Marine Biology (1998) 130: 651–662

J. B. Lewis

Reproduction, larval development and functional relationships of the burrowing, spionid polychaete *Dipolydora armata* with the calcareous hydrozoan *Millepora complanata*

Received: 6 March 1997 / Accepted: 25 October 1997

Abstract *Dipolydora armata* (Langerhans, 1880) is a small (4 to 5 mm) spionid polychaete found burrowing in the calcareous hydrozoan *Millepora complanata* Lamarck, 1816, on coral reefs at Barbados, West Indies. It excavates complex networks of interconnecting burrows and forms aggregations of worms in cavities within branches of the coral. Adult worms have a mixed feeding mode (suspension feeding and deposit feeding). Size–frequency distributions of worms in branch samples suggest that they mature in a single year and that reproduction occurs throughout the year. Burrow openings on the surface of the coral develop distinctive, erect spines caused by combined growth of worm tubes and host tissue. Millepore zooids were absent in the vicinity of tube openings and on spines, and thus the potential feeding surface of the coral will be reduced in heavily colonized branches. Burrows and openings were densest at the bases of millepore branches where weakening of the skeleton would be expected to occur. The absence of openings near the branch tips suggests difficulty in larval settlement there, amongst stinging zooids. Reproduction and larval development of the worms were examined, and a sequence of larval stages from one to 20 segments and a juvenile stage of 22 segments are described. Eggs are deposited in brood sacs attached to the burrow wall, and the larvae feed upon nurse eggs (adelphophagy). The presence of larvae and juveniles occurring free in the burrows suggests that larval development may be completed within the host coral as an alternative or in addition to a planktonic larval phase. Lack of provisional larval setae, early development of adult capillary setae, production of special spermatophores and a protracted breeding cycle in *D. armata* are all traits which would favour complete development within the host skeleton.

Communicated by R.J. Thompson, St. John's

J.B. Lewis
Department of Biology, McGill University,
1205 Dr. Penfield Ave, Montreal,
Quebec, H3A 1B1, Canada

Introduction

Polydorids are common, often inconspicuous spionid polychaetes burrowing in a variety of substrata from soft mud to hard materials. Some soft-bottom species are regarded as "pollution indicators" (Rice and Simon 1980; Weisberg et al. 1997) and may regularly colonize disturbed habitats and play an important role in early faunal successional dynamics. Other polydorids can bore into shells and limestone rock and are widely known as pests of oysters and other bivalves (Lunz 1940; Medcoff 1946; Blake and Evans 1973; Blake 1996). Considerable damage can be caused by heavy infestations of polydorids on shellfish beds (Sato-Okoshi 1994). Hutchings and Bamber (1985) have reported significant erosion and destructive effects on corals by burrowing spionids on coral reefs of the Great Barrier Reef of Australia. Polydorids are thus of interest because of their economic importance and for their ecological role as initial colonizers of disturbed habitats. Blake (1996) has provided a general account of the biology and ecology of the Spionidae.

Like many other polychaetes, spionids display diverse reproductive biologies, and their success as opportunists in disturbed habitats may be due in part to their variable reproductive and life-history patterns (Gudmundsson 1985). Examples of variation in larval development among a number of spionids have been reported by Hannerz (1956), Dean and Blake (1966), Simon (1967, 1968), Blake (1969, 1996), and Blake and Kudenov (1981). More than one developmental mode may occur within the same species (poecilogony) (Levin 1984; Hoagland and Robertson 1988; Blake 1996; Gibson 1997). The demographic consequences of alternative reproductive modes and of seasonal life-history variation have been reported by Levin (1984), Levin and Creed (1986), Levin et al. (1987), Levin and Huggett

(1990) and by Zajac (1991a, b). The evolutionary and ecological significance of poecilogony, leading to reproductive isolation and speciation, was discussed by Hoagland and Robertson (1988).

Dipolydora armata (formerly *Polydora armata*; Blake 1996) is a cosmopolitan species that bores into calcareous substrata in tropical and subtropical waters (Woodwick 1964). It has been reported living commensally with the coral *Leptastrea purpurea* in Japan (Okuda 1937), with the calcareous hydrozoan *Millepora complanata* in Barbados (Blake 1996) and associated with corals and coralline algae in the Marshall Islands (Woodwick 1964). However, there have been no detailed studies of the biology of this or other coral-infesting species (Blake and Evans 1973; Blake 1996). A purpose of the present study is to describe the occurrence, habits and interactions of *D. armata* with *M. complanata* and then to comment on life-history traits of the worm that may arise from its association with millepores.

