BULLETIN OF MARINE SCIENCE, 60(2): 482–493, 1997

SURVEY OF THE GENERA *POLYDORA*, *BOCCARDIELLA* AND *BOCCARDIA* (POLYCHAETA, SPIONIDAE) IN BARKLEY SOUND (VANCOUVER ISLAND, CANADA), WITH SPECIAL REFERENCE TO BORING ACTIVITY

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ABSTRACT

Habitat types and boring activity of 10 species of *Polydora*, *Boccardiella* and *Boccardia* from Barkley Sound (west coast of Vancouver Island, Canada) were documented from August to December 1994. Four species of *Polydora* (*P. giardi*, *P. convexa*, *P. pygidialis*, *P. limicola*) and one of *Boccardia* (*B. berkeleyorum*) were obtained from calcareous substrata: mollusc shells, coralline alga, and barnacles. Two species of *Polydora* (*P. socialis*, *P. ligni*), one species of *Boccardiella* (*B. hamata*) and two species of *Boccardia* (*B. proboscidea*, *B. columbiana*) occurred in mud deposits, including mud from crevices in shells and sandstone rocks. It is suggested that there are boring and non-boring types as none of the species used both habitat types in Barkley Sound. Morphological characteristics of burrows made by three boring species were also investigated using soft x-ray analysis. The structure of the burrows was found to be species specific. Soft x-ray was useful in both identifing the boring species and determining the degree of infestation without breaking the shells.

Spionid polychaetes of the genera *Polydora*, *Boccardiella* and *Boccardia* are found in a wide variety of substrata from soft clays or mud to hard calcareous materials (Blake and Evans, 1972; Read, 1975). Some species are widely known for their boring activities in mollusc shells, corals, coralline algae and barnacles. The effects of boring *Polydora* on their hosts have been studied in commercially important molluscs, mainly scallops (Evans, 1969; Mori et al., 1985), oysters (Korringa, 1951; Wargo and Ford, 1993), abalones (Kojima and Imajima, 1982), and mussels (Kent, 1979, 1981; Ambariyanto, 1991). The boring mechanism, however, has not yet been fully elucidated despite numerous studies on this subject (McIntosh, 1868; Hannerz, 1956; Hempel, 1957; Dorsett, 1961; Haigler, 1969; Zottoli and Carriker, 1974).

In previous papers, we examined the ecological characteristics of boring *Polydora* species such as life history (Sato-Okoshi, 1994), reproduction (Sato-Okoshi et al., 1990), condition of infestation (Mori et al., 1985), list of boring species and characters of burrow morphology (Imajima and Sato, 1984; Sato-Okoshi and Nomura, 1990), and microstructure of mollusc shells infested with boring species (Sato-Okoshi and Okoshi, 1993; 1966). Burrows of boring *Polydora* species from Japanese coasts contain morphological characters that are distinctive for each species as determined by analysis of soft x-ray photographs. This technique was found to be useful in identifying the boring species, and also in determining the degree of infestation without breaking the shells (Sato-Okoshi and Nomura, 1990).

While most species of *Polydora*, *Boccardiella Boccardia* and *Pseudopolydora* have been reported to occur mainly in either calcareous substrata or non-calcareous substrata, 6 out of 70 species occur in both calcareous and non-calcareous substrata (Blake and Evans, 1972). Moreover, there are many descriptions of species inhabiting more than one habitat type (i.e., boring into calcareous substrata and inhabiting non-calcareous substrata). In the present study we examine 10 species, documenting their use of habitat types and characterizing boring activity. The species are of either of two types: (1) inhabiting burrows excavated in calcareous substrata- boring type, or (2) inhabiting non-calcareous substrata- non-boring type.

