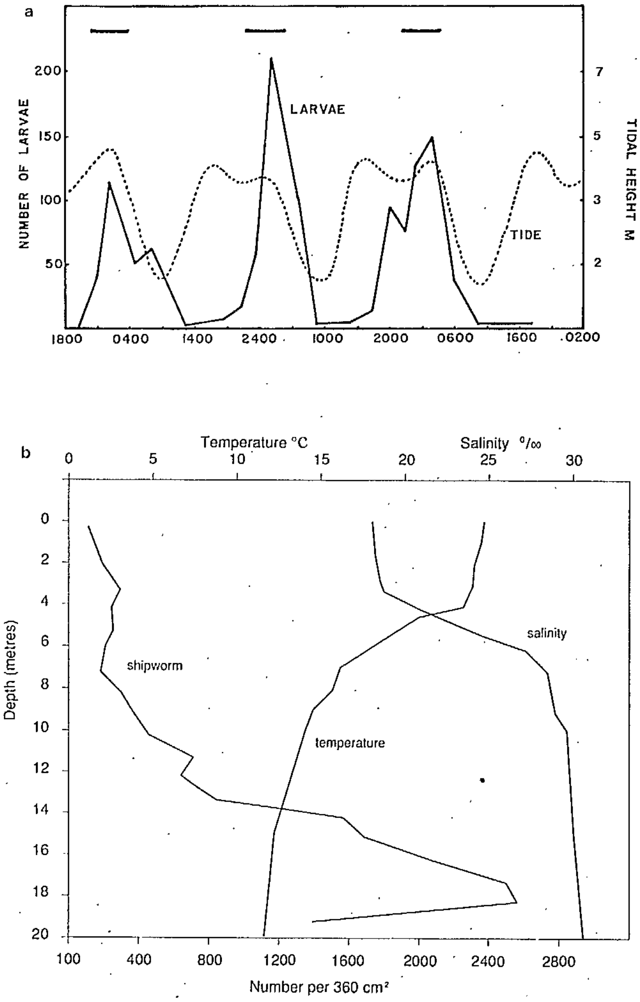

FIG. 19a. Occurrence of *Bankia setacea* larvae (total in samples from 6 to 7 depths) in Pendrell Sound, B.C., July 16–19, 1956. Bars denote periods of darkness (From Quayle 1959a); 19b. Vertical distribution of settlement of *Bankia setacea* on test panels in Pendrell Sound, British Columbia, July–August, 1966.

Temperature and Salinity

Temperature and salinity may affect settlement by restricting larvae to specific levels in the water column. In estuaries, where haloclines (areas of sharp vertical salinity change) and/or thermoclines (areas of sharp vertical temperature change) occur, the distribution of planktonic organisms is limited by these factors. At Steveston, British Columbia, about 10 km upstream from the mouth of the Fraser River, a tidal basin was formed to make a protected harbour. The basin made possible the subsurface intrusion and retention of seawater with a salinity and temperature suitable for *Bankia* settlement, survival and attack in the lower part of the basin. Previously the free flow of Fraser River water prevented attack (Tabata and LeBrasseur 1958).

Chemical

It seems obvious that shipworms would be attracted to wood and apparently this occurs. For shipworms, once contact is made by chance, it is retained initially by the wood's chemical constituents and then by byssal attachment. Harrington (1923–25) in a laboratory situation, provided shipworm larvae with wood on which they aggregated but failed to penetrate. This was before the techniques of the culture of bivalve larvae had been developed to a point where the behaviour in the laboratory paralleled that in the field. Other substances were tested but aqueous extracts of wood and malic acid were the most powerful attractants. Barger (1926–27) noted that further work at the Plymouth laboratory by C. M. Yonge confirmed chemotaxis of *Teredo* by wood extracts.

The British Columbia Research Council (1964) showed that *Bankia setacea* is able to live and grow in a synthetic medium based on a cellulose–agar mixture.

Surface Setting Angle

Of interest to students of invertebrate larval settlement patterns is the effect of the angle of the setting surface. This has been studied with oysters by a number of authors including Schaefer (1937) and Quayle (1969). To determine this for *Bankia setacea* a series of 8 wooden battens were arranged as spokes around a central hub at 45 degree angles (Quayle, unpublished data). The convention is to consider the under horizontal surface as 0 and the upper horizontal as 180. The lower and upper surfaces of the diagonals are considered 45 and 135, respectively. Both vertical surfaces are considered as 90. This study in Departure Bay in 1971–72 clearly indicated the upper horizontal or nearly horizontal surfaces were favoured (Table 2 and Fig. 20).

Settlement on upper surfaces is confirmed by British Columbia Research Council studies (1960, Tidelines, Vol. 2, No. 2), but distinct from another study in Departure Bay by Quayle (unpublished data) where the attack over a two year period was equal on the upper and under sides of panels over a range of depths (page 14).

TABLE 2. Settlement of *B. setacea* on wooden battens held at various angles, Departure Bay, 1971 – 72.

Angle	Mean number per side
0 (under horizontal)	20
45	20
90 (vertical)	10
135 (upper diagonal)	110
180 (upper horizontal)	153

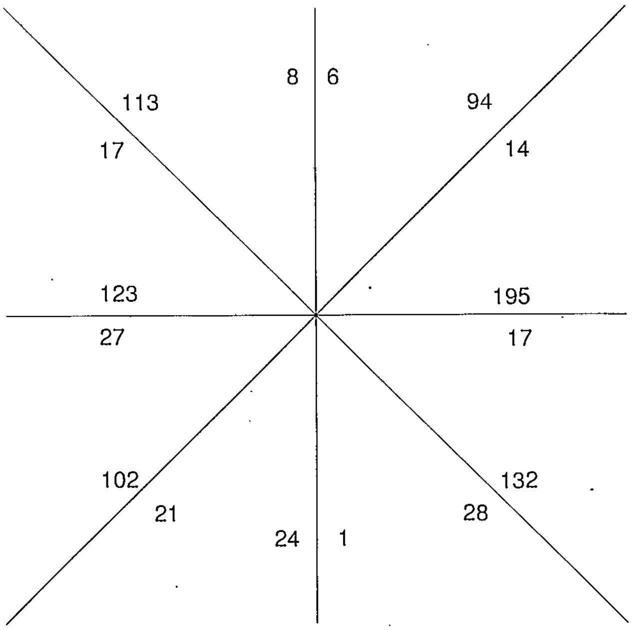

FIG. 20. Settlement of *Bankia setacea* on fir battens held at various angles. Departure Bay, British Columbia, 1971–72.

Fouling

Fouling relative to marine wood borer attack is considered to be other sessile invertebrate animals or algae that also use and may compete for space on submerged objects. Fouling organisms may compete with the marine borers in several ways. If settlement of the fouling organism, i.e. barnacles, precedes that of the borer their settlement is prevented owing to the space already being occupied. Other similar preventive organisms include oysters, mussels, hydroids (Fig. 21), colonial tunicates (sea squirts), bryozoans and algae. If settlement of these organisms occurs after that of the borers they may overgrow the borer entrance and cause mortality (Fig. 54). Some of these so-called fouling organisms, depending on the point of view, are oysters and mussels which are filter feeders which will accept shipworm larvae as food organisms, thus

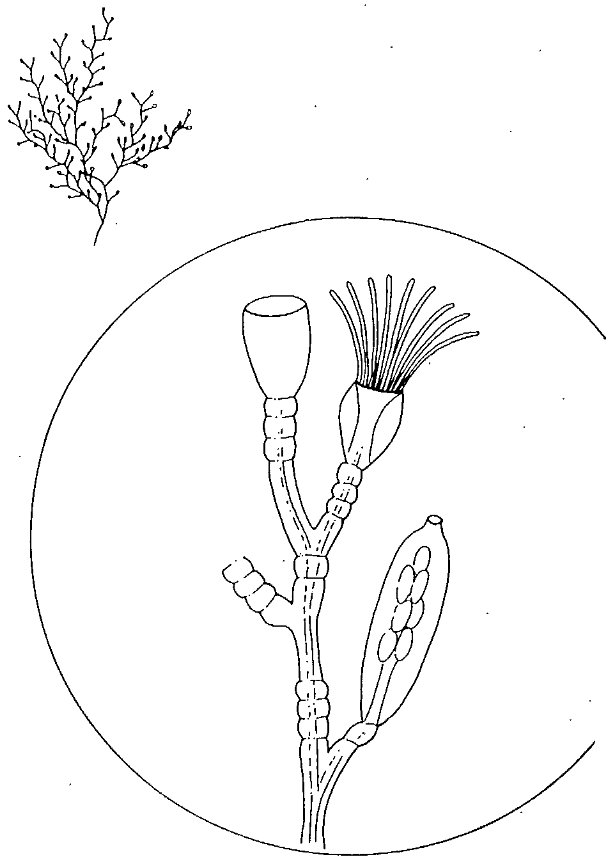

FIG. 21. The hydroid, *Obelia*. ×12.

preventing the approach to a possible settlement area. Gribbles are too large to be food items for filter feeders but fouling cover is often the habitat of polychaete annelids (seaworms) which are potential predators on these and other small crustaceans.

Pollution

The main types of marine pollution are sewage and industrial. Sewage pollution is of concern mainly to public health and generally has little impact on marine animals unless there is a large chemical component, solids deposition, or salinity decrease. The typical sewage outfall should have little or no effect on marine borers in the general area. Land drainage, often with a large agriculture fertilizer component, can affect the quantity and quality of plankton which forms part of shipworm nutrition.

Industrial pollution, however, is another matter and the discharge of toxic chemicals or wastes may affect shipworms. Either the toxic materials alone or the secondary effects such as the reduction of the oxygen content of the water, changes in hydrogen ion concentration or the development of noxious gases such as hydrogen sulphide may cause problems.

In British Columbia there is no recorded account of pollution–shipworm interaction although this may occur in the region of log dumps where hydrogen sulphide emissions may cause anaerobic conditions from bark deposition on the bottom.

Breeding Period

There have been a number of studies on the breeding periodicity of *Bankia setacea* in British Columbia, including those of Fraser (1923, 1925, 1928), White (1929c), Neave (1943), Black and Elsey (1948), Quayle (1956, 1965a), and Bohn (1975). Fraser (1925), in a coastwide study, indicated a spring and early summer months breeding period although some may occur throughout the year. White (1929c) showed 2 breeding seasons in Departure Bay, one in March and a heavier one in October.

Neave (1943) found severe attacks occurred from August to January, with some breeding throughout the year at several stations along the southeast coast of Vancouver Island.

The results of Quayle (1965a) experiments in the same area showed peak settlement in the fall and winter (Fig. 22), but, based on larval abundance in Ladysmith Harbour, the main breeding occurred there in early spring (Fig. 23). Black and Elsey (1948) in a coastwide study found considerable variation in the time of peak attacks from station to station. They considered a combination of 5–22 ‰ salinity and a temperature of 4 to 16°C were conditions for intense shipworm attack. Quayle (1959a), on the basis of larval studies in Ladysmith Harbour, showed a main spring breeding period when the 1 m water temperatures was about 10°C (Fig. 24). However, breeding in Pendrell Sound, East Redonda Island can occur when 1 m water temperatures are in the 20°C range, likely owing to spawning in populations in deeper waters where temperatures are lower. A later panel study in Departure Bay confirmed the Black and Elsey (1948) conclusion of a fall and winter breeding there from September to January when water temperature ranged from 15 to 6°C (Table 3). The British Columbia Research Council, in connection with other shipworm work, carried out extensive breeding studies at stations between Ensenada, Mexico and Ketchikan, Alaska between 1958 and 1976. Settlement was monitored monthly with test blocks hung from floating platforms at 9 depths to 7 m. Bohn (1975) analyzed these data on an annual basis for 5 Strait of Georgia stations between 1961 and 1974. This analysis showed settlement intensity was high during the early years of the study but declined significantly after 1967, with the lowest attack in 1973.

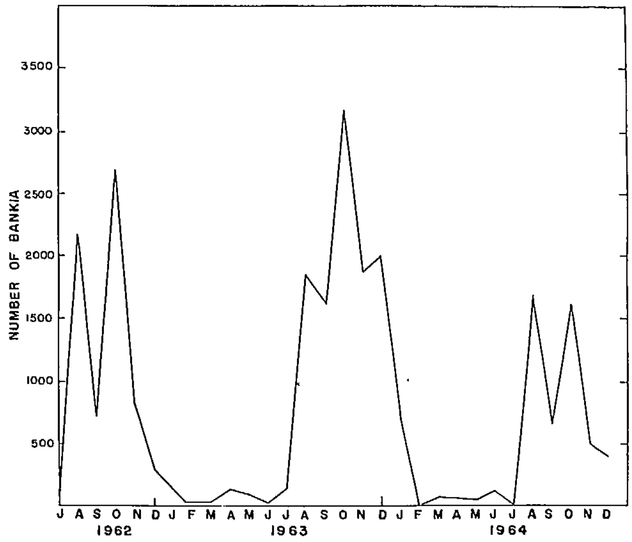

FIG. 22. Seasonal intensity of attack by *Bankia setacea* on fir panels, 1962–64. Combined data from all depths and all stations, Cowichan, Crofton and Nanaimo. (From Quayle 1965a)

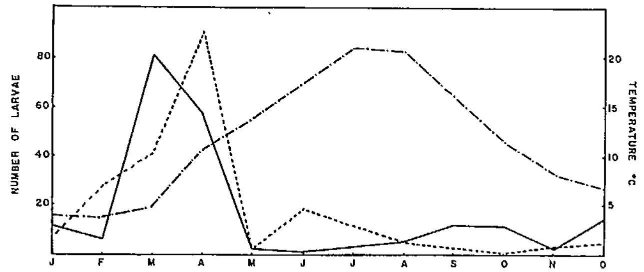

FIG. 23. Seasonal abundance of the larvae of *Bankia setacea* in Ladysmith Harbour. (———) 1951; (– – – – –) 1955; (– · – · –) thermograph temperature, 0.91 m below the surface. (From Quayle 1965a)

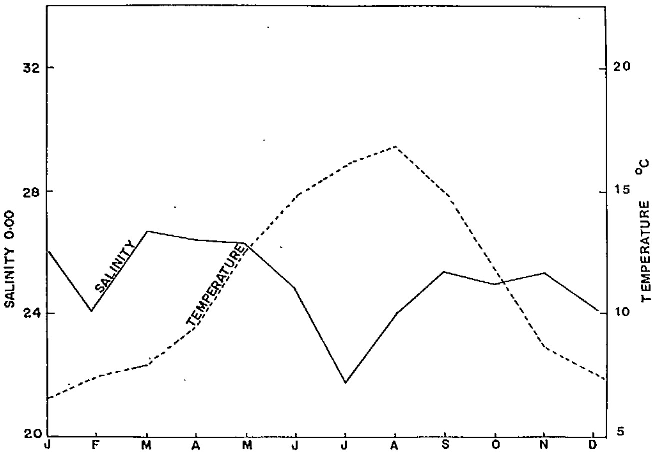

FIG. 24. Mean monthly temperature and salinity, Departure Bay, British Columbia, 1963. (Data from Hollister and Sandnes 1972)

TABLE 3. Seasonal attack of the wood borer *B. setacea* on fir panels at Departure Bay, 1981 – 83.

Date	Total attack	Mean monthly surface temperature
Aug.–Nov. 1981	2 700	12.6
Dec.–Feb.	184	5.9
Mar.–Apr.	3	8.2
May–June	11	10.6
July–Aug.	35	16.9
Sept.–Oct.	6 408	12.8
Nov.–Jan. 1982	4 264	6.6
Feb.–Mar.	28	6.4
Apr.–June	116	11.8
July–Aug.	337	17.0
Sept.–Dec.	6 115	9.9

There was no correlation between these events and temperature or salinity data nor could the data be fully explained by an improvement in log or wood debris handling techniques. The general conclusion is that *Bankia* breeding may occur during any month of the year in British Columbia and that intensity of attack is variable. All authors agreed this species is a low temperature breeder but timing varies within the breeding temperature range. Breeding can occur throughout the year at greater depths and may be an explanation for extended seasons in some areas.

Forecasting Settlement

Forecasting the time and intensity of shipworm settlement may be accomplished either from a plankton sampling program or from the trend in the actual settlement on test panels or blocks, the method used successfully for many years by the British Columbia Research Council.

Plankton Sampling

A number of methods to sample bivalve larvae have been developed, mainly for oyster spatfall forecasting (Quayle 1980, 1988; Quayle and Newkirk 1989) which may be adapted to shipworms. The main instrument is the plankton net made from bolting silk or nylon which has a specific and consistent mesh size, normally 0.65 mm for bivalve larvae.

For a relatively non-quantitative determination of the presence of bivalve larvae, a 5-min surface tow with the net often suffices. To determine the number of larvae per unit volume of water sampled requires an accurate measure of the volume filtered. Other than with pumps and water meters, an effective method of relative simplicity is the vertical tow. This overcomes the problem of diurnal variability in the vertical distribution of shipworm larvae (Quayle 1959a) and provides a measure of the volume filtered. The weighted plankton net is lowered to a specific depth and then drawn to the surface at a moderate steady pace.

With the diameter of the mouth of the net and the vertical distance, the volume of water filtered may be determined. The larvae are most readily counted in a special cell (Quayle 1980) and the number per unit volume calculated.

To separate possible discrete spawnings, the larvae are usually counted into size groups, for shipworms: straight hinge (circa 100 µm): mid umbo (circa 150 µm) and advanced (200+). Knowing the approximate length of larval life (about 3 weeks for *B. setacea*), although dependent on temperature, the approximate settlement date for a specific group of larvae may be approximated. With experience in a specific area, the intensity of the attack can be estimated from the number of advanced stage larvae. For the Pacific

MARINE BORER BREEDING-PACIFIC COAST August, 1970

Numbers per square foot to:

	2 ft	10 ft	20 ft	
				ALASKAN WATERS
	0	17	32	1. Thorne Bay
	0	7	81	2. Ward Cove
				QUEEN CHARLOTTE ISLANDS
	110	301	287	3. Shannon Bay
	20	184	219	4. Juskatla
	0	0	0	5. Skidegate
				VANCOUVER ISLAND
	0	4	18	9. Kildonan
	0	0	22	10. Honeymoon Bay
	0	26	118	11. Crofton
				SOUTHERN B. C. COAST
	0	66	273	12. Teakerne Arm
	85	360	902	13. Okeover Inlet
	0	0	42	14. Blind Bay
	55	329	570	15. Earls Cove
	0	77	708	16. Gambier Island
	0	70	783	17. Horseshoe Bay
	15	21	41	18. Vancouver
				PUGET SOUND
	0	0	2	20. Oakland Bay
				SAN FRANCISCO BAY
	40	40	37	21. Alameda
*	115	373	229	
	10	9	6	22. San Francisco
*	0	4	3	
				SOUTHERN CALIFORNIA
	0	0	7	23. Los Angeles Harbor
*	0	0	0	

* Limnoria

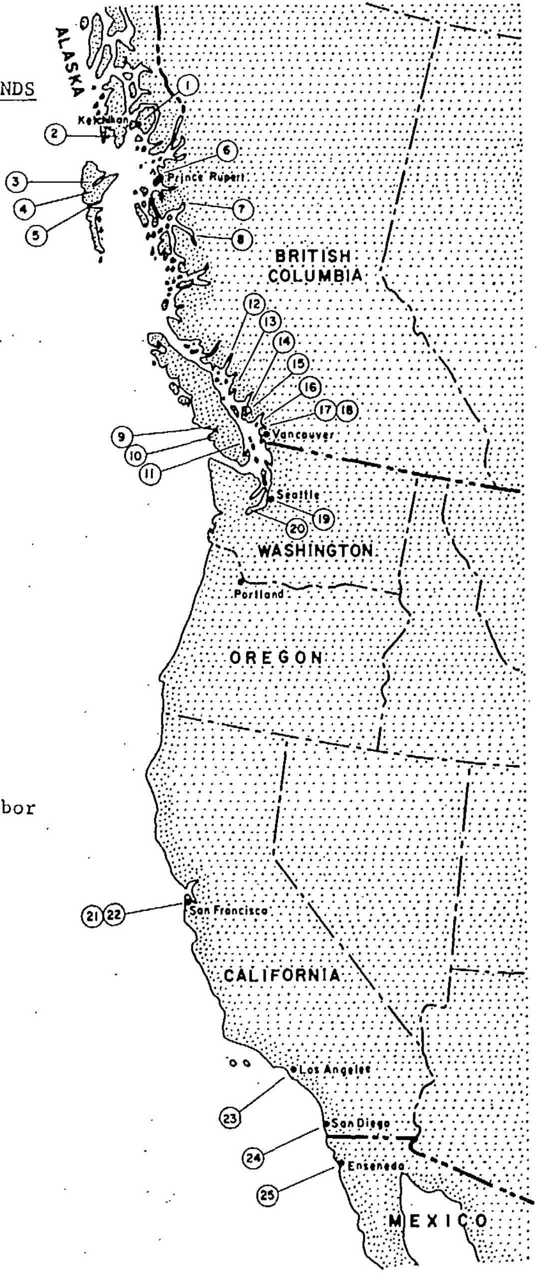

FIG. 25. Marine borer sites sampled by the British Columbia Research Council between Alaska and California. (From Tidelines, 1969. 11, No. 1)

oyster (*Crassostrea gigas*) in Pendrell Sound one advance stage larva per 4 L provides a settlement of about one spat per 15 cm². In the same area up to 5 shipworm larvae per litre have been taken.