The reproductive strategies and larval development of *Dipolydora armata* are of particular interest because its developmental life history may be influenced by the interaction of the worm with the hydrozoan coral. For example, high settlement mortality and low recruitment would be expected where larvae settle upon a living coral surface covered with stinging zooids, or initial burrowing by juveniles may be constrained by overgrowth of coral soft tissue. Moyse (1971) has reported mortality in barnacle cyprids that settled within reach of tentacles around the rim of polyps of the coral *Caryophyllia smithi*. Feeding might also be reduced by overgrowth and smothering of tube openings by coral tissue. On the other hand, there are apparent advantages to settlement on a millepore substratum free of sediment, free from competition with other epizoans and algae and from grazing by predators, all of which should lessen recruitment mortality. Foster (1987) argued that obligate commensalism, with acquired host protection, would lessen vulnerability to predation in sessile barnacles. Reproduction and larval development of *D. armata* are therefore examined in relation to association and interactions of the worm with the host coral.

Materials and methods

Branches of *Millepora complanata* Lamarck, 1816 containing *Dipolydora armata* (Langerhans, 1880) were collected from shallow water (1 to 2 m) on fringing reefs on the west coast of Barbados, West Indies in May, September and December of 1994, in March and December of 1995 and in April of 1996. Mean monthly values of temperature, salinity and water-quality variables on the reefs have been reported by Tomascik and Sander (1985). Branches were cut from colonies with strong wire cutters and, in order to minimize damage to reefs, only one or two branches were removed from each of ten separate millepore colonies on each sampling date. Individual branches were held in separate plastic bags for transport and placed in glass finger-bowls in seawater tables in the laboratory.

Worms were removed from branches by one of three methods and preserved in 5% buffered formalin. The simplest method was to break off and crush fragments of branches with a pair of stout pliers. The fragments were shaken gently in a dish of seawater and the water changed several times to clear. This method produced a high proportion of broken, damaged worms however, and thus was not suitable for subsequent size determination. Nevertheless, broken fragments of millepore branches did expose live worms and egg sacs in their tubes and allowed observations of activity in the burrows. Egg capsules containing eggs and living larvae were also obtained by this method.

The second method of obtaining samples consisted of fixation of branches in 10% formalin followed by repeated decalcification in Calex (Fisher Scientific Ltd., Montreal) over several days. Worms were then removed from the soft tissue under a dissecting microscope. This method produced samples of whole worms in good condition, suitable for size determination and allowed the detection and removal of egg sacs with their eggs and larvae. All worms contained in individual branches were removed and counted. Great care had to be taken to prevent damage during removal because worms were entangled in a dense mass of endolithic algae (Bellamy and Risk 1982) and fungal hyphae (Te Strake et al. 1988) which infested the coral skeletons. Adult size was expressed in terms of number of setigers because this was the quickest and most efficient measurement to make on worms (Zajac 1991a) and is most commonly used by other authors (Blake 1996). Linear measurements of preserved eggs, sacs and parts of larvae and juveniles were made with an ocular micrometer.

Emergence of live larvae, juvenile and adult worms from burrows was accomplished by allowing separate branches to stand overnight in a dish of seawater or immersing them in a 5% solution of epsom salts. Emergent worms were removed from the dish and preserved or transferred to fresh bowls of seawater for observation. This method also produced samples of whole worms in good condition.

Dissections, counts and observations of worms were accomplished with a Wild M5 binocular microscope with 6 to 50× objectives, fitted with a Wild MPS 46/52 photoautomat apparatus and camera as well as a Wild M20 microscope with 10 to 100× objectives, fitted with a Wild MKa4 automatic camera. Drawings of larvae were made from observations and photographs of preserved and live specimens, using a Leitz Orthomat stereomicroscope fitted with a Wild MKa photoautomat camera system. Linear measurements of whole larvae and juveniles were made with an ocular micrometer on live or freshly immobilized specimens. Nomarski phase interference optics were used to confirm observations of fine details in preserved material. Underwater photographs were taken with a Nikonos V camera, fitted with an accessory close-up lens.

Results

Appearance

Dipolydora armata is a small spionid (4 to 5 mm, with up to 50 setigers) that burrows throughout the coenosteum of branches of the hydrozoan *Millepora complanata*. It appears to be the smallest of the carbonate-boring spionids reported for the Caribbean by Foster (1971). It was found in shallow water (1 to 4 m) wherever millepores were abundant, but it was not observed on other coral species. The presence of worms in colonies was readily detected by the appearance of prominent tube openings on millepore branch surfaces (Fig. 1). Live adults obtained from emergent samples were semi-transparent, olive-green or brown in colour, with prominent dorsal and ventral blood vessels.