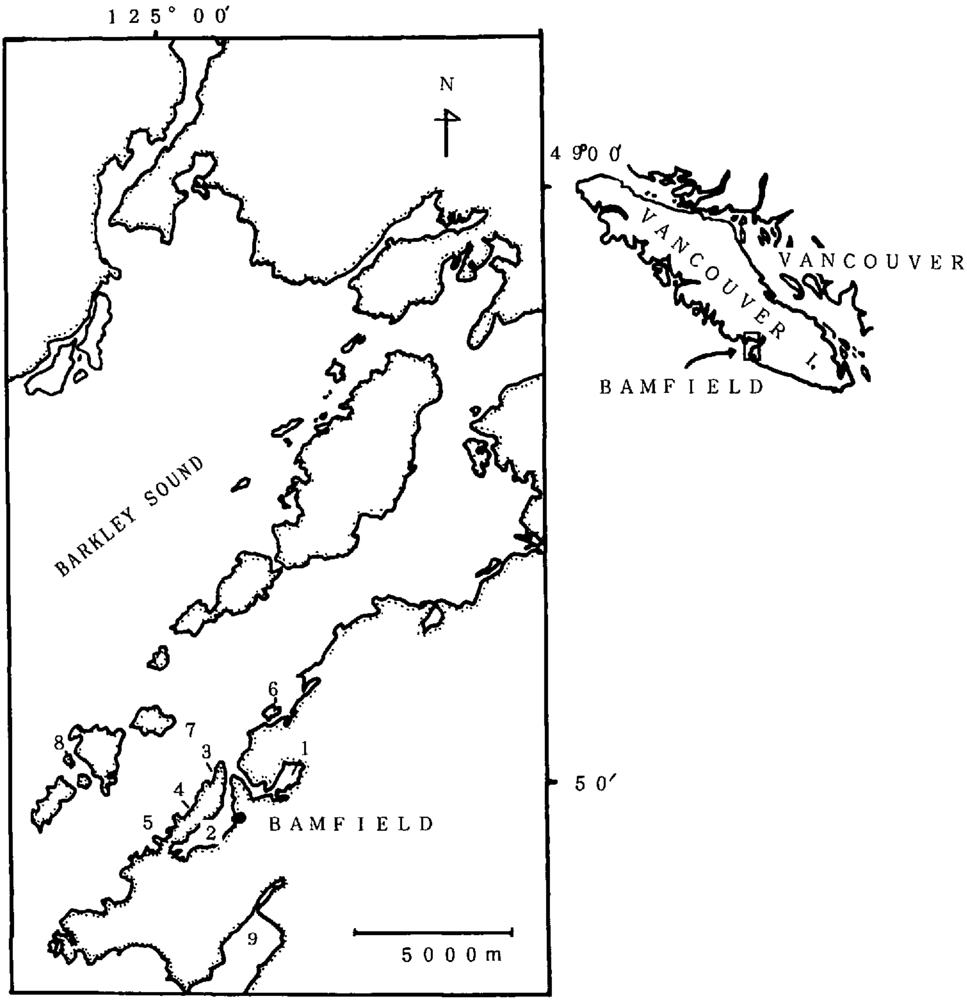

Figure 1. Sampling sites in Barkley Sound, Vancouver Island. 1. Grappler Inlet. 2. Bamfield Inlet. 3. Scott Bay. 4. Brady's Beach. 5. 1st & 2nd Beaches. 6. Dixon Island. 7. Near Self Point, Helby Island. 8. Seppings Island. 9. Pachena Bay.

Previous reports described *Polydora* and *Boccardia* species from Vancouver Island, Canada (Berkeley, E., 1927; Berkeley, C., 1968; Berkeley and Berkeley, 1936; 1950; 1952; 1954; Blake and Woodwick, 1971a; Blake, 1979; Hobson and Banse, 1981; Strathmann, 1987). However, in virtually all of these studies, samples were mostly collected from protected environments on the east coast, and very few from open coast environments. We document the occurrence of *Polydora, Boccardiella* and *Boccardia* species inhabiting open coast environments in Barkley Sound, on the west coast of Vancouver Island.

Materials and Methods

Polydora, Boccardiella and *Boccardia* species were collected at nine sites near the Bamfield Marine Station, in Barkley Sound (Fig. 1) from August to December 1994. Boring species were extracted from the shells of various molluscs (*Hinnites giganteus, Chlamys hastata, Panopea generosa, Pododesmus cepio, Mytilus californianus, Clinocardium nuttallii, Crassostrea gigas, Ostrea lurida, Haliotis* *kamtschatkana, Polinices lewisii, Acmaea mitra, Diodora aspera*), a coralline alga (*Lithothamnium* sp.), and from two barnacle species (*Balanus cariosus* and *B. nubilus*). The worms were extracted by fracturing the shells and coralline algae with cutting pliers and a hammer. *Hinnites giganteus, Chlamys hastata, Panopea generosa* and *Haliotis kamtschatkana* were obtained by scuba diving at a depth of 4.5–13.5 m near Self Point, Helby Island (48°51'N, 125°09'W), while those of the other species were collected from the intertidal zone. Non-boring species were obtained by cracking sandstone rocks with a hammer or by sieving sand and mud through a 1 mm mesh sieve.

Burrow morphology was investigated using soft x-ray analysis (SOFRON SRO-M50) after removing the flesh.

Results

Characteristics of Investigated Species and Their Habitats

Boring Species.—Five species were found to inhabit burrows excavated in calcareous substrata: *Polydora giardi, P. convexa, P. pygidialis, P. limicola* and *Boccardia berkeleyorum* (Table 1).

Polydora giardi (Mesnil)

Measuring 8 mm in length, 0.4 mm in width at 5th setiger, 80 setigers on average. Small and mucoid species. Occurred commonly in Barkley Sound. The Barkley Sound specimens match the morphological descriptions of specimens from France given by Mesnil (1896), from Australia by Blake and Kudenov (1978), and from Mexico by Blake (1981). This species was extracted from various intertidal and subtidal mollusc shells, barnacles, and coralline alga. A large number of specimens were extracted from coralline alga *Lithothamnium* sp. in tide pools. This was the only species found to bore into coralline alga. Gametocytes and egg capsules were found in the field from September through December. *Polydora giardi* was found in dense aggregations, especially in shells of living *Hinnites giganteus* and shells of dead *Panopea generosa*. In shells of living *Hinnites giganteus,* burrows were observed to overlap mostly near the hinge. On the other hand, burrows were observed all over the shells of dead *Panopea generosa*. From 10 to 186 individuals were extracted from each valve.