Test Panels

The British Columbia Research Council was active for many years in marine borer research and control. One important phase was to provide the logging industry with forecasts on the timing and intensity of bankian settlement. This covered a number of sites between Alaska and California (Fig. 25). The forecasts were based on knowledge of the breeding habits of this species and results from the attack on test blocks placed at 1, 2, and 6 m depths and replaced at monthly intervals. Studies also determined that counts from test blocks gave a clearer indication of numbers of larvae reaching an adult stage in the logs than the larval numbers attacking the logs (1966, Tidelines, Vol. VIII, No. 3). The results were presented to the industry for one and two months ahead as shown in Table 4 at monthly intervals. The reports also included information on the biology and control of marine borers, both from the Research Council's own studies and elsewhere. Accuracy of the forecasts (1967, Tidelines, IX, No. 10) was analyzed for the period 1965 to 1967 inclusive, showing little difference between 1 and 2 month forecasts (right or wrong). In Table 5 is given the degree of accuracy in 1967 based on deviation in the forecast attack intensity (0 — clear: L — low: M — medium: H — high) from the actual. An M prediction and an actual of L illustrates a one place error.

The forecasts allowed the forest industry to take preventive or ameliorative action relative to the movement of logs.

Letter designations for level of attack
0 — clear — none
L — light — 1–9 per 900 cm² (1 ft²)
M — moderate — 10–99 per 900 cm²
H — heavy — 100 or more per 900 cm²

TABLE 4. Forecast: February 1965.
(0 = Clear, L = Light, M = Moderate, H = Heavy.)

	March			April		
Station	2 ft	10 ft	20 ft	2 ft	10 ft	20 ft
Ketchikan	0	0	L	0	0	L
Watson Island	0	0	0	0	0	0
Call Creek	0	0	L	0	0	L
Teakerne Arm	0	0	L	0	0	L
Fair Harbour	0	0	L	0	L	L
Tahsis	0	0	L	0	0	L
Kildonan	0	0	L	0	0	L
Earls Cove	0	0	L	0	0	L
Burrard Inlet	0	0	L	0	0	L
Crofton	0	0	L	0	L	L
Nitinat Lake	0	0	L	0	0	L
Elliot Bay	M	H	H	M	H	H
Tacoma	M	H	H	M	M	H
Alameda (teredines)	0	L	M	0	L	M
(*Limnoria*)	M	M	M	H	H	H

TABLE 5. Degree of accuracy in 1967 forecasts.

	Forecasts	%	% expected from randomness
No error	158	51.7	25.0
One place error	109	35.6	37.5
Two place error	38	12.4	25.0
Three place error	1	0.3	12.5

Growth

Shipworm growth studies in British Columbia have been confined to *Bankia setacea*.

Growth in shipworms is quite variable, dependent on intensity of the attack (population density), species of wood, site, depth and season. Originally growth was studied by measuring sacrificed animals from wood exposed for increasing lengths of time. Now the accepted technique is based on sequential X-ray photographs since burrows with shell lining are well delineated (Fig. 26). Apparently limited exposure to X-rays affect neither growth or longevity.

Kofoid and Miller (1927) studied *Bankia* growth rate in San Francisco Bay and found a mean rate of 23–63 mm per month depending on age. Johnson and Miller (1935) in a fouling study at Friday Harbour, Washington, also with excised animal measurements, showed a rate of 10 mm per month where summer water temperatures seldom exceed 12°C, considerably less than in the Strait of Georgia.

Haderlie and Mellor (1973) examined the growth of *Bankia setacea* at Monterey Bay in California with the X-ray technique. Here surface water temperature ranges between 11 and 17°C with an annual mean of about 13°C, lower than in the Strait of Georgia. The salinity was about 33 ‰. Under crowded conditions this study showed a mean monthly growth rate of 43 mm per month while in an uncrowded situation the mean was 74 mm. In similar conditions an individual length of 976 mm and a diameter of 15 mm was attained in 9 months.

FIG. 26. X-ray photograph of a fir panel (2 × 10 × 20 cm) attacked by *Bankia setacea* in Ladysmith Harbour from August to December, 1952. (Photograph by H. Duncan. From Quayle 1956)

Quayle (1956, 1959a) studied *Bankia* growth in Ladysmith Harbour, British Columbia between November 1954 and June 1955. Fir panels 30 cm × 14 cm × 1.5 cm were covered with fibreglass except for the ends. This permitted entry only in those areas, prevented excessive attack, and allowed tunnelling with the grain, likely giving optimum boring rates. The panels were submerged a metre below the surface and X-rayed at monthly intervals. Measurements were made of length as shown on the radiographs, diameter of the burrow just posterior to the shell valves, length of the pallets and counts of the number of cones (Table 6, Fig. 7). These data were calculated from measurements of the first 27 specimens, which by July had been reduced to 5 by mortality. Shipworms in the panel with highest infestation died in 6–8 months.

The mean monthly length increment (27 animals) is shown in Fig. 27 along with the temperature regime at that time. The mean monthly growth in length of three selected specimens is shown in Fig. 28. The mean monthly growth in length, diameter and pallet length is given in Fig. 29. Results indicate a potential monthly growth of 122 mm and a length of 610 mm in about 5 months.

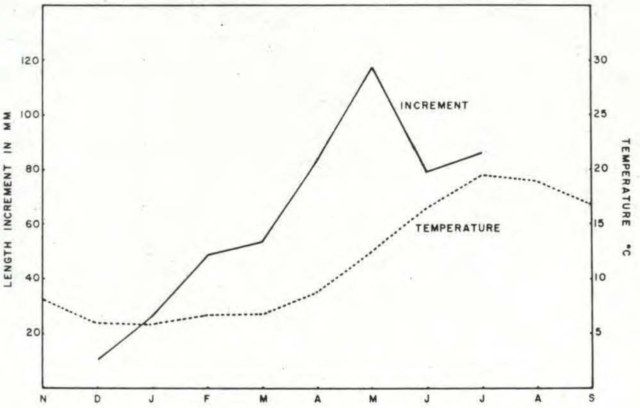

FIG. 27. Mean monthly length increment of *Bankia setacea*, Ladysmith Harbour, 1954–55. Temperature by thermograph, 0.91 m deep. (From Quayle 1959b)

TABLE 6. Growth rate of *Bankia setacea* in Ladysmith Harbour 1954–55. (From Quayle 1959b).

Date	Mean monthly temp. (°F)	Mean body length (mm)	Range	Mean body diameter (mm)	Range	Total pallet length (mm)	Range	Pallet stalk section length (mm)	Pallet blade section length (mm)	Stalk blade ratio	No. of cones	Range	No. of animals
1954 Dec.	45.0	10.5	5–17	2.2	1.5–2.5								27
1955 Jan.	43.0	36.9	12–66	4.5	3.0–6.0								27
Feb.	43.0	86.4	33–139	6.1	5.0–8.5	14.4	8–20	5.7	8.7	.660	5	4–8	27
Mar.	44.0	139.6	61–207	7.6	5.5–9.0	19.0	12–25	7.6	11.5	.669	7	5–8	27
Apr.	46.0	223.1	130–331	9.3	8.5–10.0	26.2	19–32	9.2	17.0	.543	9	7–11	27
May	54.0	340.3	255–465	10.1	9.0–12.0	34.4	32–40	12.8	23.0	.556	12	10–14	17
June	62.0	419.4	300–565	10.4	9.0–12.0	41.7	37–48	14.2	27.5	.517	15	14–17	13
July	66.0	505.0	430–570	12.0	12.0	50.0	48–59	16.0	34.0	.467	19	18–22	5

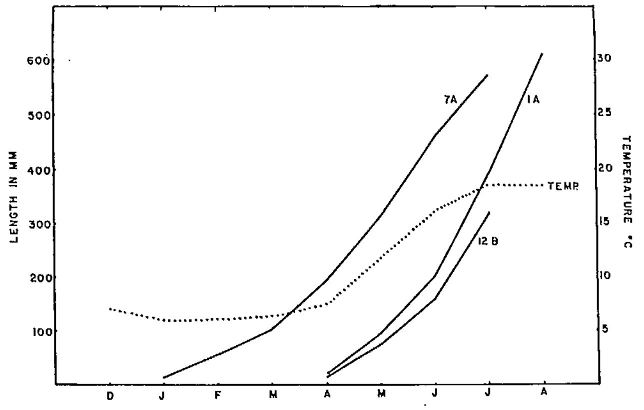

FIG. 28. Monthly growth in length of three selected specimens (1A, 7A, 12B) of *Bankia setacea*, Ladysmith Harbour, 1954–55. Temperature by thermograph 0.91 m deep. (From Quayle 1959a)

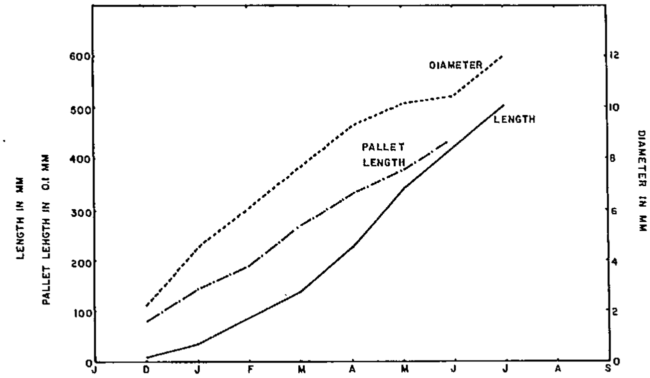

FIG. 29. Monthly growth in length, diameter, and pallet length of *Bankia setacea*, Ladysmith Harbour, 1954–55. (From Quayle 1959b)

The British Columbia Research Council (1964, Tidelines, Vol. 6, No. 2) studied the growth of *Bankia* in Vancouver Harbour and produced the growth curve shown in Fig. 30, in which is included, those for Ladysmith and Monterey, and although the conditions of the studies are not strictly comparable, the similarities are notable. In another Research Council experiment the length of *Bankia* ranged from 65 to 92 cm with a mean of 80 cm in 21 months. The largest specimen reached a length of 120 cm and a diameter of 1.5 cm at the head.

The British Columbia Research Council (1963, Tidelines, Vol. 5, No. 3) also studied the length of life of *B. setacea* by exposing individually isolated narrow strips of wood in a bundle at a depth of 8 m in Vancouver Harbour. The strips were examined at intervals over 21 months; 30% died between 17 and 21 months, while more than 25% survived for 21 months. It seems the maximum life expectancy for this species is about 2 years.

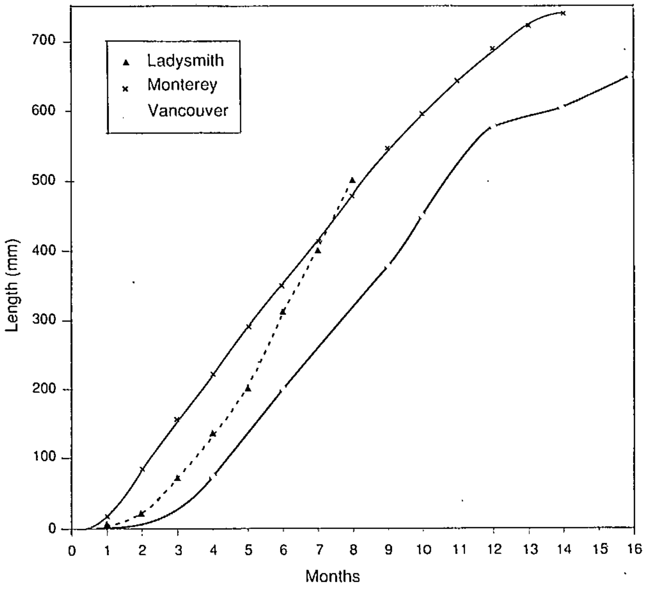

FIG. 30. Mean monthly growth rate of *Bankia setacea* at Ladysmith, Vancouver and Monterey. (From B.C. Research Council 1964; Quayle 1959b; and Haderlie and Mellor 1973)

Tunnelling

Miller (1924) first gave a reasonable explanation and description of how shipworms tunnel. He was able to do this partly by actual observations through a glass placed over an excised tunnel head of an active specimen. Later, Board (1970), with sophisticated X-ray equipment, elaborated on Miller's description. Board contended the burrows made by shipworms are larger than the dimensions of the shell valves used to make them and since the burrows are not uniform in diameter, they should be described as tunnels, rather than "burrows" or "borings".

The shipworm shell and muscular system have been described and the drilling is accomplished by their combined operation. With aid of the foot, cephalic hood and hydrostatic pressure, the shell valves are pressed against the tunnel head. With the posterior adductor muscle relaxed, the anterior adductor muscle contracts to bring the anterior part of the valves, hinged on their condyles, as close together as the position of the foot allows. This is an arc of about 20°. The powerful posterior adductor muscle then contracts, causing the anterior denticulated area of the valves to flare outward and backward against the tunnel face, enabling the denticles to perform their cutting action. This contraction brings the posterior edges of the auricles close together but the outward flare of the posterior edges prevents pinching of the body. After each cycle of the two adductor muscles, the foot repositions the shell and this change can occur 8–12 times per minute. Through this process the shipworm is rotated through 260° and then reversed, so the whole operation turns through 480°, occupying about 20 min. (Miller 1924).

Board (1970) suggested the structure of wood itself in the form of tracheids which are water conductors, is a factor in shipworm tunnelling. They assist in providing water which softens wood, in maintaining hydrostatic pressure along with lubrication and cleansing of the cutting faces of the shell valves. The tracheids are aligned in a longitudinal direction along the wood grain (spring wood) and the availability of water in this area facilitates tunnelling. Water from the suprabranchial chamber supplies water to the tunnel head and is removed from there, when necessary, by forcing it ahead through the tracheids. Also wood is softened not only by the uptake of water but also by the action of fungi and cellulolytic bacteria, both present in sea water. It is thought shipworms are sensitive to changes in wood consistency caused by alteration in the water content. Water content of wood nearest the wood–water interface is high and sensing this may be one reason teredinids seldom, if ever, break through this interface.

Another factor in tunnelling is the ability to change direction, which may occur when nearing the wood–water interface or another tunnel (Fig. 11). They can block off the vacated tunnel with a calcareous lining. Shipworms are able to pass through laminations if the spaces between layers are small.

It is often thought the tunnelling activity of shipworms can be heard, but not so, even with sophisticated sound detecting equipment (1964, Tidelines, 6, No. 3).

Timber Species and Borer Attack

Ever since marine wood borers became a problem to wooden marine installations and vessels, there has been a worldwide search for timber naturally impervious to both teredinid and limnorid wood borers under all conditions of temperature and salinity. Clapp and Kenk (1963) listed over 300 references to timbers tested for shipworms resistance. In spite of this vigorous search and subsequent testing, only a few timber species have qualified but their availability and rarity makes their use as timber impractical. There is wide variation in susceptibility to attack based partly on wood hardness, content of chemicals such as resin, silicate, and alkaloids. Most of the hardwoods and chemically toxic or highly resinous timbers occur in the tropics and this is where the search has been centred. However, as shown in Fig. 31 conifer knots are not immune to attack by *Bankia* but are too hard for gribbles. Available timbers known for a high degree of resistance to borer attack are the Greenheart (*Nectandra*) of Guyana and the Australian Jarrah (*Eucalyptus marginata*). A greenheart was tested in British Columbia for 6 months in 1953 and, while the Douglas fir controls were heavily attacked, the test timbers were free of borers. *Eucalyptus globulus* gave good service in Nanaimo Harbour for about 40 years (Bramhall 1960). Of the tropical woods, Cocobola (*Dalbergia retusa*) with a high oil content is considered to be one of the few borer resistant timbers. One chemical extract from this tropical tree prevents calcification in developing shipworms and is thus an effective control for the mollusc but not for gribbles. Another chemical from the same tree is partially effective against gribble activity and when the two chemicals are combined there is an effect on both types of borers (Boyle 1988). However, production of these chemicals as extracts is costly.

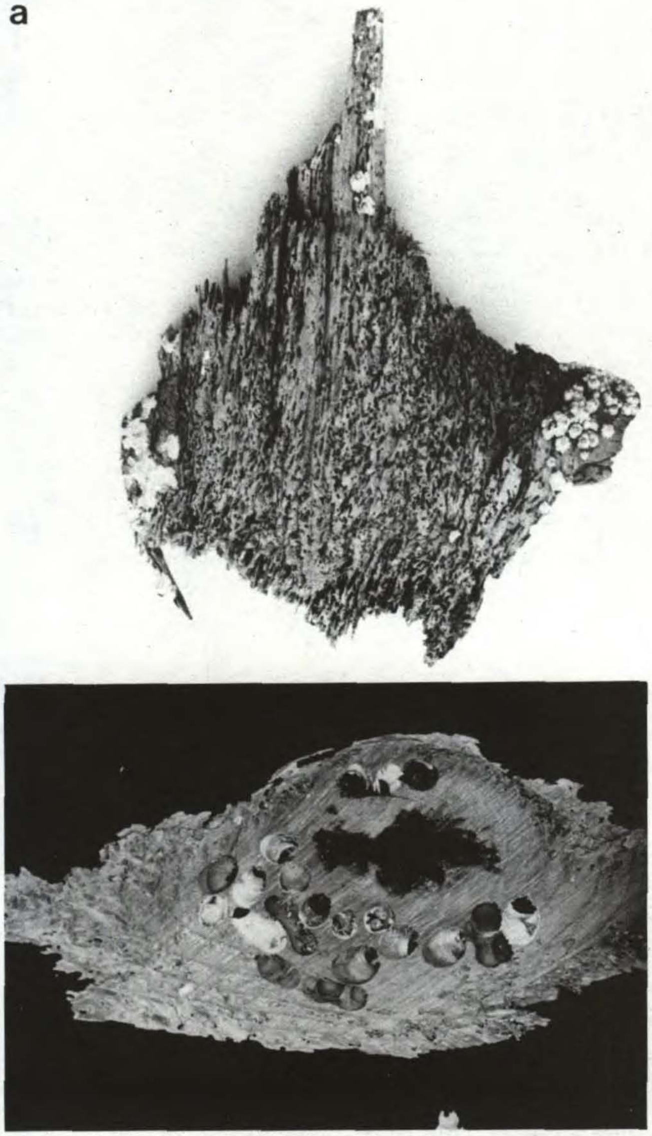

FIG. 31. Cedar knot eroded (a) externally by *Limnoria* and (b) internally by *Bankia*.

TABLE 7. Cumulative attack by months on British Columbia wood species by *Bankia setacea* at a depth of 8 m in Vancouver Harbour, B.C. (From Tidelines, 1963, Vol. 5, No. 8.)

Species	Months				
	2	3	4	5	Avg.
Western Red Cedar (*Thuja plicata*)	132	100	97	122	113
Yellow Cedar (*Chamaecyparis nootkatensis*)	209	82	95	125	128
Spruce (*Picea sitchensis*)	133	79	70	97	95
Balsam (*Abies grandis*)	250	105	102	81	135
Hemlock (*Tsuga mertensiana*)	180	76	139	133	130
Cottonwood (*Populus trichocarpa*)	203	82	93	170	137
White Pine (*Pinus monticola*)	164	116	159	97	134
Alder (*Alnus rubra*)	238	138	170	141	172
Birch (*Betula papyrifera*)	265	86	212	131	173
Maple (*Acer macrophyllum*)	266	137	165	90	165
Oak (*Quercus garryana*)	258	68	155	74	139

Juniper (*Juniperous scopulorum*) has been tested in Departure Bay and while not completely impervious to gribble attack was significantly less than the spruce control. Juniper was also tested against *Bankia*. After 6 months of exposure there were only 6 *Bankia* on 600 cm^2 of surface, indicating a modest resistance of this species. Spruce controls were completely riddled and finger crushable.

The British Columbia Research Council (1963, Tidelines, Vol. 5, No. 9) also studied the weight loss suffered by the same group of woods by exposing blocks for various lengths of time up to 7 months. Alder, yellow cedar, hemlock and white pine suffered approximately 50% loss expressed as a percentage of the original oven dry weight. Maple had least weight loss at 12% followed by oak at 21%. The others varied between 37 and 48%.

Bark is often considered resistant to borer attack and while true to a certain extent, it is not completely so.

The British Columbia Research Council (1963, Tidelines, Vol. 5, No. 10) examined the difference in attack by *Bankia* on spring (soft) and summer (lignified and hard) wood obtained from fir and hemlock logs felled in late summer. The summer wood was exposed on one side of a log section by removing the bark. The other side was planed smooth to expose a surface of both spring and summer wood. The planed surface with both spring and summer wood had 92% of the total attack; the softer spring wood was largely neglected. The suggestion is that timber felled in spring is more susceptible to shipworm attack than that cut later in the year.