Polydora convexa Blake and Woodwick

Up to 100 mm in length (range 30–100 mm), 1.8 mm in width at 5th setiger, over 200 setigers. The specimens from Barkley Sound match the morphological descriptions of specimens from California by Blake and Woodwick (1971b) and from Mexico by Blake (1981) except for body length. Body length was greater in Barkley Sound than in California (only up to 30 mm). This was the longest species and easy to distinguish according to its special notosetae in the posterior setigers. All individuals had gametocytes in their coelom throughout this survey. *Polydora convexa* occurred commonly in living and dead mollusc and barnacle shells. A maximum of 30 individuals occurred in one valve.

Polydora pygidialis Blake and Woodwick

Measuring 12 mm in length, 0.6 mm in width at 5th setiger, 100 setigers on average. Easy to identify due to its brown to blackish palps and scoop-like pygidium. However, some specimens did not have those conspicuous dark colors. The Barkley Sound specimens match the morphological descriptions of specimens from California by Blake and Woodwick (1971b). *Polydora pygidialis* was very common especially in mollusc shells in inlets. This species was also found in limpet shells. Gametocytes were present in the individuals collected in December, and one individual also had egg capsules.

Table 1. Boring species of *Polydora* and *Boccardia* from calcareous substrata in Barkley Sound (L = living, D = dead)

Species	Host	Locality
Polydora giardi	Coralline alga	
	Lithothamnium sp.[L]	1st and 2nd Beaches
		Scott Bay
		Seppings Island
	Mollusc shells	
	Hinnites giganteus[L]	Near Self Point, Helby Island
	Panopea generosa[L]	Self Point
	Pododesmus cepio[L]	Self Point
	Mytilus californianus[L]	Brady's Beach
		1st and 2nd Beaches
		Grappler Inlet
	Haliotis kamtschatkana[L]	Self Point
	Barnacles	
	Balanus cariosus[L]	1st and 2nd Beaches
P. convexa	Mollusc shells	
	Hinnites giganteus[L]	Self Point
	Chlamys hastata[L]	Self Point
	Panopea generosa[D]	Self Point
	Polinices lewisii[D]	Self Point
	Mytilus californianus[L]	1st and 2nd Beaches
		Brady's Beach
		Grappler Inlet
	Barnacles	
	Balanus cariosus[L]	1st and 2nd Beaches
	Balanus nubilus[L]	Self Point
P. pygidialis	Mollusc shells	
	Hinnites giganteus[L]	Self Point
	Panopea generosa[D]	Self Point
	Pododesmus cepio[L]	Grappler Inlet
	Mytilus californianus[L]	Grappler Inlet
	Clinocardium nuttalii[L]	Grappler Inlet
	Ostrea lurida[L]	Grappler Inlet
	Haliotis kamtschatkana[L]	Self Point
	Acmaea mitra[L]	1st and 2nd Beaches
		Scott Bay
		Seppings Island
	Diodora aspera[L]	1st and 2nd Beaches
		Scott Bay
		Seppings Island
	Barnacles	
	Balanus cariosus[L]	1st and 2nd Beaches
P. limicola	Mollusc shells	
	Hinnites giganteus[L]	Self Point
	Panopea generosa[D]	Self Point
	Mytilus californianus[L]	1st and 2nd Beaches
		Brady's Beach
		Pachena Bay
	Barnacles	
	Balanus cariosus[L]	1st and 2nd Beaches
		Pachena Bay
Boccardia berkeleyorum	Mollusc shells	
	Hinnites giganteus[L]	Self Point
	Panopea generosa[D]	Self Point

Table 2. Non-boring species of *Polydora*, *Boccardiella* and *Boccardia* in Barkley Sound

Species	Habitat	Locality
Polydora socialis	Mud in crevices of sandstone rocks and *Crassostrea gigas* shells	Grappler Inlet
P. ligni	Resistant mud tubes	Bamfield Inlet
Boccardia proboscidea	Mud in crevices of sandstone rocks and *Balanus cariosus* shells	Scott Bay Grappler Inlet Seppings Island
B. columbiana	Mud in crevices of sandstone rocks and *Crassostrea gigas* and *Mytilus california* shells	Scott Bay Grappler Inlet Pachena Bay Dixon Island
Boccardiella hamata	Mud in crevices of sandstone rocks	Scott Bay

Polydora limicola Annenkova

Measuring 30 mm in length, 0.8 mm in width at 5th setiger, 150 setigers on average. Easy to distinguish by its long palps crossed by numerous black bars. The specimens from Barkley Sound match the morphological descriptions given by Annenkova (1934) and Hartman (1969) from California except for the number of setigers. Hartman (1969) reported that the number of segments was only 80–90 in California, but the length and the width of specimens from both sites are about the same (18–25 mm in length, 1 mm in width in California). One to three individuals were found per shell.

Boccardia berkeleyorum Blake and Woodwick

Measuring 40 mm in length, 2 mm in width at 5th setiger, 120 setigers on average. Large species with transparent palps containing yellowish white dots. The specimens from Barkley Sound match the morphological description of specimens from California by Blake and Woodwick (1971a) except for body length and the color of the palps. The specimens described from California were smaller (5–14 mm in length). Collected only from the shells of living *Hinnites giganteus*. Two to 3 individuals occurred in each valve. Gametocytes were present throughout this survey.

Non-boring Species.—Five non-boring species were found: *Polydora socialis, P. ligni, Boccardia proboscidea, B. columbiana,* and *Boccardiella hamata* (Table 2). All inhabited crevices in sandstone rocks or intertidal mud deposits. Three of these species (*P. socialis, B. proboscidea* and *B. columbiana*) were also extracted from calcareous substrata, but these inhabited mud deposits located in shell crevices and did not burrow into the shell material itself.