The British Columbia Research Council also studied the relative attack on 12 species of British Columbia timbers by exposing 10 cm × 10 cm × 30 cm blocks in Vancouver Harbour for various periods beginning November 1959 (Table 7). The blocks were examined at monthly intervals to determine the cumulative attack. The results indicated all species are susceptible to *Bankia* attack and that the difference compared to attack on Douglas fir, was not significant from a practical standpoint. The comparative attack on Douglas Fir (*Pseudotsuga taxifolia*) was 100.

Parasites

Parasites of shipworms have not been well studied and none reported from British Columbia, probably because of no specific search. Tropical species appear to be more prone to harbour parasites than those in temperate waters. A variety of bacteria have been found and ciliated protozoans (*Boveria*) are quite common in the gills and mantle cavity of a variety of shipworm species. Trematodes occur as well as turbellarians although the latter may be mainly adventitious. Copepod crustaceans such as *Teredicola* occur in several species of shipworms in Hawaii and elsewhere.

Hillman et al. (1982) found a haplosporidian parasite of the genus *Haplosporidium* in *Teredo navalis* in Barnegat Bay, New Jersey with a 40% level of infection. The haplosporidian also occurred in the introduced species *Teredo bartschi*, Clapp 1923, and *Teredo furcifera* von Martens 1984, possibly the vectors for the parasite, but not in the native *Bankia gouldi* Bartsch 1908. It was considered a high infection rate followed by a decrease in shipworm abundance suggests circumstantial evidence the parasite may be a factor in the control of *Teredo* populations in Barnegat Bay.

The shipworm haplosporidum is similar in some respects to *Haplosporidium nelsoni*, a devastating oyster (*Crassostrea virginica* Gmelin 1791) pathogen.

Shipworm Distribution and Dispersal

Once ensconced in its tunnel a shipworm cannot escape the confines of that enclosure. Distribution and dispersal of the species is dependent either on the wood in which it is encased, floating or being moved to another site or by movement of the free swimming larvae. Adult movement is usually accomplished through the medium of wooden vessels, drifting wood, or in seed cases of tropical palms. In British Columbia log transport and storage and timber for construction, are important in maintaining and propagating large populations of marine wood borers in log booms, dead heads, sunken logs (sinkers) and other wood debris. River floods and freshets also bring down to the sea large quantities of timber. This is not normally merchantable so it may drift for long periods before becoming beach stranded where it may remain indefinitely unless forming an obstruction worthy of removal (Fig. 32). While there is a well-developed system of salvage for logs inadvertently lost by storm or other means, the effort is concerned only with merchantable timber. This can amount to about 10 000 m^3 of wood per month. The British Columbia Debris Control Board, formed in 1979, is a cooperative with federal, provincial and industry participation to deal with waterborne wood debris at 8 primary sites (Fig. 33). One operation is a large debris trap, 50 000 m^2 in

FIG. 32. Naturally accumulated driftwood, Long Beach, west coast of Vancouver Island.

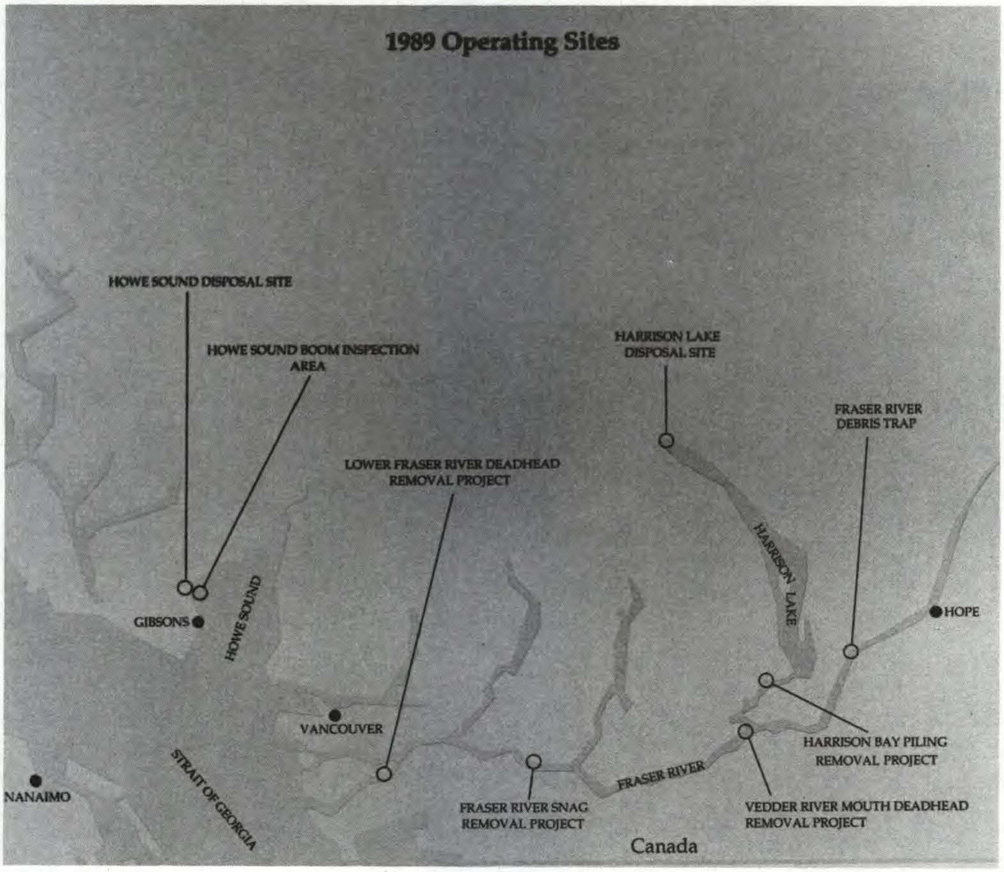

FIG. 33. British Columbia Debris Control Board operating sites, 1989. (Illustration by Debris Control Board 1989)

area (8 football fields) sometimes filled to a depth of 3 m, on the Fraser River (Fig. 34) which is a major contributor of wood debris in the lower Strait of Georgia. In Howe Sound, one of the major log booming and storage sites, there is a check on boom construction and collection of debris and deadheads, as well as at other problem sites. Merchantable timber is sorted out and unusable material burned. The extent of the debris problem is shown in Table 8, taken from the B.C. Debris Control Board Annual Reports for 1987–88 and 1989–90.

Certain ports (i.e. Horseshoe Bay) have a driftwood collection and destruction system (Fig. 35) and some yacht clubs have members flag deadheads which pose potential danger to small vessels. The advent of log barges and dry land log sorting has in some measure alleviated the log loss problem, but the logs are eventually off-loaded at the destination and stored again in the sea. Waldichuk (1978) has discussed the problems of log pollution.

Shipworm dispersal is dependent on the size of the adult population which produces larvae. The extent of movement of these larvae is determined in part by the length of its planktotrophic life, the water currents in the specific locality and the availability of wooden settling surfaces. Both *Bankia setacea* and *Teredo navalis* have quite long larval lives of up to 3 weeks, so they may be carried from the spawning site to infest wood some distance away. The Pacific oyster (*Crassostrea gigas*) has a larva about the same size as *B. setacea* and also with a larval life of 2–3 weeks. It has been shown capable of transport at least 80 km along the lower east coast of Vancouver Island from the spawning site in Ladysmith Harbour (Elsey and Quayle 1939).

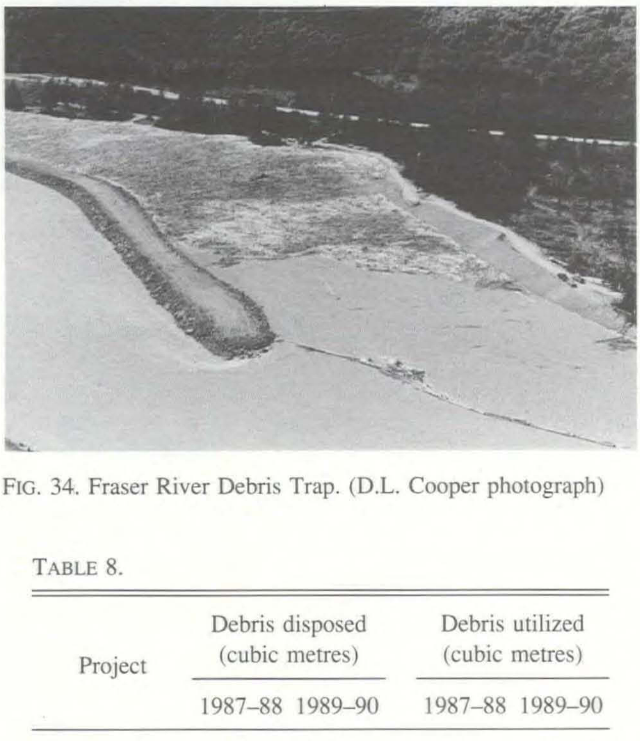

FIG. 34. Fraser River Debris Trap. (D.L. Cooper photograph)

TABLE 8.

Project	Debris disposed (cubic metres)		Debris utilized (cubic metres)	
	1987–88	1989–90	1987–88	1989–90
Fraser Trap	86 000	80 000	1 000	3 000
Howe Sound	30 000	58 000	1 000	3 000
Lower Fraser	3 000	2 000	0	0
Harrison Lake	32 000	1 000	0	200

FIG. 35. Driftwood collected in less than one month, Horseshoe Bay ferry terminal.

Scheltema (1971) showed that the larva of some shipworm species can be carried great distances in the open ocean as well as along continental shores.

Prime examples of shipworms with a potential to become widely distributed are *Teredo navalis* and *Lyrodus pedicellatus*, both non-native to British Columbia, but recorded from this province. Neither species is of great concern here at the moment. An area where at least one of these species caused devastation to untreated marine piling is San Francisco Bay in the early 1920's. It is difficult to place an exact date for exotic introductions but for *Lyrodus* it is thought to be about 1860 when it arrived in southern California. It is now circumtropical, presumably originating in the western Pacific. Its short pelagic life indicates the distributional factor is based on transport of the adult. The timing of the introduction of *Teredo navalis* is also uncertain but some estimates place it about 1913. It was presumably transported to the eastern Pacific from the Atlantic by wooden vessels and appears to have been confined to San Francisco Bay (35°N), Los Angeles Harbour and San Diego on the Pacific coast until the author found it in Willapa Harbour, Washington (46°N) in 1957. In a *Limnoria* survey in 1963, a well established population was discovered in Pendrell Sound, East Redonda Island (50°N) in the north east corner of the Strait of Georgia. Hydrographic conditions in this sound (Quayle 1965a, 1988) create conditions for summer water temperatures up to 25°C with maintenance of 20°C for several weeks and surface salinities of 20 ‰. These conditions approximate those for the breeding activity of *T. navalis* according to Miller (1926) and Hill and Kofoid (1927). The relatively low numbers of shipworm larvae, presumably *Bankia* in the 1950's relative to much higher numbers later, suggests the invasion probably occurred in the 1960's when pleasure cruisers from the State of Washington discovered the Desolation Sound area as a prime cruising area. So far *T. navalis* has not been found beyond the confines of Pendrell Sound. With reduced logging activity within the sound in recent years and conversion from wooden floating structures to plastic by the oyster seed collecting industry it appears the population of *Teredo navalis* is much reduced. Test block studies by the B.C. Research Council during the period 1966 to 1974 at 2 stations within 15 km of Pendrell Sound collected only the indigenous species. Several specimens of the tropical shipworm *Lyrodus pedicellatus* were found in Ladysmith Harbour (Popham 1983) where it does not seem to have become well established. Specimens other than the originals have not been found, indicating unfavourable oceanographic conditions for this tropical species, or inadequate searching. The means by which it reached Ladysmith Harbour are unknown, for it is not known to occur north of San Francisco Bay. However, as suggested for *Limnoria tripunctata*, a possible mechanism may have been via the wooden Japanese oyster seed creates, for Ladysmith Harbour is a well known and long established oyster growing area (Quayle 1988). However, no Japanese oyster seed has been imported into Ladysmith Harbour since about 1970.

Vertical Distribution

The vertical distribution of shipworms has been studied by larval sampling in the field (Quayle 1959a) and by larval movement in the laboratory (Isham et al. 1951). The distribution is studied by the tidal level of actual attack on marine structures like wooden piling or with collector panels placed at specific depths (Owen 1953; Quayle 1959a, 1965a; Quayle unpublished data; Nair 1966, Walden et al. 1967; Haderlie and Mellor 1973; McKoy 1981).

Isham et al. (1951) observed shipworm larvae in the dark, although negatively buoyant, swim toward the surface and concluded that during the night they concentrate near there and during daytime will disperse to less illuminated levels. Quayle (1959a) in field studies on the distribution of the larvae of *B. setacea* showed indications of diurnal movement with greater numbers near the surface at night than during the day (Fig. 19a). This has also been demonstrated for other bivalve larvae (Yasuda 1952; Quayle 1988).

Attack on submerged wood is the ultimate test of the occurrence of larvae at specific depths, for larval presence is not necessarily followed by attack, (Quayle 1959a, Fig. 19b). *Bankia carinata* (Gray 1827) was taken from wood dredged by the Danish Galathea Expedition at a depth of 7 488 m in the Banda Trench (Philippines) (Turner 1966), but the important area relative to human activities is in relatively shallow waters. The deepest record for British Columbia is 50 m (Fraser 1923). Owen (1953) found increased settlement of *Teredo norvegica* larvae with increased depth and attributed it partially to reduced illumination at those levels. In Pendrell Sound, Quayle (1959a) recorded the ratio of attack on Douglas fir test panels to be 1 at the 4 m level, 10 at 7 m, and 42 at 16 m. Nair (1966) found quite significant increases of shipworm (four species) settlement within a depth of only 3 m in Cochin Harbour, India. Walden et al. (1967) showed the attack by *B. setacea* in Elliot Bay, Washington heaviest near the mud line (10 m below zero tidal level) and decreased with decreasing depth. Haderlie and Mellor (1973) found the intensity of settlement of this species (*B. setacea*) in Monterey Bay, California increased with depth to 60 m. McKoy (1981), working in New Zealand, indicated *Lyrodus* to

TABLE 9. Total attack by *Bankia setacea* during a 30-mo period (July 1962 to December 1964) on fir panels exposed at monthly intervals and various depths at three stations, Cowichan Bay, Crofton and Nanaimo. (From Quayle 1966).

Depth	Cowichan	Crofton	Nanaimo	Total
Floating	50	933	512	1 495
Half Tide	41	1	7	49
Zero	374	759	3 625	4 758
Mud line	1 735	10 523	4 125	16 383
Total	2 100	12 216	8 269	22 685

TABLE 10. Vertical distribution of attack of the wood borer *B. setacea* on fir panels at Departure Bay, 1981–83.

Depth in metres below zero tidal level	Total attack *B. setacea*
– 0.5	19
– 1.0	270
– 1.5	728
– 2.0	1 235
– 2.5	1 618
– 3.0	1 401
– 3.5	1 697
– 4.0	1 885
– 4.5	1 884
– 5.0	2 418

have the usual increased attack with depth, while three other species had a more even distribution with depth. Settlement occurred in the intertidal zone up to mean sea level. Quayle (1965a) showed the vertical distribution of *B. setacea* at 3 stations along the east coast of Vancouver Island (Table 9). Quayle (unpublished data) in a study in Departure Bay, British Columbia, showed a gradual increase in attack with depth, nearly doubling with each metre increase in depth to 8 m (Table 10). A 1966 study (Quayle, unpublished data) in Pendrell Sound showed a similar increase in attack with depth. While vertical distribution studies in different locations may vary in detail, most are consistent in showing increase in attack with depth.

Geographical and Seasonal Distribution of *Bankia setacea* Attack

As noted previously *B. setacea* is distributed between Alaska and California and it might be expected that levels of attack from north to south would be relatively uniform. The British Columbia Research Council examined this question by comparing the attack at five locations in the years 1960 and 1964 (Table 11). The sea water temperature in San Francisco Bay where *Bankia* has been studied, varies between 12 and 15°C depending on season, site and depth. In Puget Sound the temperature range at the study site was between 5 and 16°C with approximately the same range for British Columbia and Alaska. In British Columbia attacks begin at about 13°C and cease at 7°C. Although this may not be the actual spawning temperature, it is close. In California the range is between 20°C and about 13°C. As in other species, such as oysters, the rate of temperature change rather than a specific temperature initiates spawning. Table 11 demonstrates the wide difference between years, sites and season and emphasizes the need to continuously monitor a specific site for full information on the breeding cycle there.

TABLE 11. Geographical and seasonal *Bankia setacea* attack per 9.29 square decimetres (square foot) between 1960 and 1964 at five sites. (From Tidelines, 1966. Vol. VIII, No. 9.)

	Site									
	Alaska		Mid B.C.		Lower B.C.		Puget Sound		San Francisco	
Month	1960	1964	1960	1964	1960	1964	1960	1964	1960	1964
Jan.	3	2	3	100	40	11	272	354	0	4
Feb.	1	0	2	9	2	0	594	270	2	4
Mar.	0	0	1	2	2	9	288	394	0	3
Apr.	1	7	8	378	1	14	457	1 112	0	2
May	0	2	15	24	6	18	459	218	5	9
June	16	12	1	25	43	7	74	338	10	25
July	170	2	165	107	12	90	32	312	13	1 228
Aug.	575	953	1 359	298	77	193	166	428	6	63
Sept.	1 241	2 741	688	590	122	1 062	92	230	19	43
Oct.	795	335	410	868	125	800	47	110	30	48
Nov.	136	33	1 231	1 671	143	128	292	130	5	5
Dec.	12	11	510	670	79	384	135	190	0	1
Total	2 850	4 098	4 403	4 742	652	2 716	2 908	4 096	90	1 435

Detection

Shipworm activity may be detected by the accumulation of yellow or white frass at the burrow entrance unless washed away by current or wave action. Frass is the fecal material composed of partially digested planktonic food and the wood borings (Fig. 38). In newly settled shipworms, the double aperture cones may be seen by careful examination or tips of the pallets of adults may protrude above the wood surface. Shipworm activity may also be detected in piling by examination of shavings from drilled holes for shell and tissue fragments. The holes are then filled with treated wooden plugs. On floating logs, a shaving with an axe may provide sufficient evidence.

For piling, sonic testing developed by the British Columbia Research Council (1962, Tidelines, IV, No. 9) has been used for a number of years. Sound waves tranmitted through the piling become reduced in strength and velocity and the signal is recorded on an oscilloscope. The unit can be moved up and down a pile by a diver. The degree of shipworm damage is expressed as a percentage of the retained bearing strength of the pile, and the system is able to detect as few as 3 to 6 *Bankia* tunnels in a pile. Over 50 piles per day can be examined with this apparatus.

It may be possible to confirm an anticipated attack or one in progress by exposure of test panels in the area and/or depth of concern. These may vary in size from 4.5 cm × 4.5 cm × 4.5 cm blocks suggested by the British Columbia Research Council (Walden et al. 1967) to the 15 cm × 6 cm × 1 cm panels of the Pacific Biological Station and the Clapp Laboratories design (Wallour 1958) of 30 cm × 15 cm × 2.5 cm. The Organization for Economic Co-operation and Development (O.E.C.D.) had a timber deterioration program at 23 testing sites throughout the world (Gareth Jones et al. 1972). The test panels measured 20 cm × 10 cm × 2 cm and were of pine. The Vancouver station proved to have the heaviest shipworm attack of any site.

Panels may be examined weekly for soon after settlement the burrows are readily observed with a low powered microscope or a hand lens. British Columbia Research Council studies showed blocks were twice as efficient as panels (1963, Tidelines, Vol. 5, No. 6) in showing shipworm attack at moderate or high levels. However, large panels are required to demonstrate low levels.

The Clapp Laboratories (Wallour 1958) established an arbitrary scale for shipworm attack based on the number of tunnels in the test blocks or panels, rather than on the number of pits made by newly settled larvae (Table 12).

TABLE 12. Scale of rating for Teredinidae attack.

Number of tunnels per block or panel	Attack rating
Up to 5	Trace
6–25 (10%)	Slight
26–100 or 25% filled	Moderate
101–250 or 50% filled	Medium heavy
Over 250 or 75% filled	Heavy
Filled, riddled or destroyed	Very heavy

The Research Council (1963, Tidelines, Vol. 5, No. 5) also showed floating and fixed collector strings gave essentially the same results with the slope of the depth-attack line identical.

Protection

Protection of wooden marine structures against marine borer attack is a problem only partly solved. To date the main solutions employ either mechanical or chemical means.

Mechanical

One of the earliest and quite drastic methods developed a layer of charred wood as a protective layer by applying heat in various forms, often fire. The porous friable nature of the charred wood prevented shipworm larvae from establishing a burrow. An early method of mechanical protection provided a metallic cover over the area to be protected. Closely placed flat headed nails driven into the surface was called scupper nailing. An alternative was metallic sheathing as a barrier, either on vessels or piling. Since the sheathing needed to be malleable and non-corrosive, copper was widely used. In the middle of the 1800's an alloy of 60% copper and 40% zinc, called Munz metal was used extensively. Bramhall (1960) reported Munz metal sheathed piling in Vancouver Harbour gave at least 50 years of service and at a coal wharf in Union Bay, Munz metal protected piling was in good condition after 67 years.

A wide variety of other types of coatings have been used through the years but none fully acceptable (Wakeman and Whiteneck 1960). Metallic sheathing was replaced in recent years by pliable sheet PVC plastic. This is mainly for piling and can be applied by helical wrapping or as a complete envelope either on new or already installed piling. Inside the envelope a stagnant anaerobic layer of water is developed around the pile and if there has already been an attack the lack of oxygen will kill the borers. The plastic covering prevents further attack, providing it is not breached. This is one of the main deficiencies of the system because of abrasion from drift wood or vessel movement. However, the system has been used successfully in California where the drift wood problem is not as serious as in British Columbia where a trial has given 5 years of protection.

Piles have been coated with fibreglass but abrasion and driving difficulties have prevented general use. However fibreglassed pontoons are in general use as dock floats.

Weak or damaged sections of piling or parts infested with borers may be replaced or re-enforced either by synthetic coatings or concrete sleeves.

Dynamite Blasting

Dynamite blasting for shipworm control was initiated by observation that hammer shocks from pile drivers caused mortality of shipworms in infested piling. The shock waves from explosive blasts were tested and found effective. Several British Columbia logging companies applied the system for a number of years on untreated piling, dolphins and boomsticks in booming grounds. For piling, treatment consisted of discharging 6 or 7 sticks of 60% dynamite 1 or 2 m above the mud line and 2 or 3 m from the piling. For boom sticks or floats, 3 or 4 sticks were discharged 3 or 4 m directly below. Regular treatment at 3 or 4 month intervals, sometimes adjusted for known breeding peaks, extended the life of untreated piling from about 1 up to 5 years.

In 1946 at Swansea, Wales, in an enclosed dock whose water level was controlled by gates, untreated piling began to be destroyed, presumably as a result of the introduction of shipworms in a wooden degaussing vessel. Based on experience in British Columbia (Quayle 1942) dynamite blasting was suggested to keep the docks in service until reconstruction with shipworm impervious materials. The blasting proved to be enough of a deterrent to allow this (Bell 1947; Wilson and Steven 1947).

Allen (1956) studied the effectiveness of dynamite blasting for borer control in flat log rafts. The conclusion was that reduction in number of borers by the maximum blasts possible (200 g at 2 m) was insufficient to prevent damage by the borers during future storage.

There appears to be little or no dynamite blasting for shipworm control at present, partly because of the increased use of creosote and improved methods of log transportation and handling.

Ultrasonics

Electricity and ultrasonics have long been considered for shipworm control. Charlon (1975) studied the effect of ultrasound on mussel larvae (*Mytilus edulis*) with an ultrasound disintegrator of MSE 150 W with a frequency of 20 KHz.

An exposure of 20 s at a power of 10 W/cm^2 shattered larval shells held in a small quantity of water (Fig. 36). The conclusion of the studies was that large-scale use presents many difficulties. High voltage electricity of 110 volts AC to 4500 volts DC has no effect on *Bankia* (1961, Tidelines, 3, No. 5).

Chemical

Chemical protection is based either on coatings or impregnation of wood (boat planking or marine wooden installations) with a single chemical or combinations. These must be toxic to invertebrate larvae and/or gribbles. Protection is based on slow release (leaching) of the chemicals from the coating or impregnation to form a toxic layer adjacent to the wood which prevents penetration by the larvae. If penetrated, growth and development is inhibited. The concentration of the toxic layer depends on laminar flow which may be destroyed by turbulence when protection is lost temporarily. The so-called antifouling paints are compounded to provide a long-term slow leaching rate usually preceded by a high initial release which gradually slows to an even low leach rate.

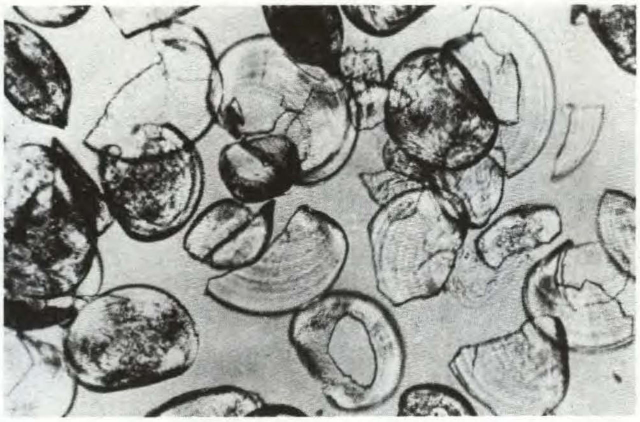

FIG. 36. Effect of ultra sound on mussel (*Mytilus edulis*) larvae. (From Charlon 1975)

Among many metals incorporated into antifouling paints, copper has been the most useful, consistent and efficacious if applied properly and frequently enough. Recently tributyl tin has formed the basis for these paints, now either curtailed or banned owing to deleterious effects on other marine organisms. In quite low concentrations it can affect invertebrate larvae and appears to cause serious shell malformations in oysters and affect sexual apparatus arrangements called "imposex" in gastropods (Gibbs and Bryan 1986).

Creosote

Of numerous chemicals tested for protection against marine borer attack none has been more successful or widely used than creosote. This is a complex mixture mainly of hydrocarbons obtained from the distillation of coal tar. Creosote may also be mixed with a proportion of coal tar itself. Admixtures with other toxic chemicals such as copper or arsenic have yielded no significant improvement in protective efficiency. However, naphthalene is toxic to *Limnoria* (McQuire 1971) and Seesman et al. (1977) have shown some efficacy with naphthalene–creosote treated wood against marine borer attack.

Creosote may be applied to wood in several ways. It may be simply painted on the surface to be protected, either hot or cold. Rough surfaces may be punctured (incising) to allow greater penetration. The most efficient method and one in general use is the full cell process. A steel chamber containing the wood to be processed is evacuated and filled with creosote oil heated to about 93°C. The pressure in the chamber is increased and maintained until the wood has absorbed the required amount of creosole. For peeled Douglas fir piling, this is usually 5.5–6.35 kg (12–14 lb) or more per 28 cubic decimetres (cubic foot) which is near the maximum retention possible. With this type of piling the significant peripheral penetration is limited to about 3 cm (Fig. 37). As with paints an initial severe loss of the toxic principle is followed by a relative steady state leaching. Well-

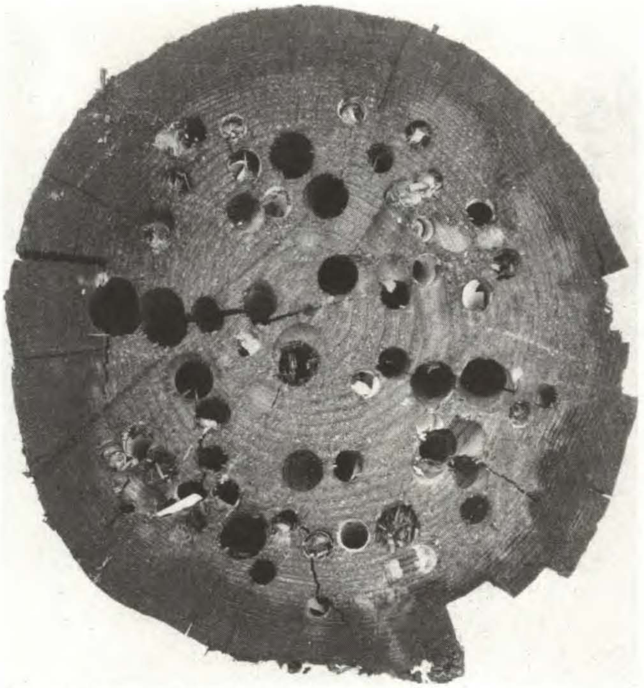

FIG. 37. Degree of creosote penetration on a 30 cm diameter treated pile. The shipworm attack due to improper installation and not to failure of the creosote treatment.

treated and properly installed fir piling in borer infested waters may have a service life of up to 40 years or more in British Columbia. Standards are set by the Canadian Standards Association and American Wood Preservers Association.

Regardless how well creosote impregnation of the pile has been carried out, it may be negated by improper installation. Bramhall (1960) lists the following faults and requirements in installation and maintenance.

1) Capping required to waterproof the top of the pile to prevent fungal infection.
2) Improper use of pike poles or other sharp instruments can penetrate the protective layer of creosote.
3) Over driving the pile may cause splitting and open the protective layer.
4) Cutting and boring for bolts should be done in a way to prevent penetration of the protective layer.
5) Bracing should be treated as well as the piling.
6) Dumping crushed rock around the base of the piling may open the protective layer.
7) Fender piling abrasion can cause a break in the creosote layer. Steel runners on the piling can prevent abrasion.

Other Chemicals

In addition to creosote impregnation, other less viscid chemicals are used in the same way. This type requires only about 0.5 kg per 0.03 m^3 (1 # per cubic foot). In 1968 the Federal Department of Public Works in co-operation with a timber preserving company investigated pile impregnation of several well known preservative chemicals (Quayle 1974). These included greensalt, boliden, double greensalt and creosote, chemnite and creosote. There were 4 replicate piles for each treatment along with an untreated control. These were arranged in a randomized block design with paired treatments at a site near Crofton, British Columbia. At the same time untreated panels were exposed at the base of each pile to determine possible attack variation over the study area (30 m x3 m). This proved to be relatively uniform between November 1968 and January 1971. The 4 untreated piling were destroyed within 13 months (Fig. 38), but all except one of the treated piling were still standing in 1988 and from external appearances were still sound.

Visual and ultrasonic examination of the piling in 1991 showed those with Greensalt, Chemonite or Greensalt-creosote were 100% sound. There was slight damage to the knots on the creosoted treated piling, but were otherwise sound. The Boliden treated piles had provided about 20 years of service against 22½ years for the others. However, the degree of penetration of this chemical was less than that of the others.

FIG. 38. Remains of an untreated fir control pile destroyed in less than 2 years in the 1969 Crofton piling protection study. Note frass at the base of the pile. (Underwater photograph. P. Fraser)

Chlorine

Chlorine has been used to control other mollusca such as mussels, particularly in sea water conduits, saltwater storage tanks and drydock pontoons. Except in special circumstances such as the latter, the problem with shipworms is the maintenance of an adequate concentration of chlorine for a long enough period of time. Studies by Richards (1953) indicate that lower residuals of chlorine applied continuously are more effective than higher concentrations applied intermittently. Adult *Bankia gouldi*, an Atlantic species of shipworm, is able to withstand 3.00 parts per million of chlorine up to 5 h.

Sodium Arsenite

For most permanent marine wooden installations chemical pretreatment has advantages, evidenced by the success of creosote impregnation.

Pretreatment is not economical or practical for log booms or wooden floats, where destruction of the borers by externally applied treatment is possible. This means applying materials toxic to the borers in the water surrounding infested surfaces (Trussell et al. 1956a, b, c). Through the years many chemicals have been employed for this purpose with limited success. However, the British Columbia Research Council (Trussell et al. 1955) investigated over 100 chemicals and discovered sodium arsenite met the required criteria. These are toxicity to the imbedded shipworms and insensitivity of the siphons to the chemical permitted the intake of the toxin to the body cavity. Studies showed time-lethal concentrations (sodium trioxide) ranged from 10 min at 1 000 ppm to 12 h at 25 ppm. For *Limnoria* there was little difference in tolerance between the two British Columbia species and the lethal concentration varied between 12.5 and 25 ppm with 18 h of exposure. However, sodium arsenite is also toxic to other marine organisms and care was exercised with its employment cleared by pollution control and fisheries authorities (Fig. 39).

Sodium arsenite has been employed in the treatment of flat rafts, bundle rafts, Davis rafts, wooden dock floats, booming ground installations, barges and scows. Some were treated by spraying with sodium arsenite solutions (Allen et al. 1966), others by enrobing with polyethylene sheathing to maintain concentrations of the chemical. This is one way piling was treated with sodium arsenite. A particularly successful application was the protection of wooden floating drydock pontoons where it is possible to maintain the concentration of the chemical. Repeated applications (3 times per year) or less depending on the breeding cycle in the particular area were required (Trussell 1959). In recent years employment of sodium arsenite treatment has ceased partly owing to permit difficulties, awareness and opposition of environmentalists and federal law now prohibits the importation of this chemical.

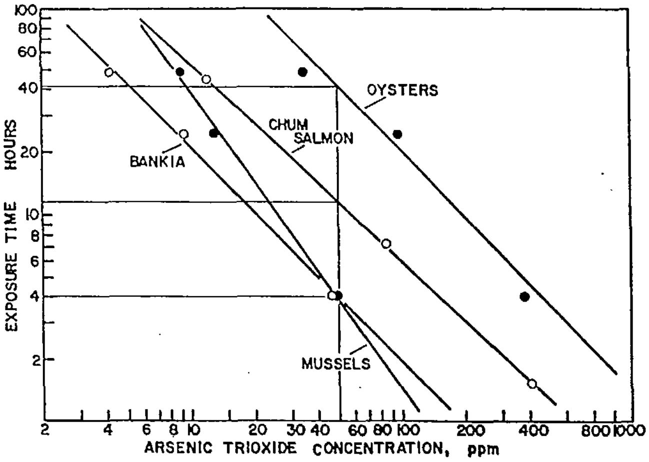

FIG. 39. Concentration of sodium arsenite needed to kill half the population (LD50) of shipworms, mussels, oysters and chum salmon. (From Tidelines, 1961, 3, No. 8)

Drying

Drying, requiring a reasonable time interval, is useful for structures used intermittently and moveable. When removed from water the shipworm pallets seal off the entry hole and the calcareous lining of the tunnel buffers acids of anaerobic metabolic processes to maintain proper pH of the body fluids for some time. However, this system eventually breaks down, resulting in mortality.

Industrially, many logs are stored intertidally partly in the expectation of a measure of protection against borer activity. The British Columbia Research Council (Tidelines, 1972, XIV, No. 2) studied *Bankia* survival out of water by exposing 4.5 cm x 4.5 cm x 30 cm blocks in the open sea for periods of 2, 4, and 6 weeks. After removal from the sea, the blocks were kept cool and damp (10°C), again for periods of 2, 4, and 6 weeks. The longest survival period recorded was 41 days but most specimens did not live more than a month. Logs stored intertidally have periods of re-immersion depending on the tidal cycles, so survival can be indefinite, although with a reduced rate of boring activity according to tidal level.

Logging and Borers

In British Columbia the three main areas of concern with marine wood borers in British Columbia are wooden vessels, docks and logging. Wooden vessels are adequately and relatively inexpensively protected by the timely application of antifouling paints. Marine structures (docks, etc.) can be built of steel, concrete or wood safeguarded by pre-impregnation with toxic chemicals. From the nature of the industry, logs cannot be protected by either of these methods. The best means of protection is by limiting the time and place of access to the borers.

The destructive ability of shipworms is illustrated in Fig. 40 which compares an unexposed control and a heavily attacked section of the same piece of wood. Figure 41 is a 15 cm log split longitudinally through the centre to show the level of destruction possible. B.C. Research (1964, Vol. 6, No. 4) debarked 40 cm fir and hemlock logs and floated them for varying periods in Burrard Inlet. Figure 42 shows the relative amount of damage at specific intervals and Table 13 indicates the loss in lumber value.

The majority of logs in the British Columbia lumber industry are salt water borne between the forest and the mill when exposed to attack by wood borers. The process involves dumping logs from the forest into the sea. Here they may be sorted as to size, quality and species and stored for some time to allow accumulation of sufficient quantities for shipping. For long distances or through exposed waters, self propelled or towed barges are now in general use (Fig. 43). For medium distances the logs are often bundled and made up into booms. These are formed into seaworthy rafts by enclosures of boomsticks (13 m logs with chain holes drilled at each end) linked together with chains and swifter lines or logs. In 1980, bundled booms were used for about 70% of the volume of logs moved in coastal British Columbia (Duval 1980). For short distances flat rafts of single logs is the usual format. Rafts are towed by one or more tugboats at about 2 knots. There are also flat bag and bundle bag booms (Fig. 44) for local transport.

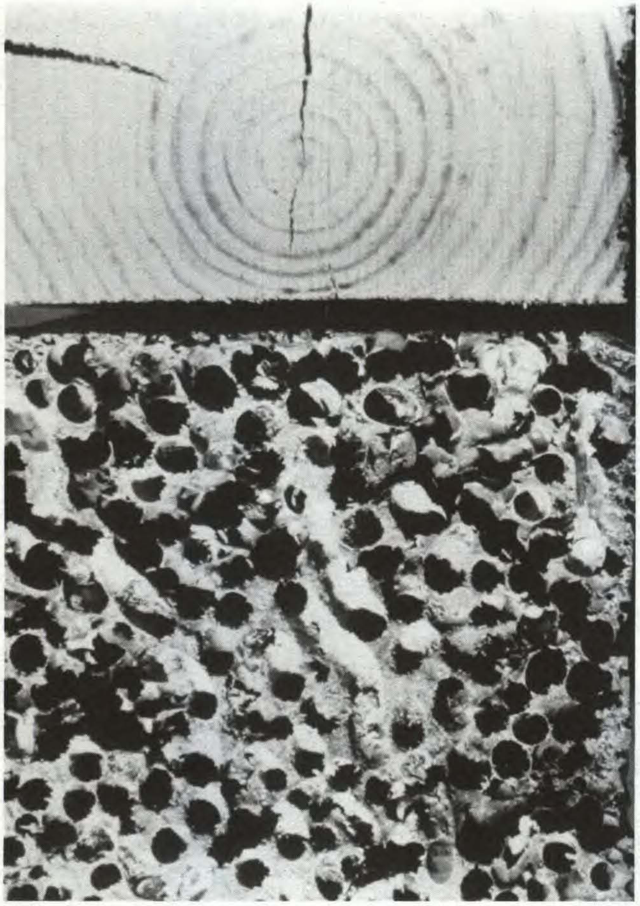

FIG. 40. Pre and post attack by *Bankia* on a fir batten. (B.C. Research Council photograph)

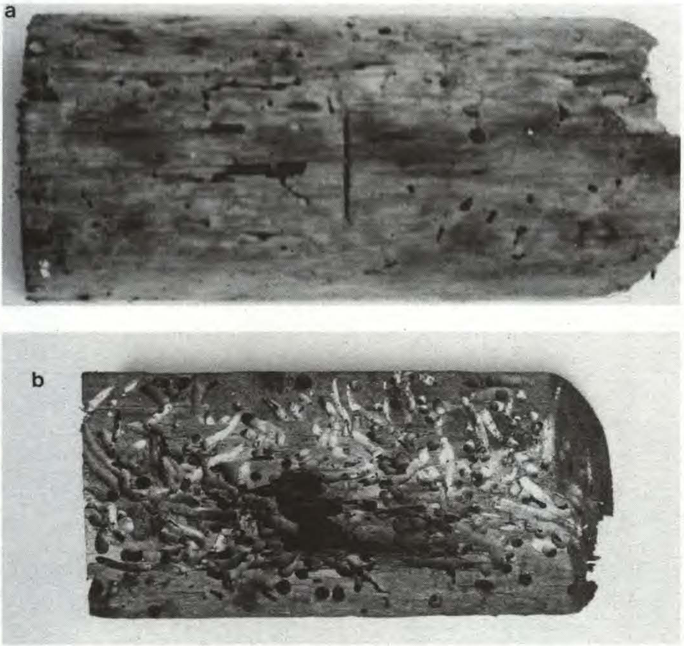

FIG. 41. Illustration of *Bankia* attack. (a) outer view and (b) interior view of a 15 cm diameter fir log.

Destination of the logs may be directly to the mill or to intermediate sorting and storage grounds. These may be in deep water, river mouths or intertidal areas where the booms dry at low tide.

There are about 6 000 ha of log storage area in British Columbia where logs may remain for up to 2 months although every effort is made to keep this period to a minimum.

The advent of log barges (Fig. 43) and the practice of dry land sorting has reduced significantly the time of the log in seawater.

TABLE 13. Loss in lumber value of floating Douglas fir and hemlock logs by *Bankia setacea*.