Polydora socialis (Schmarda)

Up to 50 mm in length, 1.5 mm in width at 5th setiger, 130 setigers on average. The specimens from Barkley Sound match the morphological descriptions of the specimens from the east coast of North America by Blake (1971) and from west coast of Canada by Blake (1979). The caruncle extends to setiger 7; larval pigmentation is retained on the dorsal and ventral side of most adults. This is a large species, occurring commonly in mud within the crevices of sandstone rocks. Only one individual was extracted from the mud within the crevice of a shell of living *Crassostrea gigas*. However, no burrows were found in the shell material. Gametocytes and egg capsules were present in October and November.

Polydora ligni Webster

Measuring 20 mm in length, 1.5 mm in width at 5th setiger, 80 setigers on average. The specimens from Barkley Sound match the morphological descriptions of the specimens from the east coast of Vancouver Island by Berkeley and Berkeley (1952), from the east coast of North America by Blake (1971) and from Australia by Blake and Kudenov (1978). Occurred commonly in intertidal mud. This species builds resistant mud tubes. High densities were observed in the Bamfield Inlet.

Boccardia proboscidea Hartman

Measuring 40 mm in length, 1.6 mm in width at 5th setiger, 100 setigers on average. Large species with strong transparent palps. Notosetae of setiger 1 are short, average of 0.1 mm in length. The specimens from Barkley Sound match the morphological descriptions of the specimens from California by Hartman (1940), from the west coast of Vancouver Island by Berkeley and Berkeley (1952), by Woodwick (1963) and from San Francisco Bay by Light (1978). Black pigmentation along the prostomial ridge and the palpal grooves can be seen in live specimens. Very common in Barkley Sound, inhabiting mud in crevices of sandstone rocks. Many egg capsules were present from August to October. This species exhibited lecithotrophic development and had different development characteristics (unpublished).

Boccardia columbiana Berkeley

Measuring 40 mm in length, 1.5 mm in width at 5th setiger, 100 setigers on average. Large species, common in Barkley Sound. It is important to distinguish this species from *B. proboscidea* as these two are very similar both morphologically and ecologically. Identification is possible by carefully examining the length of the first notosetae. Notosetae of setiger 1 are very long, average of 0.55 mm in length, and reach to the anterior end of peristomium, whereas they are much shorter in *B. proboscidea*. The specimens from Barkley Sound match the morphological descriptions of specimens from Vancouver Island by Berkeley (1927), Woodwick (1963) and Hartman (1969), except for body size. Specimens from Barkley Sound are larger than the specimens reported previously (maximum of 15 mm in length). Therefore, body length cannot be used as a character to distinguish *B. columbiana* from *B. proboscidea* as previously suggested. The species mainly inhabits mud within the crevices of sandstone rocks. Only two individuals were extracted from mud in the crevices of *Crassostrea gigas* shells, but they had not bored into the shells.

Boccardiella hamata (Webster)

Measuring 20 mm in length, 1.3 mm in width at 5th setiger, 110 setigers on average. The specimens from Barkley Sound match the morphological descriptions from California given by Blake (1966). Only two individuals were found during this survey. Inhabits mud in the crevices of sandstone rocks.

Burrow Morphology

Soft x-ray analysis was used to investigate burrow morphology and degree of infestation for three common boring species: *Polydora convexa, P. giardi,* and *P. pygidialis* (Figs. 2, 3).