	Douglas Fir		Hemlock	
Months immersed in sea	% Loss dry weight	% Lumber shrinkage	% Loss dry weight	% Lumber shrinkage
3	0	10	0	10
4	0	40	0	40
5	0	45	0	55
6	0	50	0	70
7	3	75	5	90
8	9	75	8	100
9	18	100	18	100

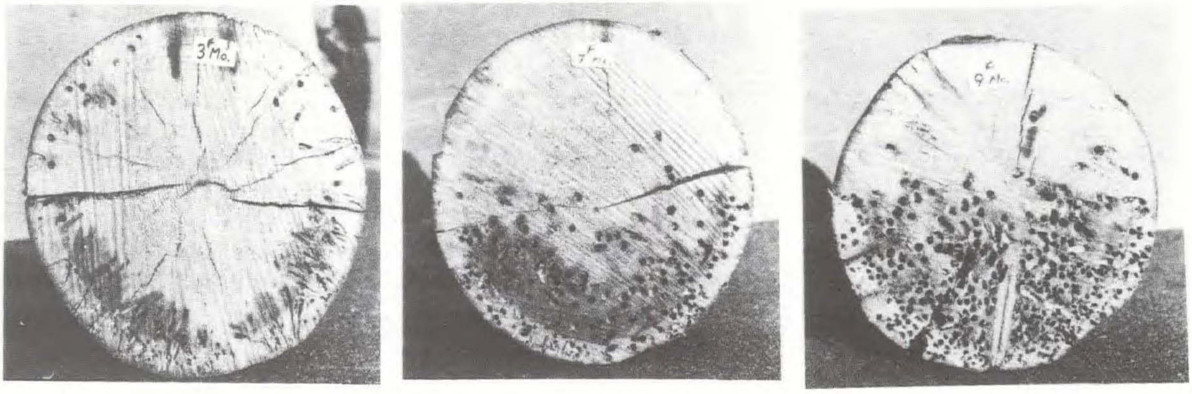

FIG. 42. Relative degree of damage caused by *Bankia setacea* on 40 cm diameter fir logs exposed for 3, 7, and 9 month intervals in Burrard Inlet, 1960. (From Tidelines 1964, 6, No. 4)

In this extensive complex transport and storage system there are some unavoidable losses. These may occur because of storms or accidents and the high specific gravity of some logs (particularly hemlock) causes them to sink either partially or completely. The partial sinkers, usually with less than a metre protruding vertically above the surface are called ''deadheads'' and are a serious navigational hazard (Fig. 45). Upon reaching the bottom complete sinkers form a reservoir of breeding shipworms. Formerly dead heads were congregated into areas called ''graveyards'' where they were allowed to remain until destroyed by the shipworms themselves, but this no longer occurs. Quayle (1956) called attention to this practice as unnecessarily increasing the population of shipworms and consequently the intensity of attack and advocated the elimination of graveyards. Deadheads are readily recoverable and Scuba diving has made the recovery of sinkers economical.

A government organized log salvage system is in operation whereby logs (owner marked) escaped from booms or sorting areas are recovered usually from beaches by licensed operators. There are other systems

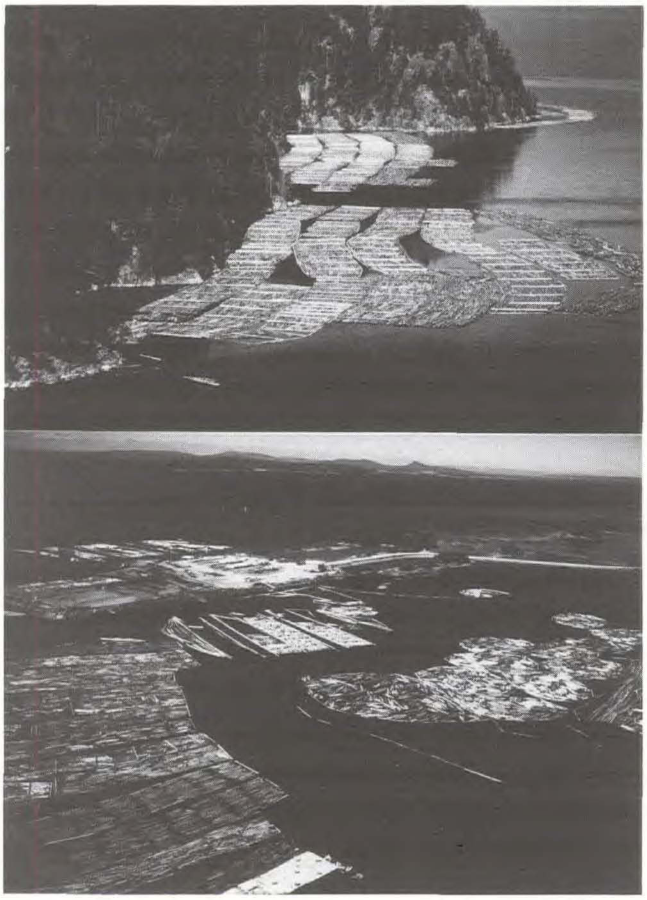

FIG. 44. Various types of log booms. (Council of Forest Industries photograph)

FIG. 43. Typical British Columbia log barge discharging its load. (Council of Forest Industries photograph)

FIG. 45. ''Deadheads'' in a ''graveyard''. (D. L. Cooper photograph)

of collecting wood debris originating from material swept down rivers in times of freshet or discarded miscellaneous wooden items and refuse from industrial operations. The British Columbia Debris Control Board has already been mentioned. Despite these efforts at marine sanitation and better transport methods, non commercial grade wood debris stranded on beaches (Fig. 32) or caught in dock piling remain important reservoirs of wood borer populations, whose larvae can be widely distributed. Most of the 150 samples collected in the 1962 *Limnoria* survey (Quayle 1965a) were collected from water-logged beach stranded logs.

It may be concluded that marine wood debris will continue to be an important habitat for the maintenance and distribution of marine wood borer populations in British Columbia waters. This requires increasing attention to marine sanitation and an efficient log flow through the lumber production system.

CRUSTACEA (*Limnoria*)

Introduction

Gribbles are marine wood boring isopod crustaceans belonging to the family Limnoriidae. Isopods are flattened dorso-ventrally, and generally small. A well known land representative is the common wood louse. Gribbles are smaller and seldom exceed 5 mm in length (Fig. 3), but cause considerable damage to wooden marine installations. The mud line pencil point of untreated intertidal piling is the result of gribble activity (Fig. 46). The family Limnoriidae contains one species of the genus *Paralimnoria*, 19 species of *Limnoria* (all wood borers) and 9 species of *Phycolimnoria* (algal borers) (Menzies 1957, 1959). In British Columbia there are two species. One, presumed to be native, is *Limnoria lignorum*; and the other, introduced relatively recently is *Limnoria tripunctata*.

FIG. 46. Pencil pointed piling resulting from gribble attack along with replacement piles. (From Hill and Kofoid 1927)

Distribution

Limnoria lignorum is a temperate zone species with a boreal distribution above 40° N latitude in both the Pacific and Atlantic Oceans. The range on the Pacific coast of North America is between Point Arena, California (39°N) and Amchitka Island (51°N) (Richards and Belmore 1976). It also occurs in northeast Europe and Japan.

Limnoria tripunctata is a temperate–tropical species, occurring approximately between 20° and 40°N latitude. On the Pacific coast of North America it occurs between Mazatlan, Mexico and the Strait of Georgia in British Columbia. Menzies described the species in 1951 and identified British Columbian specimens as *L. tripunctata* when first discovered there in 1961, but unfortunately gave the northern limit of its Pacific coast distribution as Point Arenas, California as late as 1972 (Menzies 1951, 1972). It occurs on the Atlantic coast of the Americas, from

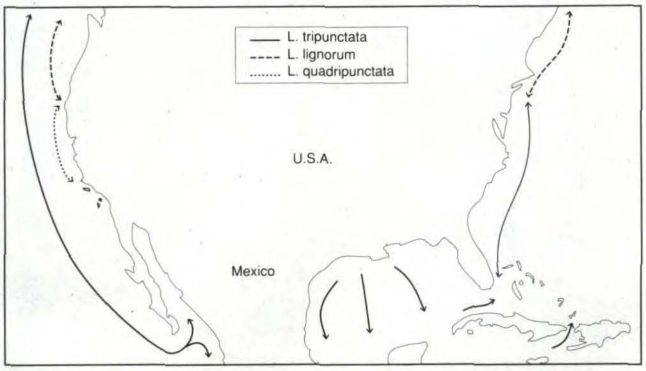

FIG. 47. The lower half of North America showing the distribution of the main species of *Limnoria*.

New York Harbour, south to the Panama Canal and in Argentina (Fig. 47). In the Eastern Atlantic it extends from the south coast of Great Britain south to Senegal. It is in the Mediterranean and Red Seas, in Hawaii, Japan and south to northern Australia, New Zealand and in the Indian Ocean.

Distinguishing Characters

The two species may be distinguished partly on the basis of size with *L. tripunctata* (3 mm) little more than half the length of *L. lignorum* (5 mm). Also, in the latter species, the flagellum (outer tip) of the second antenna has 4 parts (articles) while that of *L. tripunctata* has 5 articles. In *L. lignorum* the fifth somite of the pleon has a longitudinal ridge (carina) along the back, while on the same segment *L. tripunctata* has two raised nodes and behind these a single one. However, the most apparent and useful feature to distinguish the two species is the pleotelson. That of *L. lignorum* is broad and flat with a smooth periphery while in *L. tripunctata* it narrows at the anterior end where the edges are raised into a strongly denticulated rim. The central anterior area of the telson of *L. lignorum* has a raised ridge in the form of an inverted "Y". *L. tripunctata*, as the name indicates, has three punctations (nodes or tubercles) on the telson, a single anterior one and a posterior pair (Fig. 48). These features may be masked by debris or by *Folliculina*, an attached green protozoan.

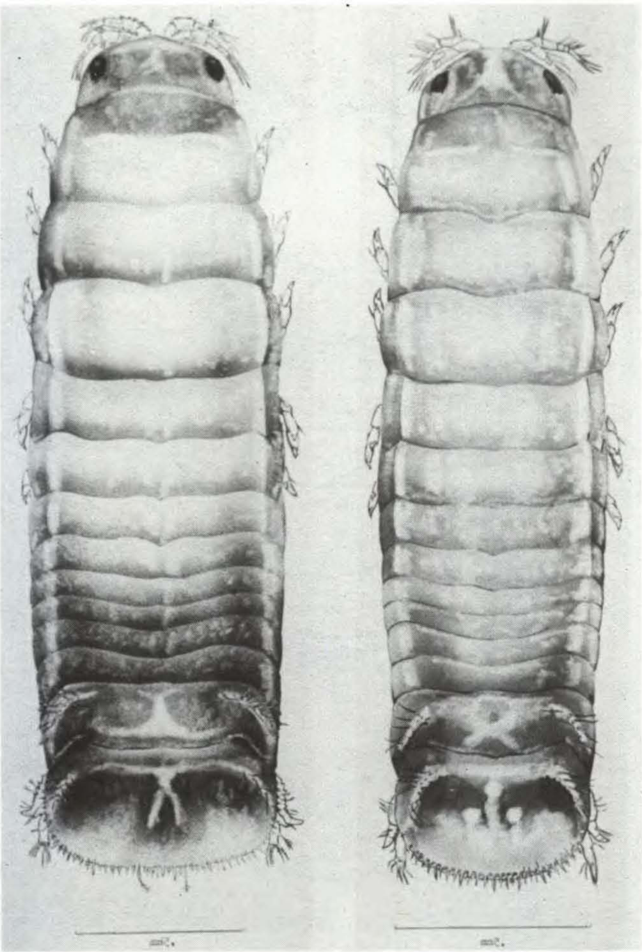

FIG. 48. Dorsal view of gribbles found in British Columbia. Left, *Limnoria lignorum* (Rathke). Right, *Limnoria tripunctata* Menzies.

Anatomy

The anatomy of *Limnoria* has been described in detail by Hoek (1893) some of whose illustrations appear in the more readily accessible Hill and Kofoid (1927). Menzies (1954) has an account of the reproductive anatomy.

Body

The *Limnoria* body (Fig. 49) consists of a cephalon or head, the peraeon or thorax, and the pleon or abdomen. The head carries the eyes, two pair of antennae as well as a set of complex mouth components, the important parts of which are the two mandibles. These are the wood rasping instruments (Fig. 50). The peraeon consists of seven segments (somites), each of which is furnished with a pair of walking legs. Each leg is composed of seven segments, the last one ending in a simple claw. During the breeding season females form a brood pouch from outgrowths at the base of the legs on the second to fifth segments inclusive. The abdomen has six segments with the last one (sixth) fusing with a flat plate (telson) to form the pleotelson. The abdomen also carries five pairs of pleopods which are flap-like appendages for swimming and respiration, plus one pair of uropods. The body exoskeleton is flexible and of a chitinous nature with a small amount of calcium. The colour is variable, ranging from white or beige to light reddish brown due to granular pigments in the cuticle.

Nervous system

The nervous system is simple with a two lobed "brain" and a single main nerve cord. There are sensory setae (fine hairs) on the short antennae likely responsible for site selection and type of wood (sap or heartwood) in which they tunnel. There is a preference for rough surfaces although planed surfaces are acceptable. The eyes are compound and not stalked as in many crustaceans.

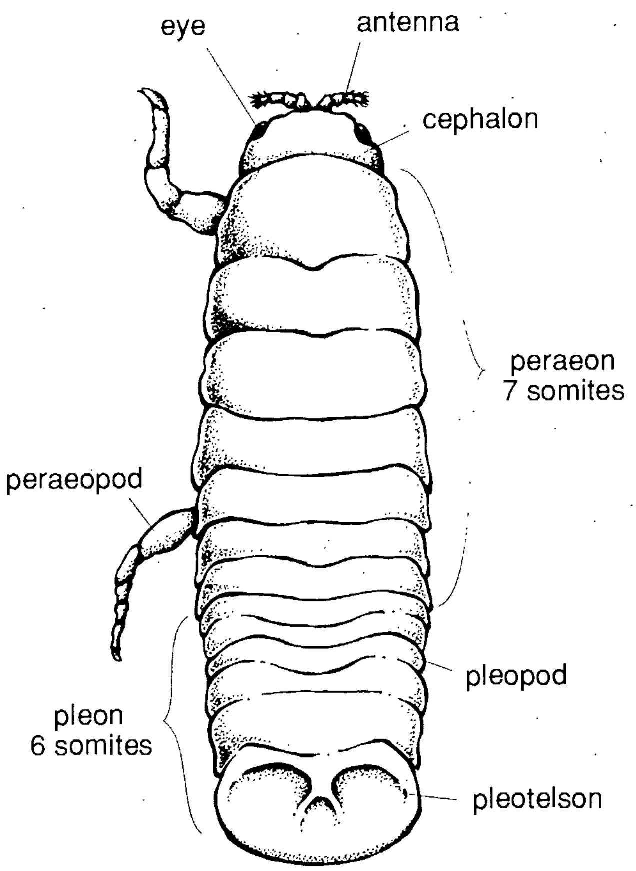

FIG. 49. Diagram of the main features of the gribble body and appendages, ×25.

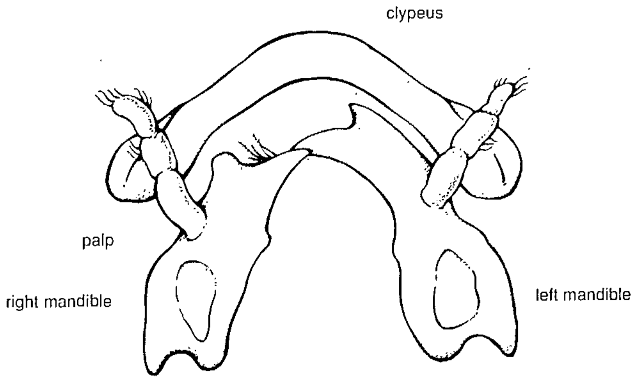

FIG. 50. Mandibles of the gribble, *Limnoria tripunctata*. ×130.

Circulatory System

A heart, pericardium and blood sinuses compose the simple circulatory system of gribbles. The tubular heart, about one quarter the length of the body, is surrounded by the pericardium and lies in the median line between the fifth abdominal and fourth thoracic somites, extending partially into each of these. The pericardium is in close association in position with the ovaries. There are anterior and posterior aorta and two openings (ostia) into the heart, which receive blood from the pericardial sinus. Blood is oxygenated by the continuous activity of the pleopods.

Digestive System

From the mouth there is a short oesophagus which leads into a gastric mill, essentially the stomach. From there a straight digestive tract ends in the anus on the under side of the telson. At the posterior end of the gastric mill are four blind sacs (digestive diverticula), two large and two small, concerned with digestion apparently in the form of enzyme activity but not production. Crystals of unknown function up to 28 µm in length and tetragonal or bipyramidal in shape occur in the walls of these diverticula. Posterior to where the digestive diverticula enter the gut, and lining the stomach, is the peritrophic membrane, a non-permanent structure which is a tube partially separated from it by the peritrophic space. It protects the lining of the stomach from ingested material. A number of studies have shown quite conclusively that the gribble gut does not contain digestion assisting microorganisms such as those found in termites (Boyle and Mitchell 1978).

Food

After many years of study gribble nutrition, if not yet completely understood (Lane 1959), it is now accepted the burrow is made by chewing action of the mouth mandibles. The wood particles are ingested and taken into the digestive tract in part insulated from it by a peritrophic membrane. Wood has certain nutritional constituents not readily available except by enzymatic action. The absence of microorganisms in the stomach to assist in the digestive process is well confirmed. Cellulase activity but not cellulase production itself has been demonstrated in the digestive diverticula and it is possible necessary enzymes are present in the ingested food (Ray and Julian 1952). Estimates of the daily ingestion of wood is about 0.15 mg per animal per day (Boyle 1988) and about 18 complete passages per day through the intestine (Oliver 1962) provides little opportunity for digestive processes to operate on the wood fragments. There is considerable bacteriological and fungal activity in wood immersed in sea water and these activities have often been considered necessary precursors to borer attack. These organisms are taken in with the wood particles and may complement a wood only diet. On burrow walls and also attached to the exterior surface of gribbles, particularly on the pleopods and under surface of the pleotelson, are considerable numbers of bacteria, fungi and diatoms which when dislodged by grooming and pleopodal activities may have some nutritional role, as a source of protoplasm, nitrogen and microbial cellulases (Sleeter et al. 1978; Boyle and Mitchell 1981; Boyle 1988).

In tropical and semi-tropical waters *L. tripunctata* thrives in creosote treated timber which harbours a greater number and diversity of bacteria than untreated wood. Some of these bacteria seem able to metabolize some of the creosote constituents, reducing its toxicity for the gribble, and providing a source of nutrition, particularly nitrogen, which is lacking in the wood part of the diet (Zachary and Colwell 1979; Zachary et al. 1983).

Dissolved organic material (D.O.M.) in sea water is being increasingly considered as an additional source of limnorian nutrition.

Reproductive System

In *Limnoria* sexes are separate and the gonads are located in the central part of the pereaeon. In females, paired ovaries are between the second and seventh segments above the intestine and below the heart. The oviduct emanates from the centre of each ovary opening at the fifth somite near the base of the fifth leg. There is a vulva but no vagina as such. In the male the paired testes are between the fourth and fifth somite below the heart. The vas deferens from the testes to the seventh somite of the peraeon ends in the genital apophysis (penis) at the mid line and the pointed appendix masculinum. The apophysis structure (two skin folds) makes possible external sex differentiation. Female secondary sexual characteristics are the oostegites or brood pouches attached to the base of the legs in somites two to five inclusive. They become readily evident only at the moult prior to egg deposition. It is probably at this time that copulation takes place for sperm are found in the oviduct at the time of egg release. After this there is another moult when the oostegites return to the pre-breeding state. Like all crustaceans *Limnoria* moult at regular intervals for during the growth period it is the only way and time they increase in size. *Limnoria lignorum* moults every 60 — 90 days at about 12°C.

Breeding

Male *Limnoria* make the initial burrow and when long enough for two animals (circa 1 cm), is joined by a female. Pairing of an individual couple can last up to a year. At breeding time the pair exchange positions and the female occupies the front of the tunnel. Copulation seemingly occurs in the burrow and oostegites develop to form a brood pouch to receive eggs as they are laid. These are oblong and 0.3 x 0.1 mm in size (Fig. 51). According to the literature, *L. lignorum* lays a maximum of 40 eggs with an average of between 20 and 25. *Limnoria tripunctata* deposits a maximum of 25 with an average of about 5 to 10, over most of its range. The brood size apparently depends partially on the degree of crowding. Less crowded test panels or blocks have higher brood sizes than the densely crowded populations in infested piling.

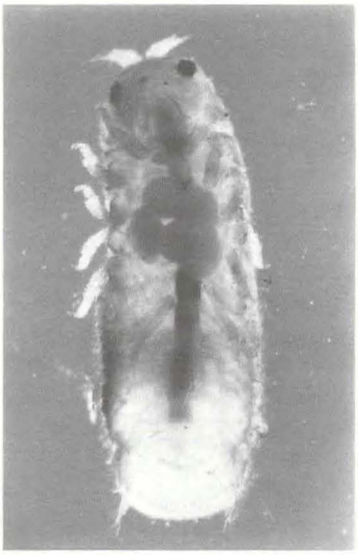

FIG. 51. Gravid female *Limnoria tripunctata* with 5 ova. ×15.

In a general life span of 2 years, the first brood occurs near the end of the first year with several broods in the succeeding year. The embryonic period may last up to 6 weeks, depending on temperature. *Limnoria tripunctata* females are gravid (carrying embryos in the brood pouch) in the range of 15 to 25°C while in *L. lignorum* it is between 8 and 20°C. In Departure Bay the earliest breeding observed in *L. lignorum* was in late March at a temperature of 8°C. The mean number of eggs was 20 per animal and the ova measured 0.36 mm x 0.30 mm. Gravid females can occur in small numbers as late as November in Departure Bay.

Growth

Growth varies considerably depending on temperature and species. From a mature egg size of 0.5 mm the embryos have a length of about 1.0 mm when released from the brood pouch (Fig. 52). The incubation period for *L. lignorum* at 15°C is 5 weeks and at 22°C it is 2 weeks for *L. tripunctata*. In Departure Bay the period is closer to 5 weeks for this species.

At release the mouth parts are not functional and become so only after the first moult. As indicated previously, like all crustaceans, a gribble may grow only by periodic moulting (ecdysis) which allows the soft body to increase in size when the hard casing is shed and a new covering formed. In about 3 months a length of 1.3 mm is attained and 2 mm after 5 months by *L. tripunctata*. There is little or no growth in temperate waters during the winter, for the 1988 brood had not grown significantly by April of 1989 in Departure Bay.

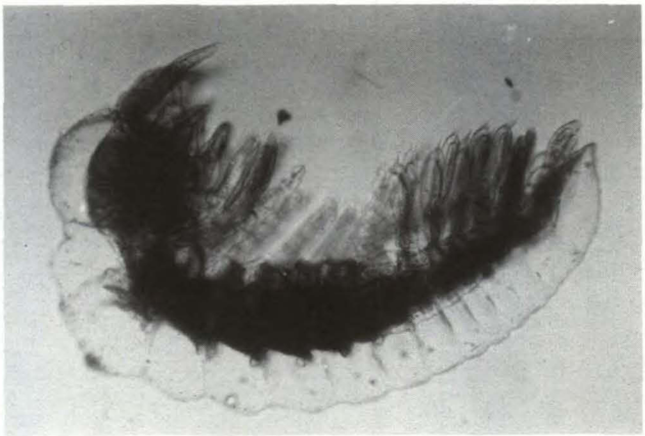

FIG. 52. Newly hatched young of *Limnoria tripunctata*. ×100.

Ecology

Temperature

The temperature regime in the southern half of the British Columbia coast accommodates the existence of both species of gribble while the north coast conditions are suitable in the main only for *L. lignorum*. Situations may occur where, given the opportunity, *L. tripunctata* would be able to survive and possibly multiply there. This may have already occurred for the area has been sparsely sampled.

The literature (Becker 1959; Kampf 1957; Somme 1940; Eltringham 1967; Menzies 1957; Beckman and Menzies 1960) indicates some mortality at the extreme temperatures of −1°C and 38°C with a higher upper level of 44°C for *L. tripunctata*. These temperatures are for exposed animals and in nature the insulation provided in burrows must extend these limits appreciably. For intertidal limnorian populations on the lower British Columbia coast air temperatures fall as low as −10°C with no apparent effect. The minimum ovigerous temperature for *L. lignorum* is about 7.5°C and for *L. tripunctata* near 15°C. In British Columbia *L. lignorum* can be gravid in November at a temperature of about 8°C.

Temperature also affects the rate of boring which is greatest during initial creation of the burrow. Boring activity of mixed species (*L. lignorum*, *L. tripunctata*, *L. quadripunctata*) at 17°C increased by 1.5 fold at 27°C. For *L. tripunctata* the length of life in the laboratory decreased by one third as the temperature increased from 20 to 30°C, but under 20°C it lived for a year (Kampf 1957). Eltringham (1965) and Vind and Hochman (1961) also studied the effect of temperature on boring activity on the same species in California and the rates are shown in Fig. 53 a,b.

Characterization of *L. tripunctata* as a temperate–tropical species raises the question of its tolerance to British Columbia hydrographic conditions which cannot be described as tropical. The opinion is that this species requires a breeding temperature of 15°C for about 3 weeks. Water temperatures at selected sites in British Columbia are shown in Table 14.

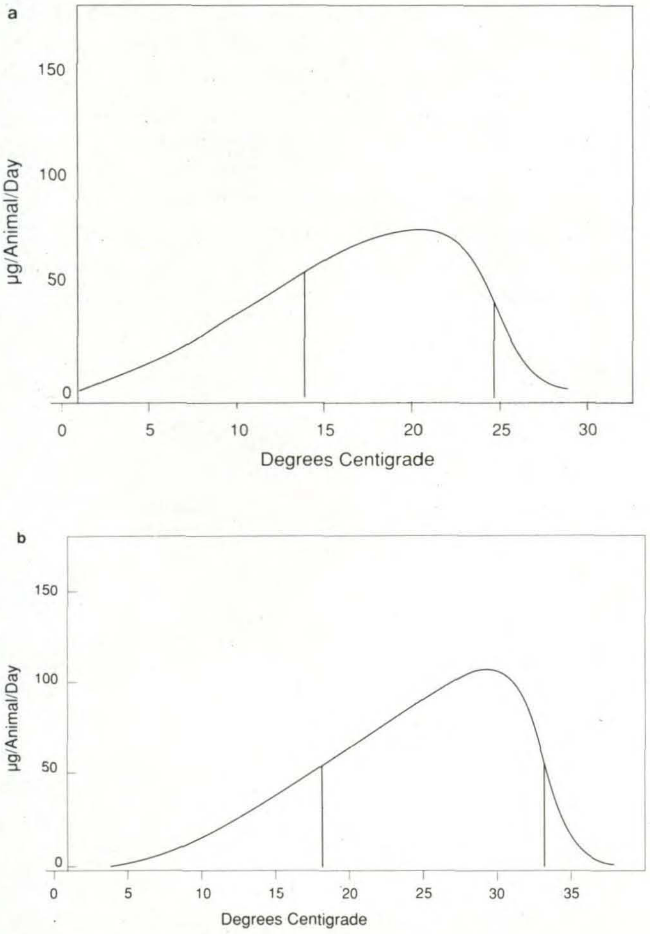

FIG. 53. a, b. Fecal (frass) production by the gribbles, *Limnoria lignorum* and *L. tripunctata*. (From Vind and Hochman 1961)

TABLE 14. Surface water temperatures at selected sites on the British Columbia Coast. (From Hollister and Sandnes 1972).

Minimum	Maximum	Temperature held
Cape Mudge 6.7	14.0	above 15°C for 5–10 days
Chrome Island 6.7	17.6	" " 60 days
Departure Bay 6.5	17.8	" " 90–120 days
Pendrell Sound 7.2	25.0	" 18°C for 60 days
East Point 7.2	11.6	" 13°C for a few days

Mean minimum temperatures described here are at or above the instantaneous lethal temperatures for both gribble species as cited by Jones (1960) in Oliver (1962). Minimum breeding temperatures occur for both species giving adequate time for embryonic development in most areas. The centre of *L. tripunctata* distribution in British Columbia is the Strait of Georgia, the area of highest water temperatures along the coast. So far *L. tripunctata* has not been found beyond the north end of the Strait of Georgia, where water temperatures decline quite drastically. The July–August water temperature at Pultney Point at the north end of Johnson Strait between Vancouver Island and the mainland averages about 10°C. There are no known oyster seed plantings from wooden Japanese oyster seed boxes north of the Strait of Georgia and low water temperatures are probably too great a barrier for development of breeding populations of *L. tripunctata* from infested driftwood that might have found its way north. The occurence of *L. tripunctata* at sites distant from the immediate vicinity of oyster seed plantings at Fatty Basin in Barkley Sound are not so readily explained with similar occurrences at Sidney Inlet, Zeballos and Fair Harbour, the latter about 200 km to the north. The movement of logs is away from the latter sites rather than towards them, and with considerable stretches of open Pacific Ocean between the intervening inlets, although there is considerable wooden fishing boat traffic.

In Pendrell Sound surface water temperatures in summer can reach 25°C and remain above 20°C for several weeks, *L. tripunctata* is the only gribble species that occurs there.

Salinity

In British Columbia *L. lignorum* appears to be euryhaline, tolerating a wide range of salinities, able to withstand extremes for brief periods. At Shannon Bay in the Queen Charlotte Islands the surface salinity varied between 9‰ and 28‰ in the 1948 Black and Elsey study. *Limnoria tripunctata* is also relatively euryhaline, withstanding salinities less than 20‰ in the Strait of Georgia and oceanic salinities up to 32‰ on the west coast of Vancouver Island. Regardless of the effects of salinity, the overriding factor in distribution and survival is probably temperature as suggested by Jones (1963) for the three British species of *Limnoria*. Also in Great Britain, Eltringham (1961a) examined the effect of salinity on boring activity and survival of *Limnoria*. With reduced salinity he found less boring activity which ceased completely below 10°C, but varied inversely with temperature. A salinity of 5‰ proved to be lethal in 15–20 days for *L. tripunctata* which was able to survive briefly in a 4‰ salinity.

Oxygen

Except in areas of pollution extreme enough to cause anaerobic conditions, (log dumps, pulp mill discharge sites), the concentration of oxygen in British Columbia waters is relatively high. Menzies et al. (1963) found that dissolved oxygen concentration of less than 2.9 ppm reduced *Limnoria* settlement in Los Angeles–Long Beach Harbours. Anderson and Reish (1967) with the three Californian gribble species, studied the effect of low dissolved oxygen concentration at various temperatures on wood boring activity as measured by mortality and fecal pellet production. They found that all three species can burrow at low levels of oxygen but their activity was less than at higher levels.

The 28-day median tolerance limit for *L. lignorum* was 1 mg/L of dissolved oxygen at 15–16°C and for *L. tripunctata* 1 mg/L at 22–25°C.

Eltringham (1961b) examined the wood boring activity of *Limnoria* in relation to oxygen tension and concluded that if the level of dissolved oxygen in the under surface of infested timber falls below 2% saturation, boring activity ceases. He also confirmed that oxygen tension less than 3% saturation causes exodus of most of the gribbles (*L. lignorum* and *L. tripunctata*) from the burrows.

Light

The literature (Eltringhan 1971b; Isham et al. 1951) indicates a correlation between a reduction in light intensity and increased attack. This is in conformity with the widespread impression of an increase in attack with depth as illumination is reduced. Since *L. tripunctata* occurs at somewhat higher levels than *L. lignorum* it may be more light tolerant. However, tank studies in full darkness, with mainly *L. tripunctata*, showed nearly equal attack (total 6 335 burrows) on the upper and lower surfaces of horizontal panels (12% greater on the upper) in full darkness. With a normal day and night light sequence, the attack (3 088 burrows) was 12% on the upper and 88% on the lower surface of the panel indicating a large measure of negative phototropism (Quayle, unpublished data).

Current

The effect of current speed on gribbles has been studied by Doochin and Smith (1951). Experimentally the limiting velocity for settlement is between 1.5 and 1.9 knots (2.8–3.5 km/h or 100 cm/s). Current speed is probably more important in distribution than settlement.

Fouling

Fouling by barnacles, bryozoans, hydroids and other sedentary invertebrate animals can provide a surface covering able to prevent gribble attack. This depends on the seasonality of settlement of these organisms relative to the limnorian migratory period. In the Strait of Georgia the peak settlement period for the most abundant and ubiquitous barnacle (*Balanus glandula*, Darwin 1854) takes place in most years within 10 days of April 1. On a suitable surface the barnacle abundance and growth are sufficient to inhibit gribble attack in about 10 days after settlement. Figure 54 demonstrates the surface cover possible by bryozoa, in this case *Schizoporella unicornis*, Johnson 1847. The common bush-like hydroid (*Obelia*, Fig. 21) presents a network of branches difficult for a gribble to penetrate.

Associated Organisms

Because of its sessile nature, with most of the time in its burrow, *Limnoria* is available as a host for other organisms. The association with bacteria has already been explained. Gribbles carry a variety of protozoa, none of which appears to be particularly harmful, and therefore classed as commensals. There is little evidence of parasites, and predators appear to be few. In British Columbia the common protozoan associated with *Limnoria* of both species is the readily visible heterotrichidan green coloured *Folliculina* about 0.2 mm in length (Fig. 55). Mohr (1959) found three species of *Folliculina* in a single gribble population at Friday Harbour, Washington, with *Microfolliculina limnoriae* as the most common species, particularly on the upper surface of the telson. *Folliculinopsis gunneri* attaches to the underside of the thorax. In British Columbia specimens the majority of folliculinids occur on the dorsal surface of the telson, with fewer on the abdomen. A dozen species of *Folliculina* have been recorded from British Columbia (Andrews 1955) including *Lagotia viridis* which infests *Limnoria*. Folliculinids occurs more frequently on *L. lignorum* than on *L. tripunctata* in British Columbia waters.

Peritrichidan and chonotrichidan (collar ciliates) also occur on gribbles but have not been well studied in British Columbia, although Mohr (1959) cites the occurrence of a common chonotrichidan from the north west coast of Vancouver Island. This cosmopolitan protozoan attaches to the bristles of the pleopods.

Limnoria in British Columbia may be infested, although not universally, with tiny nematode worms in considerable numbers in the ventral abdominal region, either within the brood pouch or loosely clustered under the head. Like the protozoa they may be more commensal than parasitic. In B.C. nematodes tend to occur on gribbles where the water temperature is relatively low.

In California, Reish (1954) examined the role of polychaetous annelids (sea worms) which frequent the abandoned tunnels of the gribbles. Several species, such as *Halosydna brevisetosus* (Kinberg 1855), *Nereis vexillosa* (Grube 1851), and *Ophiodromus pugettensis* (Johnson 1981), which also occur in British Columbia, were found to feed on *Limnoria*. Polyclad turbellarians of at least one species, were shown to consume gribbles. These flatworms also

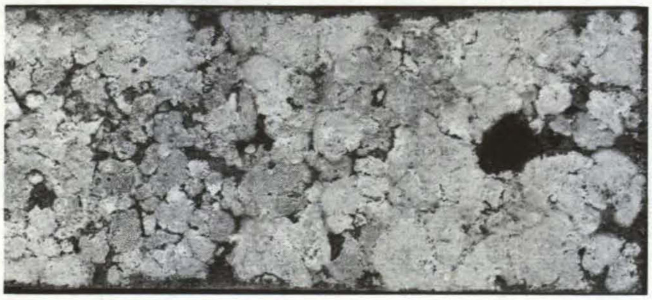

FIG. 54. The bryozoan, *Schizoporella unicornis*, completely covering a 15 × 6 cm test panel, preventing borer attack.

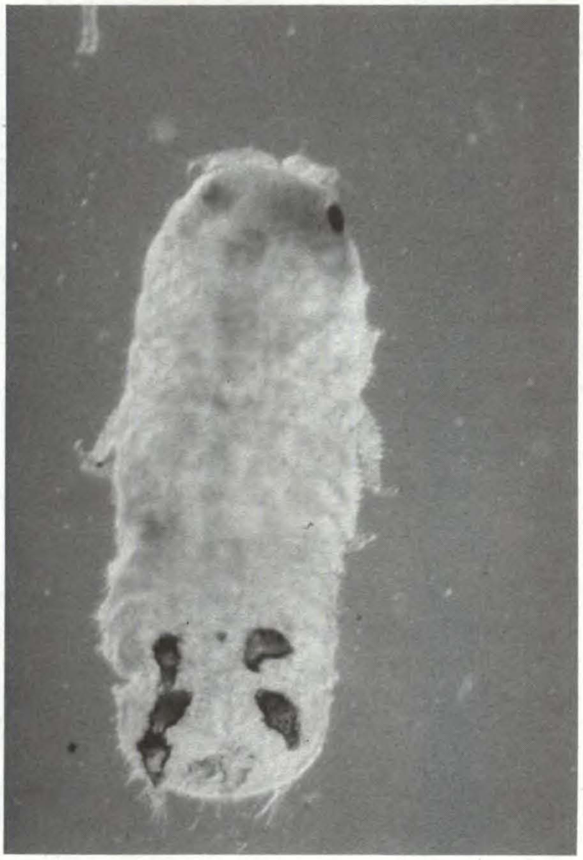

FIG. 55. *Limnoria* with the heterotrichidan, *Folliculina* attached to the telson. ×18.

occur in infested wood in British Columbia. The active amphipod *Corophium ascherusicum* Costa, 1857 about the same size as *Limnoria*, also occur with it in small numbers, but does not appear harmful.

An assortment of other animals occur adventitiously on or in wood attacked by gribbles but do not have any apparent effect on the *Limnoria* populations. Some are temporary visitors, but others become permanently attached as fouling organisms. Among these are algae, hydroids and barnacles which in some circumstances may prevent marine borer attack by forming a protective shield.

In summary gribbles are relatively free of disease as far as known and parasites appear to be few.

Behaviour

The activities of *Limnoria* may be listed as tunnelling, crawling and swimming.

Tunneling

The tunnelling apparatus is composed essentially of two slightly dissimilar mandibles which are said to operate on a ''rasp and file'' principle. A saw and file description might be more appropriate for the right mandible with a sharp point and toothed edge like a saw, works in conjunction with the denticulated flat surface of the left mandible (Fig. 50). Each mandible has an attached 3 segment palp and complex jointed first and second maxillipeds aid in directing the abraded wood particles to the mouth.

Tunnels are first started by males, initially on a slope. After reaching a depth just sufficient to cover the animal, the burrow proceeds at a level parallel to the surface, but close enough to allow perforations in the tunnel roof for ventilation (Fig. 56). Faecal pellets may be found near the adit but not in the tunnel itself for they are fanned by the force of the pleopod induced current. In the tunnelling action, walking leg claws enable the gribbles to secure a firm anchorage to burrow walls, necessary to hold the body close to the tunnel face and provide purchase for the mandibular action.

Crawling

Gribbles seldom leave the burrow, but when this occurs they are able to crawl about quite actively but do not wander far. The chemotactic response to wood is weak or non-existent; there is avoidance of strong light but contact stimulus (thigmotropism) is strong. On infested floating panels in aquaria, small numbers may be found on the dry upper surface where they perish. Menzies (1961) suggested a nocturnal migration.

Swimming

The third activity is non-directional swimming which is accomplished in a limited way by action of the pleopods. Without this activity they sink. Considerable literature exists on the migratory habits of gribbles on the basis of time and intensity of infestation of test panels. There are few studies on the actual mechanism, whether swimming only, coupled with current action, or combined with floating infested timber.

In Departure Bay panels suspended near the surface from a styrofoam raft 30 m from a floating *Limnoria* infested fir log for 4 months (August to November) collected no *Limnoria* but panels suspended from the log at the same time were infested (Quayle, unpublished data).

Tank studies, mainly with *L. tripunctata*, at the Pacific Biological Station (Quayle, unpublished data) demonstrated a marked tendency to swim at the same or lower level than the source population. Horizontal panels held 1 m from there had an attack only slightly greater (9%) than those 2 m away. This study (Fig. 57) also confirmed the conclusion of Menzies and Widrig (1955) that distribution becomes aggregated after the initial attack.

In a study using a 6 m flume, with collector panels spaced at 1 m intervals, the maximum swimming distance of both species was 3 m at a temperature of 18°C and a salinity of 28‰ (Quayle, unpublished data).

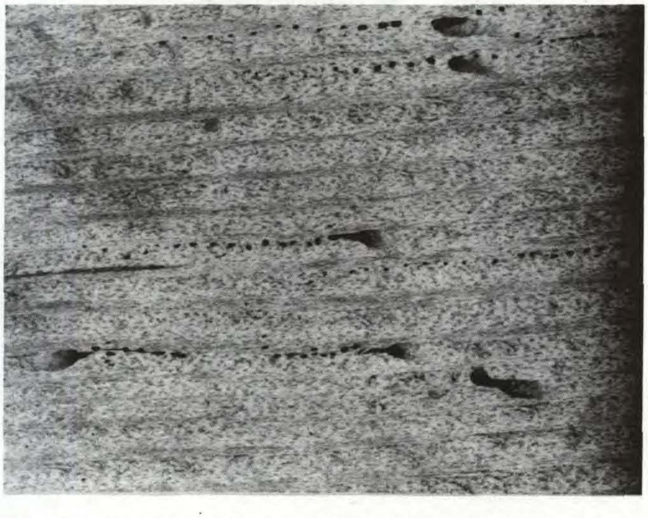

FIG. 56. *Limnoria* entrances with ventilation pores above the tunnels. ×2.

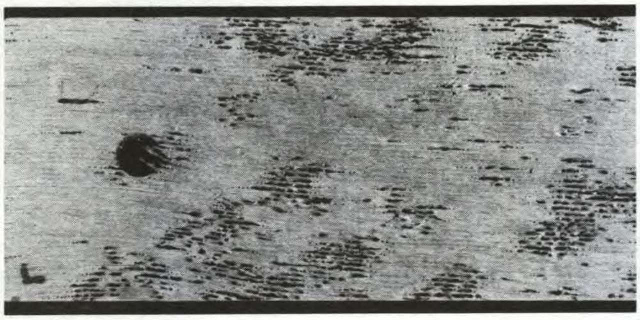

FIG. 57. Fir panels (15 × 6 × 1 cm) showing the aggregative behaviour of *Limnoria*.