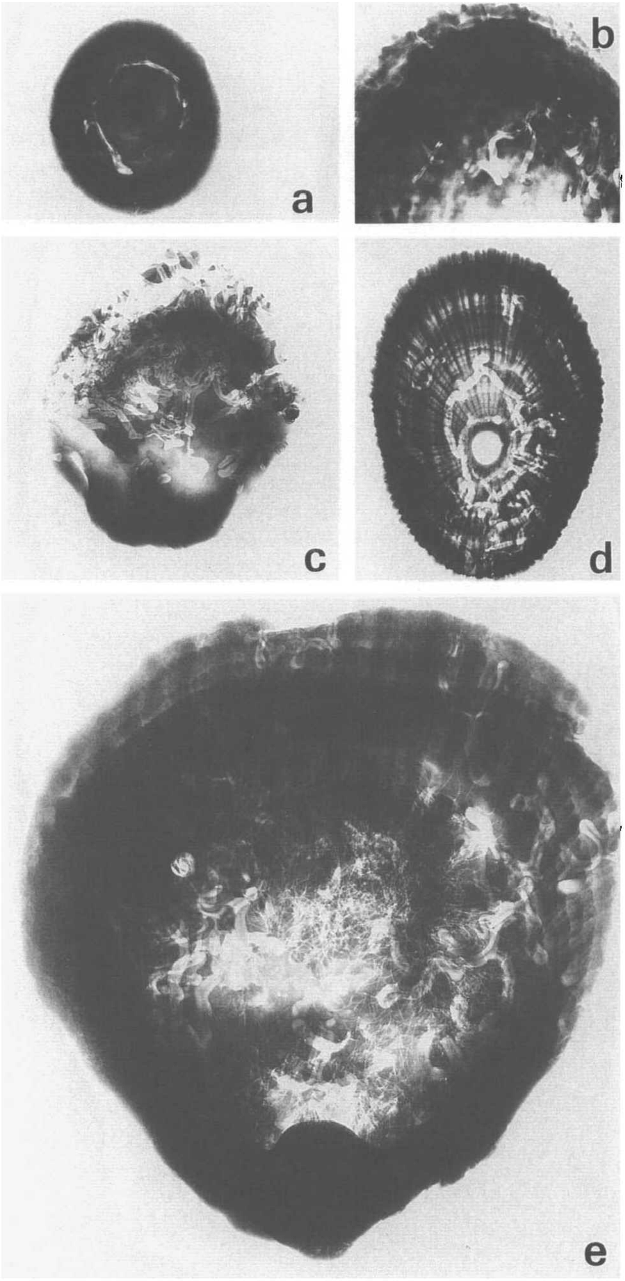

Figure 2. Soft x-ray photographs showing burrows of *Polydora*. a. Burrows of *P. pygidialis* in an *Acmaea mitra* shell. b. Burrows of *P. pygidialis* in a *Pododesmus cepio* shell. c. Burrows of *P. pygidialis* in an *Ostrea lurida* shell. d. Burrows of *P. pygidialis* in a *Diodora aspera* shell. e. Burrows of *P. convexa* and *P. giardi* in a *Hinnites giganteus* shell.

Although all burrows were basically elongated and U-shaped, each species had a distinctive burrow morphology. Burrows of *P. giardi* showed typical slender U shape. Those of *P. convexa* and *P. pygidialis* were branched. Especially in *P. convexa*, the burrows were repeatedly branched. The burrows of adult *P. convexa* were

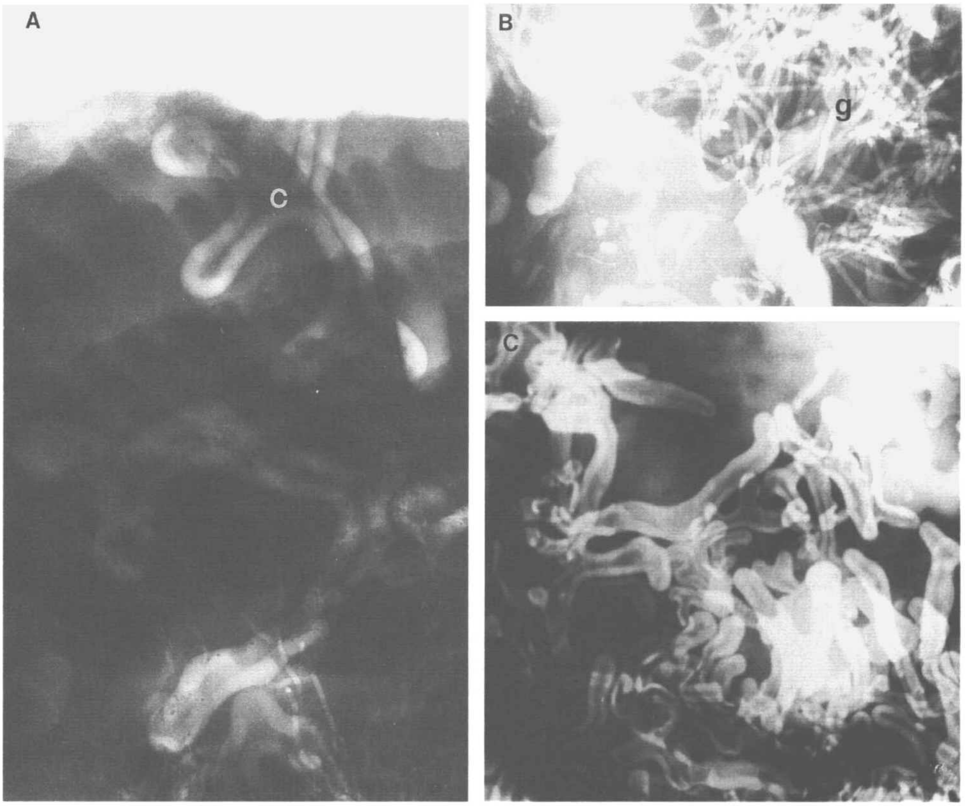

Figure 3. Soft x-ray photographs of burrows of *Polydora* at higher magnification. A. Burrows of *P. convexa* (c) in a *Hinnites giganteus* shell (×4). B. Burrows of *P. giardi* (g) in a *Hinnites giganteus* shell (×5). C. Burrows of *P. pygidialis* in an *Ostrea lurida* shell (×5).

larger than those of *P. pygidialis* both in length and width as a result of large adult size in *P. convexa*. *Polydora giardi* had a tendency to aggregate and many burrows were observed to overlap one another, but never to intersect. Burrows of *P. pygidialis* formed concentric lines within the shells of the white cap limpet *Acmaea mitra*. It would appear that the larvae of *P. pygidialis* settle at the periphery of the shell and burrow toward the center based on the distribution of the burrows of adult worms.