Site Selection

Panel studies show *Limnoria* select burrow sites in soft spring wood rather than in denser winter wood (Fig. 58). This ability to select exists although there is no evidence of chemotaxis. Once ensconced, burrowing is nearly always in the direction of the grain. Menzies and Widrig (1955) state selection of burrowing sites is non-random, for after some wandering over an area of 25–50 square cm there is a tendency to burrow near an adjacent tunnel. As described later, with test panels in an aquarium there is also the tendency for *L. lignorum* to select areas already inhabited.

From attack on fixed test blocks Eltringham (1971b) concluded that *Limnoria* (presumably a mixture of three species) tend toward positive geotaxis when searching for a burrow site, but become negatively so when burrowing. On floating panels in a lighted aquarium, small number of gribbles, once on the panel, find their way to the upper surface where they perish. This behaviour is contrary to the positive geotaxy cited above and to the observations of both Eltringham (1971a) and Isham et al. (1951) which indicated negative phototaxis. The former author also showed evidence of strong thigmotropism.

Since *Limnoria* has limited swimming ability, current speed affects selection as shown by the experiments of Doochin et al. (1951).

Surface Selection

In an experiment to compare the attack on smooth and rough surfaces, 10 smooth surfaced panels (6 × 15 cm) were compared to 10 slightly roughened, in a randomized block design between December 9, 1987 and May 4, 1988. These were submerged horizontally in a covered (dark) aquarium about 60 cm away from a fairly large block of wood with a large population of *Limnoria* of both species. At this time of year *L. lignorum* was the main migrant. To count, the panels were marked off into 2 cm^2 sections, and the gribbles in each of the 21 squares on each side of the panel recorded. This provided a total of 420 squares for comparison.

The roughened panels had 62% of the attack, with 415 gribbles on the upper, to 450 on the lower side. There were 260 gribbles on the upper to 275 on the lower surface of the smooth panels. Most studies show greatest infestation on the undersides and confirms the effect of light on site selection. The mean level of attack in this experiment was 3.3/cm^2, with a range between 0 and 10, or 70 per panel, but 80% of the squares contained no gribbles. The panel with the greatest number of gribbles contained 147 on the upper and 156 on the under side.

The design of this experiment allowed an analysis similar to that employed by Menzies and Widrig (1955) in their study of *Limnoria* aggregation. They concluded that the distribution of the infestation became markedly aggregated as the attack proceeded. Data from the Nanaimo experiment also showed this; the variance was 1.8 times the mean indicating a non-

TABLE 15. Vertical distribution of *Limnoria lignorum* attack on panels at fixed depths in Departure Bay, B.C. August 1981 to December 1983.

Depth (m) below Chart Datum	Total attack
–0.5	2
–1.0	9
–1.5	28
–2.0	21
–2.5	25
–3.0	33
–3.5	67
–4.0	111
–4.5	124
–5.0	167

TABLE 16. Total attack by two species of gribbles during the period from July 1962 to December 1964 on fir panels exposed at monthly intervals at four depths and three stations. Mean tidal range 0–4 m. (From Quayle 1965a).

Mean tidal range (0–4 m)	Cowichan Bay	Crofton	Nanaimo	Total
		Limnoria lignorum		
Surface	0	89	2	91
Half	0	0	0	0
Zero	1	89	46	136
Mud line	84	739	57	880
Total	85	917	105	1 926
		Limnoria tripunctata		
Surface	0	829	2	831
Half	0	0	0	24
Zero	0	16	8	24
Mud line	0	10	7	17
Total	0	855	17	872

random distribution (Elliot 1971). Other panel studies without design or statistical analysis showed that aggregative behaviour exists (Fig. 57).

Between August and September of 1989, a similar experiment with smooth panels and with full light exposure showed similar aggregative behaviour, but with nearly 100% of the attack on the under (dark) surfaces of the panels.

Vertical Distribution

As Jones (1963) has stated *L. lignorum* in Great Britain occupies mainly the lower section of the intertidal zone often extending to the mud line.

This is also the situation in British Columbia along with its occurrence at the surface on unprotected wooden floats.

Limnoria tripunctata, which also occurs in Great Britain, occupies a higher zone. No specific studies have been done on the vertical distribution of this species in British Columbia. A crude experiment with large collectors at Talbot Cove on East Redonda Island showed 76% of *L. tripunctata* at the 4 m tidal level against 28% at 1 m.

Naturally occurring populations of both species may be found at the 4 metre tidal level in the Strait of Georgia where the large tides of higher high water is about 5 m. In Departure Bay *L. lignorum* showed the typical pattern of increased attack with depth (Table 15).

The vertical distribution of both species along the lower east coast of Vancouver Island is shown in Table 16 (Quayle 1965a). At Crofton the mean seawater temperature varies between 7°C in winter to 13°C in summer.

Resistance of Timber to Gribble Attack

Neave (1960) investigated the comparative attack, by presumably *L. lignorum*, on six species of native British Columbia woods at Kyuquot on the west coast of Vancouver Island (Table 17). He showed that both heart and sapwood of all species to be susceptible to attack.

However, in general there is a decided preference for the softer, less lignified spring wood (Fig. 58).

A further series of monthly observations were carried out in 1955 and 1956 with fir panels 90 cm × 3 cm × 0.75 cm exposed only 60 cm from heavily infested logs. The results are shown in Table 18.

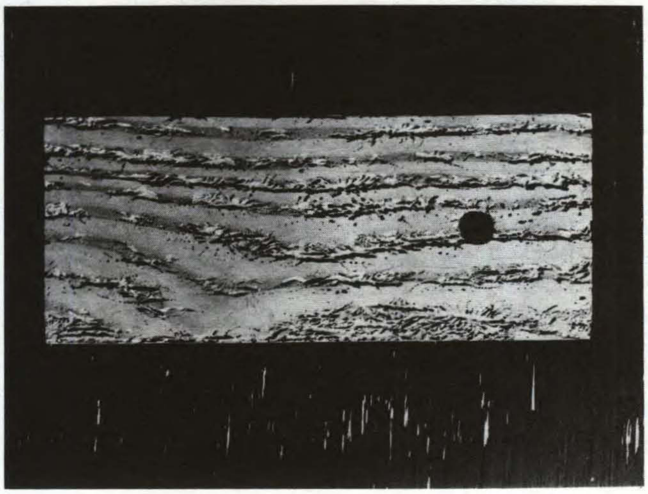

FIG. 58. Fir panels (15 × 6 × 1 cm) showing preference by *Limnoria* for the soft spring wood.

TABLE 17. Gribble attack expressed as number of points of entry per 900 sq. cm of submerged area at Kyuquot, 1934. (From Neave 1960).

Month	Fir Heart	Fir Sap	Hemlock	Alder	Cedar Red	Cedar Yellow	Spruce	Mean
Mar.	2 190	936	947	936	918	950	889	1 109
Apr.	1 152	468	1 215	144	846	360	819	715
May	711	693	450	171	729	468	459	526
June	90	103	183	24	88	8	138	91
July	12	34	60	21	24	28	30	30
Aug.	8	12	9	14	20	8	14	12
Sept.	0	0	0	0	0	0	0	0
Oct.	0	0	0	0	0	0	0	0
Nov.			22	0	16	24	12	11
Total	4 163	2 246	1 886	1 310	2 641	1 846	2 361	

Neave believed decreasing surface area as the wood flakes away may be the cause of enforced displacement of excess numbers. In the case of the pencil pointed intertidal untreated piling the wave action may be sufficient to remove the loose surface material and allow access to new wood. This is normally not the case with untreated floating logs where the gribble penetration is relatively shallow in most instances, for the enjoined surface tunnels prevents disposal of fecal materials and reduced access to fresh water for respiration.

Juniper (*Juniperous scopulorum*) was tested in Departure Bay and while not completely impervious to gribble attack it was significantly less than the spruce control.

TABLE 18. Gribble attack expressed as number of holes per 900 cm^2 after 1 month. (From Neave 1960).

Immersion period	1955	1956	Mean temperature °C
Jan. 15 – Feb. 15	810	810	5.2
Feb. 16 – Mar. 15	1 325	870	5.4
Mar. 16 – Apr. 15	3 420	3 360	6.6
Apr. 16 – May 15	1 084	2 300	10.1
May 16 – June 15	155	432	10.5
June 16 – July 15	14	218	11.0
July 16 – Aug. 15	56	60	12.5
Aug. 16 – Sept. 15	15	37	12.8
Sept. 16 – Oct. 15	21	15	7.2
Oct. 16 – Nov. 15	18	27	8.7
Nov. 16 – Dec. 15	27	42	8.9
Dec. 16 – Jan. 15	128	88	8.5

Migration

Migration studies have been based largely on the seasonality and intensity of attack on test panels and from these, conjectures on the migration stimulus. There is no mass migration in the general sense, but sporadic movement of a few individuals from the home base, and a gradual implementation of numbers after pioneer settlements. The limited swimming ability of gribbles carries them only a few metres (probably 3 or 4) from the home burrow. Doubtless currents are significant in migration, for to achieve any distance on their own, maintenance of a constant level is only by considerable effort. Once away from the burrow and partial transport by currents, chance of striking a suitable wood surface other than in an area of dense marine structures such as docks, moorings and slipways, is fairly remote, especially with no measurable chemotropism. Mortality of migrating *Limnoria* must be relatively high. Transport of populated driftwood, wooden vessels or equipment or water ballast are the obvious means of long distance transport. In British Columbia, where the concentration of driftwood is as high as anywhere in the world (Fig. 32) this would seem a prime method for gribble distribution but free floating pieces of gribble infested timber are uncommon. Other than at dock sites and log booming operations the main populations of *Limnoria* occur in waterlogged beach stranded logs (Fig. 59) or felled trees with the ends lying on the beach. Most samples in the distributional surveys in British Columbia were obtained from these sources.

Migration in *Limnoria* is studied by exposing wooden test blocks or panels and recording the number of burrows per unit area. Wallour (1958) established an arbitrary scale, given in modified form in Table 19 and similar to that for the Teredinidae. The time of exposure and the seasonal element should also be considered.

TABLE 19. Scale of ratings for *Limnoria* attack. (From Wallour 1958).

Number of tunnels per 6.5 cm^2	Attack rating
1	Trace
10	Slight
25	Moderate
50	Medium Heavy
75	Heavy
100[a]	Very Heavy

[a] This is near the limit of accurate counting.

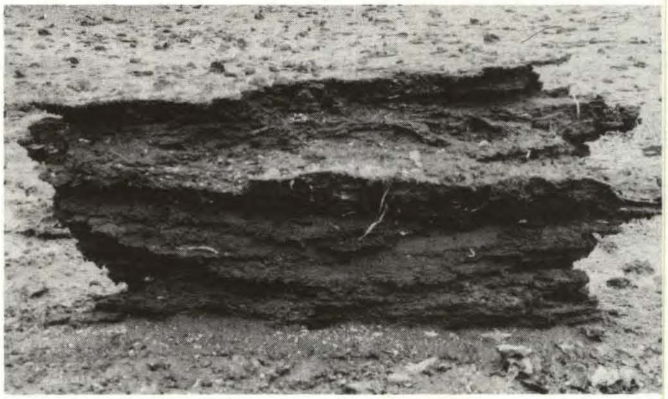

FIG. 59. Stranded portions of 1 m diameter yellow cedar log partially destroyed by both *Bankia* and *Limnoria* activity, mainly the latter.

Migration in British Columbia

Limnoria migration has been studied at widely separated geographical areas such as southern California, southern England and Japan. In British Columbia similar studies are those of Fraser (1923, 1925, 1928), Black (1934), Black and Elsey (1948), Neave (1960), Eltringham and Hockley (1961), and Quayle (1965a, b, 1974).

The earliest study of gribble (presumably *L. lignorum*) migration in British Columbia was by Fraser (1925) in 1923 at 7 sites over the British Columbia coast between Victoria and Prince Rupert. Quantitative data on the infestation rate or level were not given but the conclusion was that attack may occur throughout the year and areas with similar temperature and salinity conditions may have a wide variation in infestation levels.

Black and Elsey (1948) studied *Limnoria* migration at Departure Bay, Crescent Beach, and Vancouver Harbour in the Strait of Georgia; Bentinck Island, William Head and Esquimalt Harbour in the Strait of Juan de Fuca; and Masset Inlet and Prince Rupert on the north coast. The results for 1931 to 1933 are summarized as follows. It is presumed the gribble species involved was *L. lignorum*.

Prince Rupert Harbour

Gribble attack occurred throughout the year with up to one gribble per 3 cm² per month.

Masset Inlet

A light attack occurred throughout the year with a maximum of 1 per 5 cm² per month.

Crescent Beach

A heavy attack occurred in summer and in the early fall with a peak of 4 per cm² per month in July.

Vancouver Harbour

Attack was light or non-existent. One gribble per 10 cm² was found in August 1933.

Departure Bay

Attack was continuous and severe with infestation in 45 of the 51 months of the study. A maximum attack of nearly 2 gribbles per cm² per month occurred in the early spring of 1932.

Bentinck Island

Attack was consistent throughout the year.

William Head

The infestation was severe and continuous with up to 4 gribbles per cm² per month.

Esquimalt Harbour

The attack was continuous throughout the year with a peak of one gribble per cm² per month.

Results of this study demonstrated clearly that neither temperature or salinity was the principle element influencing intensity of settlement. It could be inferred that high salinity and low temperature were generally conducive to high levels of attack, as in the Juan de Fuca site, with Departure Bay an exception. Here water temperatures are relatively high and salinity relatively low, yet with a significant infestation rate. As the authors state there was no information on population levels in any of the areas. Placement of collectors relative to indigenous populations, shape and arrangement to the test panels may have considerable effect. Low rates of infestation at Prince Rupert and Masset Inlet may have been the effect of salinity. That *L. lignorum* migrates at quite low temperatures is shown at William Head where the annual near surface (1.8 m depth) temperature varies only between 7 and 11°C (1933) and a salinity between 30 and 31‰. At Departure Bay the 1 m temperature in 1933 ranged between 5 and 18°C and the salinity from 17 to 28‰. In Biological Station aquarium studies *L. lignorum* migration occurred regularly throughout the winter at water temperatures as low as 8°C, but only occasionally by *L. tripunctata*.

At about the same time as the Black and Elsey study in the early thirties, Johnson (1935) described in some detail the seasonal migration of *L. lignorum* at Friday Harbour, Washington where oceanographic conditions are similar to many areas in British Columbia. His studies showed 93.6% of the migration, by swimming animals, occurred from January to June inclusive, and 48.8% settled in March and April. He also associated seasonal migration with the main breeding season and Johnson and Menzies (1951) studied the migratory habit of *Limnoria tripunctata* in San Diego Harbour.

Port McNeil Study

An unpublished study of marine borer activity at Port McNeil on the north east coast of Vancouver Island in cooperation with a local logging company was conducted in 1941–42. Peak limnorian attack (almost certainly *L. lignorum*) occurred in November in 1941 and in June, July, and August in 1942 at a level 5 times greater than in 1941.

Kyuquot Study

Neave (1960) studied gribble (presumably *L. lignorum*) attack at Kyuquot on the west coast of Vancouver Island. He showed maximum attack at Kyuquot occurred in the period January to May when water temperatures ranged from 5° to 10°C. The level of attack reached 3 to 4 gribbles/cm^2 per month in March and April 1955.

Crofton Study

With the discovery of *L. tripunctata* at Crofton in 1961, the Forest Products Laboratory, Department of Public Works Canada and the Fisheries Research Board initiated a test panel study of gribble settlement at Nanaimo, Crofton and Cowichan Bay on the south east coast of Vancouver Island (Quayle 1964, 1965a). Fir panels (15 cm × 10 cm × 1 cm) were exposed (a) at monthly intervals at 4 depths from government wharves of creosote piling at those sites between July 1962 and December 1964 (Fig. 60) and (b) a group of 12 panels were exposed simultaneously and single panels removed at monthly intervals to provide an increasing period of exposure up to 12 months (Fig. 61).

At Cowichan Bay no *L. tripunctata* occurred, confirming results of field sampling that *L. lignorum* attack was slight although large populations occur on boomsticks and sinkers stranded on adjacent beaches. At Crofton the major attack by *L. tripunctata* was at the surface during summer; *L. lignorum* attack occurred in approximately the same total numbers but was spread throughout the year and heaviest at the mud line. At Nanaimo the attack of *L. tripunctata* was light in spite of large populations in the general area. Infestation by *L. lignorum* was also light, only 10% that at Crofton. The temperature profile as shown in Fig. 24 for Departure Bay is generally representative for the other stations.

Crofton Piling Study

In 1968 the Federal Department of Public Works established a study at Crofton to compare various pressure impregnated chemical treatments applied to Douglas fir piling for protection against marine borers. To determine the variability of the attack pattern of borers over the area of the experiment (30 m × 3 m) untreated fir test panels (15 cm × 10 cm × 1 cm) were attached to stainless steel stakes placed close to each test pile to float 0.5 m above the bottom and 4 m below the zero tidal level. Panels were changed at various intervals between November 15, 1968 and July 22, 1971 (Quayle 1974).

There were 5 chemical treatments: greensalt, Boliden, double greensalt and creosote, chemnite, and creosote, along with an untreated control, each treatment replicated 4 times. Thus each exposure utilized 24 panels and *L. lignorum* was the only gribble species to attack the panels. Probably the reason for this was depth, conforming to studies elsewhere which show *L. tripunctata* occurs near the surface. Also the nearest known concentrated population of this species was 1 km distant. The peak *L. lignorum* attack in 1969 was in mid-winter, and in 1970 and 1971 in late winter with a maximum attack of one burrow per cm^2 per month. The variability between pile positions was low. The indication from the panel study was that a direct comparative analysis of the treatment effects on the piling would not be affected by variations in the borer attack over the area of the experiment. The untreated control piling, driven in September 1968, were so damaged by *Bankia* attack they were no longer standing by the October 1969 inspection (Fig. 38).

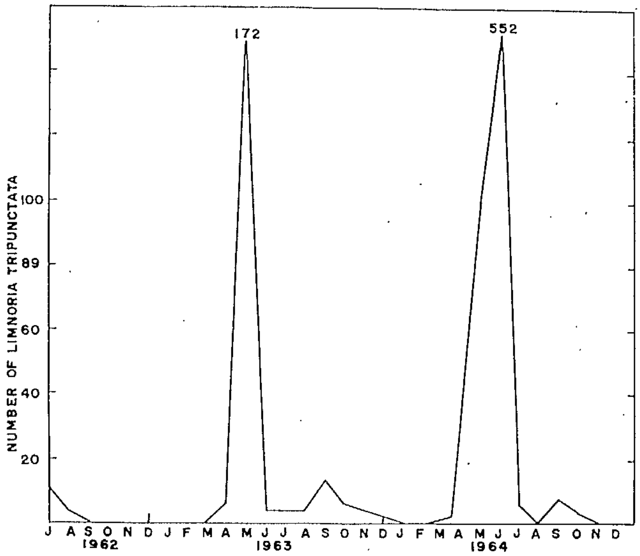

FIG. 60. Seasonal intensity of attack by the gribble (*Limnoria tripunctata*) on fir panels, 1962–64. Combined data from all depths and all stations, Cowichan, Crofton and Nanaimo. (From Quayle 1966)

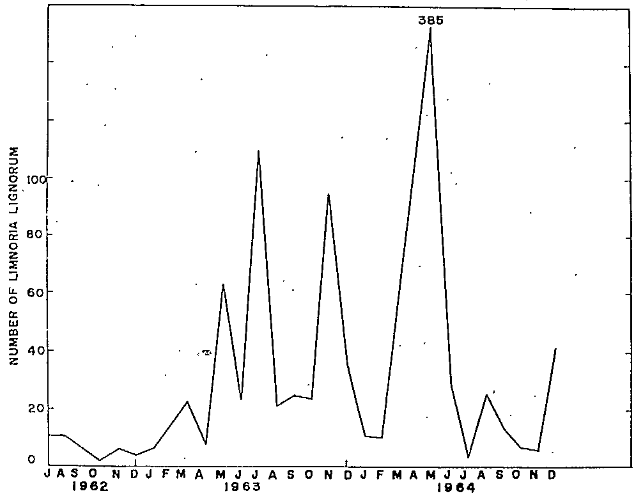

FIG. 61. Seasonal intensity of attack by the gribble (*Limnoria lignorum*) on fir panels, 1962–64. Combined data from all depths and all stations, Cowichan, Crofton and Nanaimo. (From Quayle 1966)

Departure Bay Study

In connection with a 1982–84 study on the possible changes in the distribution of *L. tripunctata* in the Strait of Georgia since 1961, a panel experiment to determine the migratory pattern of this species in Departure Bay was arranged (page 43). This consisted of a string of Douglas fir panels 15 cm × 10 cm × 1 cm held horizontally 50 cm apart and suspended from the Pacific Biological Station dock in 8 m of water. The deepest panel was close to the bottom, with the topmost panel at the +1.5 m tidal level. The panels were changed at intervals of 3 months between August 1, 1981 and December 15, 1983.