Discussion

In previous papers, 19 *Polydora* species (*P. socialis, P. cardalia, P. armata, P. pygidialis, P. websteri, P. convexa, P. commensalis, P. giardi, P. ligni, P. spongicola, P. alloporis, P. brachycephala, P. quadrilobata, P. bioccipitalis, P. elegantissima, P. limicola, P. narica, P. neocardalia, P. nuchalis*) and 11 *Boccardia* and *Boccardiella* species (*B. proboscidea, B. columbiana, B. hamata, B. polybranchia, B. berkeleyorum, B. truncata, B. tricuspa, B. basilaria, B. ligerica, B. pugettensis, B. natrix*) were reported from Western Canada or from the west coast of North America (Berkeley, 1927; 1968; Berkeley and Berkeley, 1936; 1950; 1952; 1954; Blake, 1966; 1971; 1979; Blake and Woodwick, 1971a; 1971b; Hartman, 1969; Hobson and Banse, 1981; Light, 1978; Woodwick, 1963). During our survey, we described 6 *Polydora*, 1 *Boccardiella* and 3 *Boccardia* species from an open coast environment in Barkeley Sound. From west coast of Vancouver Island, 4 species of *Polydora, Boccardiella* and *Boccardia* (*P. socialis, B. proboscidea, B. hamata, B. pugettensis*) are described out of 10 species from all over the Vancouver Island previously (add *P. spongicola, P. commensalis, P. ligni, P. cardalia, B. polybranchia, B. columbiana* to the above species to complete the species described from Vancouver Island) (Berkeley, 1927; Berkeley and Berkeley, 1936; 1950; 1952; Blake, 1979; Blake and Woodwick, 1971a). According to our results, 7 species (*Polydora ligni, P. giardi, P. pygidialis, P. limicola, P. convexa, Boccardia columbiana,* and *B. berkeleyorum*) are new additions to the list of species occurring on the west coast of Vancouver Island. Therefore, a total of 9 *Polydora*, 1 *Boccardiella* and 5 *Boccardia* species are recorded from Vancouver Island. Three species, *P. convexa, P. limicola,* and *B. berkeleyorum* are new not only to Vancouver Island but also to Western Canada.

It is said that there is taxonomical confusion in many *Polydora, Boccardiella* and *Boccardia* species. Many species are reported to use more than one habitat type. The habitats include soft bottoms and hard substrata, in which they bore. Blake and Evans (1972) listed 26 species of *Polydora, Boccardia* and *Pseudopolydora* which occur mainly in calcareous substrata, 6 species from both calcareous and non-calcareous substrata, and 33 species mainly from various non-calcareous substrata based on published reports. However, they stated that the identification of the species which occur in both habitats was doubtful.

There have been many discussions especially regarding the *Polydora ciliata* complex. Whether boring activity itself can be used alone as a distinguishing character was discussed by Rasmussen (1973), Kendall (1980), Ramberg and Schram (1982), Mustaquim (1986, 1988) and Manchenko and Radashevsky (1993). Mustaquim (1986, 1988) concluded that the non-boring and boring forms of *P. ciliata* are different both morphologically and genetically based on scanning electron microscopy and starch gel electrophoresis. Manchenko and Radashevsky (1993) examined the systematics of the *P. ciliata* complex by means of starch gel electrophoresis and stated that boring activity itself can be used as a distinguishing character in the *Polydora ciliata* complex.

In this study, we classified 10 species with respect to boring activity. None of the species found used both habitat types. Five species of *Polydora* and *Boccardia* were only extracted from burrows they had excavated in calcareous substrata, and five other species inhabited mud deposits, including mud located in crevices of shells and sandstone rocks.

Similarly, we did not find species of both boring and nonboring types in northern Japan (Mori et al., 1985; Sato-Okoshi and Nomura, 1990). Although hundreds of boring *Polydora* belonging to the 4 species *P. variegata, P. websteri, P. concharum,* and *P. convexa* were observed in the left valve of the scallop *Patinopecten yessoensis* in Abashiri waters, no species inhabited soft bottoms in that area. However, we found several different species in the soft bottom in nearby shallow waters (unpublished).

Moreover, we found three common species that live along the Pacific coasts of both Canada and Japan. These were *P. convexa, P. giardi,* and *B. hamata*. The former two were extracted from burrows they had excavated in calcareous substrata. Their hosts in Japan were *Patinopecten yessoensis* from the coast of Hokkaido (Sato-Okoshi and Nomura, 1990) and *Haliotis diversicolor aquatilis* from southern Japan (Kojima and Imajima, 1982), respectively. *B. hamata* did not bore, but inhabited mud in the crevices of oyster shells *Crassostrea gigas* in Japan (Sato, 1988) or of sandstone rocks in Canada.

During the present survey, we observed differences in the laboratory between two species of *Boccardia* of different habitat types. *Boccardia proboscidea,* which does not bore, is capable of rapid crawling and can quickly hide itself in mud deposits and form a new burrow when removed from its former one; it has strong and vigorous palps, and branchiae in which thick blood vessels can be observed. On the other hand, *B. berkeleyorum,* which bores into calcareous substrata, is a slow crawler and is incapable of either forming a new burrow or of hiding itself in mud deposits; palp activity is slower than in *B. proboscidea,* and only thin blood vessels are present in the branchiae. Characters and structures of muscles and blood vessels may also differ between other boring and non-boring species. It can be argued that a species able to bore has the advantage of a stable habitat due to the stout calcareous substrata, low predation pressure and limited exposure to unfavorable conditions when bored into non-sessile live mollusc shells. On the other hand, a species which does not have the ability to bore has the advantage of free movements and does not need to expend energy for boring into hard substrata.