Departure Bay proper now has no known significant populations of *L. tripunctata* as all the docks have creosote protections or steel with little or no driftwood on the shore because of a large public beach and waterfront homes. However, there is a considerable population of both gribble species (dominantly *L. tripunctata*) in several large stranded logs about 200 m from where Newcastle Island Channel enters Departure Bay proper at Brechin Point in the southwest corner of the bay. This population is 1.8 km from the Biological Station, and while beyond the direct swimming reach of a gribble, current assisted transport by swimming or by drift wood should be possible for distribution over this distance. However, limnorian attack during this study was light and consisted only of *L. lignorum* with a maximum attack of 8 per panel per month. The mean attack on all panels at all depths over the 29 month period was 5 per panel of 180 cm^2. As expected for *L. lignorum*, maximum attack was near the bottom with some infestation within each 3 month period.

Results of this study (Table 20) are in marked contrast to that of Black and Elsey (1948) for Departure Bay where the attack was continuous and severe with infestation in 45 of the 51 months of the study and a peak attack of 1.8 per cm^2 per month. Since then (1931–33) there have been significant changes within Departure Bay with reduced numbers of marine structures, and a switch from untreated to treated construction timbers, with a consequent reduction in limnorian populations. There was a slight indication of reduced attack during the summer (18°C), but there is some movement throughout the year. Migration occurred at temperatures as low as 7°C. As with other studies the intensity of attack increased with depth. It is significant there was no *L. tripunctata* attack. Figure 24 shows a typical temperature profile for Departure Bay.

TABLE 20. Seasonal attack of the wood borer *L. lignorum* on fir panels in Departure Bay, 1981–83.

Date	Total attack	Mean monthly surface water temperature °C
Aug.–Nov. 1981	69	12.6
Dec.–Feb.	69	5.9
Mar.–Apr.	89	8.2
May–June	47	10.6
July–Aug.	26	16.9
Sept.–Oct.	32	12.8
Nov.–Jan. 1982	110	6.6
Feb.–Mar.	99	6.4
Apr.–June	44	11.8
July–Aug.	69	17.0
Sept.–Dec.	23	9.9

Latitude and *Limnoria* Attack

As with *Bankia* the British Columbia Research Council studies (1966, Tidelines, Vol. VIII, No. 8) showed similar wide variations in limnorian attack between site, season and year (Table 21). Except for San Francisco Bay, where three species of *Limnoria* occur, the single species involved at all other sites was *L. lignorum*. These variations also emphasize the need for continuous monitoring to provide adequate control.

TABLE 21. Geographical differences in *Limnoria* attack per 0.9 m^2 at three depths to 6 m for the years 1960 and 1964.

Month	Alaska		Mid B.C. Coast		Lower B.C. Coast		Puget Sound		San Francisco Bay	
Jan.	0	1	14	8	6	0	0	1	1	0
Feb.	2	3	7	17	2	0	0	1	24	0
Mar.	5	6	43	58	12	1	2	0	344	53
Apr.	34	9	15	198	14	0	0	4	2 263	388
May	11	12	27	233	12	0	0	4	285	181
June	0	2	29	389	6	0	0	0	73	84
July	0	0	14	294	4	0	1	0	11	4
Aug.	0	1	32	100	8	0	4	0	52	38
Sept.	0	1	24	17	18	0	5	0	170	10
Oct.	0	2	11	14	3	1	1	0	285	13
Nov.	0	3	20	25	2	0	0	1	1	1
Dec.	2	10	11	10	3	0	3	4	19	0
Total	54	44	247	1 363	90	2	22	15	3 528	772

Origin of *Limnoria tripunctata* in British Columbia

Until 1951 it was assumed that *Limnoria lignorum* was the only species on the west coast of North America. In that year *L. tripunctata* from Pacific Beach, California was described as a new species (Menzies 1951). Its range extended from San Francisco south to Mexico.

In May 1961 this species was reported from Crofton, B.C. with the identification confirmed by Menzies himself. A survey of 150 sites between south eastern Alaska and the State of Washington (Quayle 1965a) indicated a discontinuous distribution and a high correlation between its occurrence and sites of Japanese oyster seed plantings. Of 21 such sites in British Columbia and Washington State, 19 contained *L. tripunctata*.

Beginning about 1930, seed of the Japanese oyster (*Crassostrea gigas*), now known as the Pacific oyster, was packed in wooden cases for annual shipments to the west coast of North America (Quayle 1969). After packing in Japan the cases were stored in the intertidal zone until enough had accumulated to form a freighter deck cargo for shipment. During this time the wooden cases were capable of being infested with *Limnoria*. As deck cargo, a covering of wetted rice matting permitted survival conditions for the oyster seed as well as any gribbles which may have entered the wood of the containers. On arrival at the west coast the cases were frequently stored again in the intertidal zone prior to the seed spreading operation. Wood from these cases often escaped to become driftwood, providing an opportunity for *Limnoria* to be distributed in the new environment.

An alternative route might have been the northward extension of established populations from San Francisco Bay by means of wooden vessels. If this were so it would be expected that the temperate water *L. quadripunctata*, which also occurs in San Francisco Bay would be the species to invade boreal waters rather than the more tropical *L. tripunctata*. This has not occurred.

There has been a question as to whether the British Columbia *L. tripunctata* is in fact that species (Carlton 1979), but recent studies at Oregon State University have provided confirmation (Gonor, correspondence).

Distribution of *Limnoria tripunctata* in British Columbia

As soon as the existence of this species in these waters became known, a broad study of its distribution between Prince Rupert (54° N) and Yaquina Bay, Oregon (43° N) was made. More than 150 samples containing about 13 000 specimens were collected (Quayle 1965a, b). Of these samples, 122 were taken from the Strait of Georgia and the lower west coast of Vancouver Island (Fig. 62). Of these 71 samples contained only *L. lignorum* and 31 had only *L. tripunctata*. Of the total number of specimens in these samples the proportion of the two species was nearly equal although the sample size varied considerably.

In 1982–84 another survey was made to determine whether changes in distribution had occurred. This was confined mainly to the Strait of Georgia and the lower part of the west coast of Vancouver Island (Quayle, unpublished data).

As in the previous survey, samples were obtained by chipping gribble infested wood from standing or floating structures, or from beach stranded logs whose appearance and situation indicated a long-term stay at that site. Samples of an adequate size (circa 200 gribbles) were not always available. The gribbles were dissected from the wood chips, identified and counted.

Survey Results

A total of 78 samples containing 11 000 animals of both species were taken in the 1982–84 survey. Several samples were obtained from the west coast of Vancouver Island between Barkley Sound and Esperanza Inlet. There were 48 new sites and 30 repeat samplings from the previous survey. Of the 78 samples, 30 contained both species, 21 with only *L. lignorum* and 14 with *L. tripunctata* alone. At the 48 new sites, 15 contained both species, 26 with only *L. lignorum* and 7 with *L. tripunctata* alone. The occurrence of the latter species in the new sampling sites was not unexpected because of contiguity with sites containing that species. Five resampled sites had a significantly changed status with 3 showing increased numbers of *L. tripunctata*.

The proportion of this species in the total gribble population did not differ significantly in the 20 years between the 2 sampling periods, with 52.8% in 1962 and 51.7% in 1982–84. At repeated sampling sites in the 2 periods, the *L. lignorum* to *L. tripunctata* ratio changed from 0.89 in 1962 to 0.60 in 1982–84.

Along the British Columbia coast there is an enormous quantity of stranded and floating miscellaneous wood debris as described on page 34. This

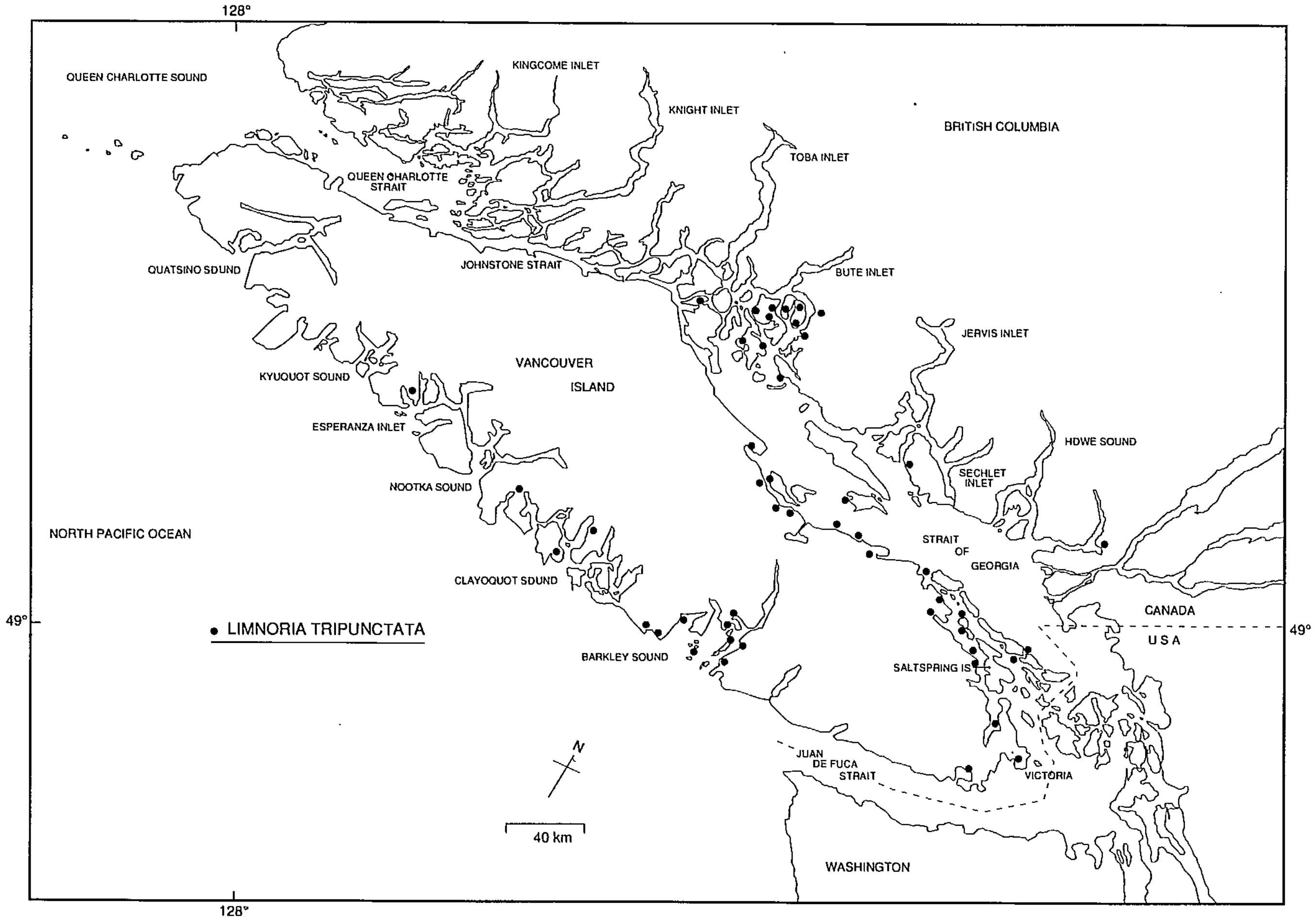

FIG. 62. Vancouver Island, British Columbia showing the distribution of the gribble, *Limnoria tripunctata*, as of 1984.

moves about from area to area with wind and tide, providing a habitat and transport for wood borers. The native gribble species is ubiquitous throughout British Columbia coastal waters wherever suitable habitat and salinity conditions occur, yet a number of stations had only *L. tripunctata* and no *L. lignorum*. It appears the introduced species has been successful to the point where it can compete with, and in some cases possibly supplant the indigenous species. In the 21 new sampling sites with *L. tripunctata* there were 5 with no direct connection with oyster seed plantings from Japan, which ceased in the early 1960's. Others were reasonably close to previous sampling sites containing that species. Only in a few instances were *L. tripunctata* associated with log storage sites without oyster planting implications. However water temperature must be an important factor. There is a rough correlation between the occurrence of this species and enclosed or semi-enclosed bays where there is more potential for higher water temperatures than in open waters. Wave protected bays tend to be oyster growing sites. The high correlation between Japanese oyster seed plantings and *L. tripunctata* maintained in the 1982–84 survey.

In summary there has been no significant change in the distribution of *L. tripunctata* between 1962 and 1982, beyond unexplained new occurrences 200 km further up the west coast of Vancouver Island (i.e. from Sidney Inlet to Esperanza Inlet), although this may have been due to the sampling program.

Control

The destructive ability of *Limnoria* lies in numbers rather than size. A piling of intermediate size has been estimated to contain a population of 200 000 animals (Menzies and Turner 1957), each capable of consuming 20 g of wood per year. Before the advent of chemical treatments (i.e. creosote) for marine timber installations, *Limnoria* was a concern in British Columbia as demonstrated by intertidal piling where the wood at the mud line could almost be completely destroyed, with the attack receding up the piling for a half metre or so, giving the appearance of a sharpened pencil (Fig. 47). These are now rarely seen for most permanent piles are now creosote treated. Figure 59 shows a section of a beached yellow cedar log more than a metre in diameter that has been almost destroyed by both species of gribbles.

Wooden vessels can be protected if care is given to the application of antifouling paints. At present the main cause for concern lies with untreated float logs or boom sticks, whose buoyancy would be materially reduced by creosote treatment.

However, *Limnoria* damage is slight relative to that by shipworms and an initial gribble attack provides a friable layer of wood 1 or 2 cm thick which reduces the possibility of shipworm attack.

In British Columbia creosoted treated marine piling, properly installed and maintained, provides adequate protection against gribbles, including *L. tripunctata*. In Los Angeles, California, this species can reduce the life of a creosote treated piling to about 6 years instead of a possible 40 years in northern waters (Beckman et al. 1957). The reason for intolerance to creosote in northern waters is not known unless related to different bacterial flora and water temperatures. However, in British Columbia, if the outer creosote layer is ruptured, both gribble species will attack the non-creosoted interior of the piling and cause damage. A minimum temperature of 21°C appears to be required for this species to attack creosoted material.

Detection of initial activity by *Limnoria* is shown by shallow etchings on the wood surface. There can be no mistaking serious attack evidenced by the eroded surface of the wood (Fig. 58). Species determination requires microscopic examination.

Bramhall (1960) in his survey of service records of marine wooden installations in British Columbia attributes damage by gribbles only to improperly treated or installed creosoted or untreated material. Of nearly 60 records of piling installations considered, only 4 showed significant damage by *Limnoria*.

Although wide spread and abundant it is doubtful *Limnoria* can be incriminated as a major destructive force in wooden marine installations in British Columbia waters since the introduction of adequate preventive measures.

Marine sanitation, as suggested by Quayle (1956) for *Bankia setacea*, could also reduce maintenance and decrease in *Limnoria* populations significantly. The main source of samples used in the British Columbia gribble surveys were infested logs stranded on intertidal beaches. The increased use of log barges rather than rafts for transporting logs and dry land sorting are factors in reducing marine borer breeding populations. Replacement of float logs by pontoons of synthetic materials also assists.

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Glossary

adductor muscle	muscle attached to both valves of a mollusc
afferent	carrying toward the heart
alkaloid	organic chemical found in plants
amphipod	a group of small crustaceans with both swimming and walking appendages
anaerobic	without oxygen
antenna	an anterior appendage of crustaceans
aorta	principal blood vessel from the heart
appendix	in shipworms a blind tubal attachment of the stomach (also called the caecum)
apophyses	curved calcareous elongate rods from the umbonal region of all teredinid and some pholad shells
aragonite	a form of crystalline calcium carbonate
article	a section of a crustacean appendage
auricle	chamber of the heart
auricle	lobed extension of the teredinid shell
awn	lateral extension of the pallet cone
bag boom	a loose cluster of logs enclosed by a connected circle of other logs
bivalve	a mollusc with two valves making up the shell
boom	a rectangular collection of logs arranged longitudinally and enclosed by a connected string of other logs
branchia	a respiratory organ made up of filaments
bryozoa	a colony of minute invertebrates either encrusting or erect
caecum	in shipworms a blind tubal attachment of the stomach (also called the appendix)
carina	a rib-like structure
cephalic	pertaining to the head
cephalon	head with eyes and antennae
cellulolytic	having ability to hydrolyse cellulose
chemotactic	movement of an organism in the direction of a chemical stimulus
chitin	exoskeletal material of most crustaceans
cilia	microscopic vibrating hair like projections
connective	a bundle or nerve fibres uniting two nerve centres
condyle	a smooth rounded protuberance on the shipworm shell
copepod	small mainly pelagic crustacean
crustacea	jointed leg animals with a chitinous exoskeleton (crabs and shrimps)
crystalline style	in some molluscan stomachs, a rod shaped gelatinous organ concerned with digestion
ctenidia	a comb-like structure of filaments concerned with respiration and food collection
dead head	a floating log with one end submerged
demibranch	a leaf of a molluscan gill
denticle	a small tooth-like structure
diurnal	during a day
diverticula	in mollusca, sac-like extensions of the stomach
dorsal	the back or upper part
ecdysis	casting off of a shell or outer skin
efferent	away from the heart
enzyme	chemical produced by living cells which aid but do not take part in chemical reactions
epibrachium	that part of the body cavity above the gills
euryhaline	adaptable to a wide salinity range
excurrent	discharge stream
extracellular	referring to digestion outside individual cells
faeces (feces)	indigestible residues of the digestive tract
flagellum	a large cilium
follicle	a small sac-like structure
frass	any type of excrement
gastropod	a single valved mollusc often coiled
ganglia	an aggregation of nerve cells
gamete	a mature reproductive or germ cell
genus	a category of closely related species
gonad	tissue from which eggs or sperms are formed
gonopore	aperture through which germ cells leave the body
gribble	common name for the wood-boring isopod *Limnoria*
halocline	an area of sharp vertical salinity change
hermaphrodite	having both male and female reproductive organs
hydroid	colonial phase of a medusa

incurrent	drawing in of a liquid
intracellular	within the cell
invertebrate	an animal without a backbone
labial palp	a sensory appendage in the mouth region
lamella	a gill plate of filaments
larva	a motile immature stage between the fertilized egg and the adult form
mantle	a shell secreting soft fold of tissue enclosing the body of some mollusca
mandible	a jaw part
maxilliped	a mouth appendage of many crustaceans
metabolize	utilization of nutritive materials
micron	one thousandth of a millimetre
Mollusca	a group of invertebrate animals, with shells of various forms
myoglobin	a red iron-containing protein pigment in muscles
nacre	iridescent calcareous inner layer of a molluscan shell
nematode	slender unsegmented worm
oesophagus	canal between the mouth and stomach
oostegite	brood pouch formed by plates on the thoracic limbs of some higher crustacea
ostia	mouth-like apertures
otocyst	sac lined with sensory hairlets
ovocyte	egg cell
oviparous	egg laying
pallet	calcareous plug of various forms to close the entry of shipworm tunnels
palp	a sensory appendage
periostracum	horny outer layer of a molluscan shell
pedal	pertaining to the foot
pericardial	space or membrane surrounding the heart
peraeon	the 7 somites of the thorax of some Crustacea
peritrophic	surrounding the gut
pile	large timber driven into the sea bed
plankton	floating or weakly swimming small animals and plants
planktotrophic	feeding on plankton
pleon	abdominal region of some Crustacea
pleotelson or telson	the posterior terminal segment of some Crustacea
pleopod	abdominal appendages for swimming and respiration of some Crustacea
polychaete annelid	segmented worm with setae
protoporphyrin	a purple porphyrin acid
protractor	muscle causing movement away from the body
protandry	initial sex male
protozoa	unicellular animals
pseudofeces	false feces – waste material not discharged through the digestive tract
radiograph	an X-ray picture
retractor	muscle causing movement toward the body
resorption	conversion to another form
relict	germ cells remaining after spawning
salinity	in oceanography, the salt content of sea water usually measured in parts per thousand
seed	young molluscs also spat
setting	the process whereby molluscan larvae become attached to a substrate
shipworm	a wood-boring marine mollusc
siphon	in mollusca a tubular structure by which water enters or leaves the shell cavity
sinus	an ill defined blood vessel
sinker	a waterlogged log which sinks to the bottom
somite	one division of a segmented animal
species	a group of closely allied individuals
spermatocyte	a male reproductive cell
spatting	another term for setting, the attachment of molluscan larvae to a substrate
spawn	common collective term for eggs and sperms
suprabranchial	that part of the body cavity above the gills
swifter	a log or a steel cable holding together the two sides of a log boom
telson	the last or sixth somite of the abdominal region of some certain Crustacea
thigmotropism	response or reaction of an animal to the stimulus of contact or touch
tracheid	water conducting element in wood
turbellarian	one of a group of flatworms
typhlosole	a longitudinal infolding of the wall of an intestine increasing the absorptive area
umbo	beak-like projection representing the oldest part of a molluscan shell
uropod	an appendage of the abdominal somite preceding the telson of some Crustacea
valve	one of the sections comprising the shell of some mollusca
veliger	the second larval stage of most Mollusca and characterized by a velum
velum	a protrusile ciliated platform of molluscan larvae
ventricle	the main contractile chamber of the heart