Given these results, we propose that boring activity is an important distinguishing character for identifying *Polydora, Boccardiella* and *Boccardia* species at least in the studied area. Boring activity is suggested to be species specific.

It is of interest to compare the characteristics of boring and non-boring species from the point of view of morphology and ecology. Some morphological characters may be associated with the boring activity, but these have yet to be identified.

Although the boring mechanism has not yet been fully clarified, it has been suggested that some substance which attacks the calcium matrix of the shell is secreted along the animal's body; this hypothesis is supported by results of microstructure analysis of scallop and oyster shells infested with boring *Polydora* using SEM (Sato-Okoshi and Okoshi, 1993; 1996).

Further investigation is needed to determine if all *Polydora, Boccardiella* and *Boccardia* species are dependant on a single habitat type (i.e., boring or non-boring), and to clarify the different characteristics based on boring activity.

ACKNOWLEDGMENTS

We wish to express our appreciation to Dr. F.-S. Chia for providing the opportunity to carry out this study in Canada. Sincere thanks to Dr. L. A. Gosselin for his kind help in advising us about sampling sites and critically reading and improving the manuscript. Critical reviews by Dr. D. Reish and two anonymous reviewers were also of great help in later improvements of the manuscript. We are grateful to all the staff of the Bamfield Marine Station especially Dr. A. N. Spencer, Mr. J. Boom and Ms. A. Stewart for providing facilities and support when carrying out this study. Ms. L. Rimmer was of great help in obtaining the papers cited herein. Our heartfelt thanks are given to Drs. A. Taniguchi and Y. Sugawara for their continuous and kind support.

LITERATURE CITED

Ambariyanto, S. R. 1991. The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy Estuary, North Wales. J. Moll. Stud. 57: 413–424.

Annenkova, N. 1934. Kurze Übersicht der Polyxhaeten der Litoralzone der Berling-Insel (Kommandor-Inseln) nebst Beschreibung neuer Arten. Zool. Anzeig. 106: 322–331.

Berkeley, C. 1968. A checklist of Polychaeta recorded from British Columbia since 1923, with references to name changes, descriptions, and synonymies. 2. Sedentaria. Can. J. Zool. 46: 557–567.

Berkeley, E. 1927. Polychaetous annelids from the Nanaimo district. 3. Leodicidae to Spionidae. Canad. Biol. Ottawa, Contr. n.s. 3: 405–422.

——— and C. Berkeley. 1936. Notes on Polychaeta from the coast of western Canada. 1. Spionidae. Ann. Mag. Nat. Hist. ser. 10, 18: 468–476.

———, ———. 1950. Notes on Polychaeta from coast of western Canada. 4. Polychaeta Sedentaria. Ann. Mag. Nat. Hist. ser. 12, 3: 50–69.

———, ———. 1952. 9. Annelida. 9b(2) Polychaeta Sedentaria. Canadian Pacific Fauna. Fish. Res. Board Canada. 139 p.

———, ———. 1954. Additions to the polychaete fauna of Canada, with comments on some older records. J. Fish. Res. Board Canada. 11: 454–471.

Blake, J. A. 1966. On *Boccardia hamata* (Webster), new combination (Polychaeta, Spionidae). Bull. So. Calif. Acad. Sci. 65: 176–184.

———. 1971. Revision of the genus *Polydora* from the east coast of North America (Polychaeta: Spionidae). Smiths. Contr. Zool. 75: 1–32.

———. 1979. Revision of some Polydorids (Polychaeta: Spionidae) described and recorded from British Columbia by Edith and Cyril Berkeley. Proc. Biol. Soc. Wash. 92: 606–617.

———. 1981. *Polydora* and *Boccardia* species (Polychaeta: Spionidae) from western Mexico, chiefly from calcareous habitats. Proc. Biol. Soc. Wash. 93: 947–962.

——— and J. W. Evans. 1972. *Polydora* and related genera as borers in mollusk shells and other calcareous substrates (Polychaeta: Spionidae). Veliger. 15: 235–249.

——— and J. D. Kudenov. 1978. The spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. Mem. Nat. Mus. Victoria 39: 171–280.

Blake, J. A. and K. H. Woodwick. 1971a. A review of the genus *Boccardia* Carazzi (Polychaeta: Spionidae) with descriptions of two new species. Bull. So. Calif. Acad. Sci. 70: 31–42.

———, ———. 1971b. New species of *Polydora* (Polychaeta: Spionidae) from the coast of California. Bull. So. Calif. Acad. Sci. 70: 72–79.

Dorsett, D. A. 1961. The behavior of *Polydora ciliata* (Johnst.). Tube building and burrowing. J. Mar. Biol. Assoc. U.K. 41: 577–590.

Evans, J. W. 1969. Borers in the shell of the sea scallop, *Placopecten magellanicus*. Amer. Zool. 9: 775–782.

Haigler, S. 1969. Boring mechanism of *Polydora websteri* inhabiting *Crassostrea virginica*. Amer. Zool. 9: 821–828.

Hannerz, L. 1956. Larval development of the polychaete families Spionidae Sars, Dismidae Mesnil and Poecilochaetidae N. fam. in the Gullmar Fjord (Sweden). Zool. Bidr. Uppsala. 31: 1–204.

Hartman, O. 1940. *Boccardia proboscidea*, a new species of spionid worm from California. J. Wash. Acad. Sci. 30: 382–387.

———. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles. 828 p.

Hempel, C. 1957. Uber den Rohrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta, Sedentaria) der deutschen Küsten. Helgol. Wiss. Meeresunters. 6: 100–135.

Hobson, K. D. and K. Banse. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. Can. Bull. Fish. Aquat. Sci. 209: 1–144.

Imajima, M. and W. Sato. 1984. A new species of *Polydora* (Polychaeta, Spionidae) collected from Abashiri Bay, Hokkaido. Bull. Natn. Sci. Mus., Tokyo (Ser. A), 10: 57–62.

Kendall, M. A. 1980. Variations in some morphological characteristics of *Polydora ciliata* (Johnston). J. Nat. Hist. 14: 405–411.

Kent, R. M. L. 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. 59: 289–297.

———. 1981. The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. J. Cons. Int. Explor. Mer. 39: 252–255.

Kojima, H. and M. Imajima. 1982. Burrowing polychaetes in the shells of the abalone *Haliotis diversicolor aquatilis* chiefly on the species of *Polydora*. Bull. Jap. Soc. Scient. Fish. 48: 31–35. (In Japanese with English abstract)

Korringa, P. 1951. The shell of *Ostrea edulis* as a habitat: observations on the epifauna of oysters living in the Oosterchelde, Holland, with some notes on polychaete worms occurring there in other habitats. Arch. Neerl. Zool. 10: 32–152.

Light, W. J. 1978. Spionidae. Polychaeta Annelida. Cal. Acad. Sci. The Boxwood Press, California. 211 p.

Manchenko, G. P. and V. I. Radashevsky. 1993. Genetic differences between two sibling species of the *Polydora ciliata* complex (Polychaeta: Spionidae). Biochem. Syst. Ecol. 21: 543–548.

McIntosh, W. C. A. 1868. On the boring of certain annelids. Ann. Mag. Nat. Hist. ser. 4, 2: 276–295.

Mesnil, F. 1896. Études de morphologie externe chez les Annélides. 1. Les Spionidiens des côtes de la Manche. Bull. Sci. France Belg. 29: 110–287.

Mori, K., W. Sato, T. Nomura and M. Imajima. 1985. Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes, *Polydora*, on the Okhotsk Sea coast of Hokkaido, especially in Abashiri waters. Bull. Jap. Soc. Scient. Fish. 51: 371–380. (In Japanese with English abstract)

Mustaquim, J. 1986. Morphological variation in *Polydora ciliata* complex (Polychaeta: Annelida). Zool. J. Linn. Soc. 86: 75–88.

———. 1988. Electrophoretic variation of isozymes in *Polydora ciliata* complex (Polychaeta: Spionidae). Comp. Biochem. Physiol. 91: 197–205.

Ramberg, J. P. and T. A. Schram. 1982. A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data (Polychaeta: Spionidae). Sarsia 68: 233–247.

Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1–495.

Read, G. B. 1975. Systematics and biology of polydorid species (Polychaeta: Spionidae) from Wellington Harbour. J. Royal Soc. New Zealand 5: 395–419.

Sato, W. 1988. Infestation and life history of the boring polychaetes, *Polydora*, living in Japan. Ph.D. Thesis, Tohoku University, Sendai, Japan. 115 p.

Sato-Okoshi, W. 1994. Life history of the polychaete *Polydora variegata* that bores into the shells of scallops in northern Japan. Mém. Mus. Natn. Hist. Nat. 162: 549–558.

——— and T. Nomura. 1990. Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes *Polydora* on the coast of Hokkaido and Tohoku District. Nippon Suisan Gakkaishi. 56: 1593–1598. (In Japanese with English abstract)

——— and K. Okoshi. 1993. Microstructure of scallop and oyster shells infested with boring *Polydora*. Nippon Suisan Gakkaishi. 59: 1243–1247.

——— and ———. 1996. Microstructure of scallop shells infested with young boring polychaete, *Polydora variegata*. Bull. Inst. Océanogr. Monaco. 14: 203–207.

———, Y. Sugawara and T. Nomura. 1990. Reproduction of the boring polychaete *Polydora variegata* inhabiting scallops in Abashiri Bay, north Japan. Mar. Biol. 104: 61–66.

Strathmann, M. 1987. Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle. 670 p.

Wargo, R. N. and S. E. Ford. 1993. The effect of shell infestation by *Polydora* sp. and infection by Haplosporidium nelsoni (MSX) on the tissue condition of oysters, *Crassostrea virginica*. Estuaries. 16: 229–234.

Woodwick, K. H. 1963. Comparison of *Boccardia columbiana* Berkeley and *Boccardia proboscidea* Hartman (Annelida, Plychaeta). Bull. South. Calif. Acad. Sci. 62: 132–139.

Zottoli, K. A. and R. M. Carriker. 1974. Burrow morphology, tube formation, and microarchitecture of shell dissolution by the spionid polychaete *Polydora websteri*. Mar. Biol. 27: 307–316.

DATE ACCEPTED: May 21, 1996.

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