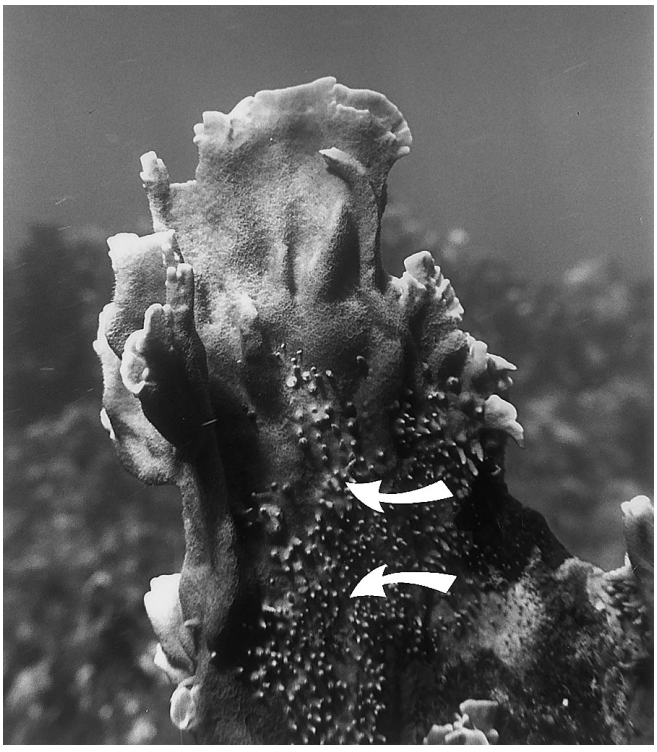

Fig. 1 Underwater photograph of branch of *Millepora complanata* showing burrow openings of *Dipolydora armata* (indicated by arrows). Note the absence of burrow openings in distal region of branch

Population size structure

Size–frequency distributions of *Dipolydora armata* obtained from decalcified branch samples (brood sacs excluded), expressed as numbers of setigers, are shown in Fig. 2. Samples from several branches were pooled for each date in order to increase the total sample size. Larval worms bearing 15 to 20 segments and juveniles of 20 to 25 setigers were found in all samples, and adult worms with as many as 46 setigers were recorded. Means of numbers of setigers varied by only a few setigers between samples (29.45 ± 3.06 SD to 31.56 ± 4.07 SD).

Burrowing

The burrows of *Dipolydora armata* are complex, interconnecting, branching tunnels within the coenostem of the coral (Fig. 3A). Openings to the burrows are single, tubular limbs lined with mucus, scattered over the coral colony surface. Each opening is surrounded by a rounded, convex swelling or mound of host skeletal and soft tissue. Continued growth of the host tissue and the worm tubes causes these swellings to grow into long spines which may extend outwards for several millimeters. Spines are often bent and misshapen (Fig. 3B) and their coral surface tissue lacks zooids. In other cases where fouling organisms or other agents have caused partial mortality to coral tissue, burrow openings remain flush with the skeleton surface. The distal end of the tube lining is mixed with detritus and fine sand and projects beyond the opening for a distance of about 1 mm. Tube openings are 0.5 to 0.6 mm in diameter.

Tube openings and burrows are densest at the bases of millepore branches and decrease towards the branch tips. No tube openings were observed at the distal ends of branches (Fig. 1). Extension of the burrows takes place within the coenosteum, and new openings are produced by the worm boring upwards towards the surface. Prior to the opening of a new burrow mouth, coral growth produces a rounded mound on the corallum surface (Fig. 3D) above the presumptive opening lying below. Linear arrangements of these mounds frequently track the paths of burrows below. Aggregations or clusters of worms are found within cavities excavated by other cryptofauna in the coenosteum (Hutchings 1983) and in empty calcareous tubes of the large polychaete *Spirobranchus polycerus* which is commonly found on millepore branches (Marsden 1992). Several cross-sections of *S. polycerus* tubes with enclosed *Dipolydora armata* tubes are shown in Fig. 3C.

The number of worms per unit area of branch surface generally exceeded the number of burrow openings on the same branches. The mean number of worms (40.26 ± 1.33 SE cm^{-2} branch surface) in ten decalcified branches was significantly higher than the mean number (24.61 ± 1.06 SE) of burrow openings on the same branches by paired sample *t*-test ($t = 2.95$, $p < 0.05$). This indicates that burrows and their openings are used by more than a single worm. In preserved branch samples, several worms were often found in the same burrow, oriented in opposite directions and frequently entangled with one another. Observations on live worms (in fractured blades) indicated that they move freely back and forth within the burrows and can reverse directions. Movement was by peristaltic action, aided by purchase provided by erect setae against the tube wall.

Feeding

Dipolydora armata has a mixed feeding strategy common to other boring spionids (Dauer et al. 1981; Blake 1996). It feeds by the capture of suspended material in the water column and the collection of particles from the substratum surface. In the laboratory, the worms lie within their burrows with the prostomium more or less flush with the opening and the palps waving about rhythmically in the water. The palps were also seen to bend towards the substrate and gather particles from the surface. Field observations of feeding showed that palp posture and movement were less deliberate than in the laboratory and that palp movement was uneven and random in response to water currents and wave surge.

Palps are thin and lanceolate, highly flexible and are 1 to 2 mm in length when extended in adult worms. They are transparent with prominent longitudinal blood vessels. Movement of water-borne particles towards the

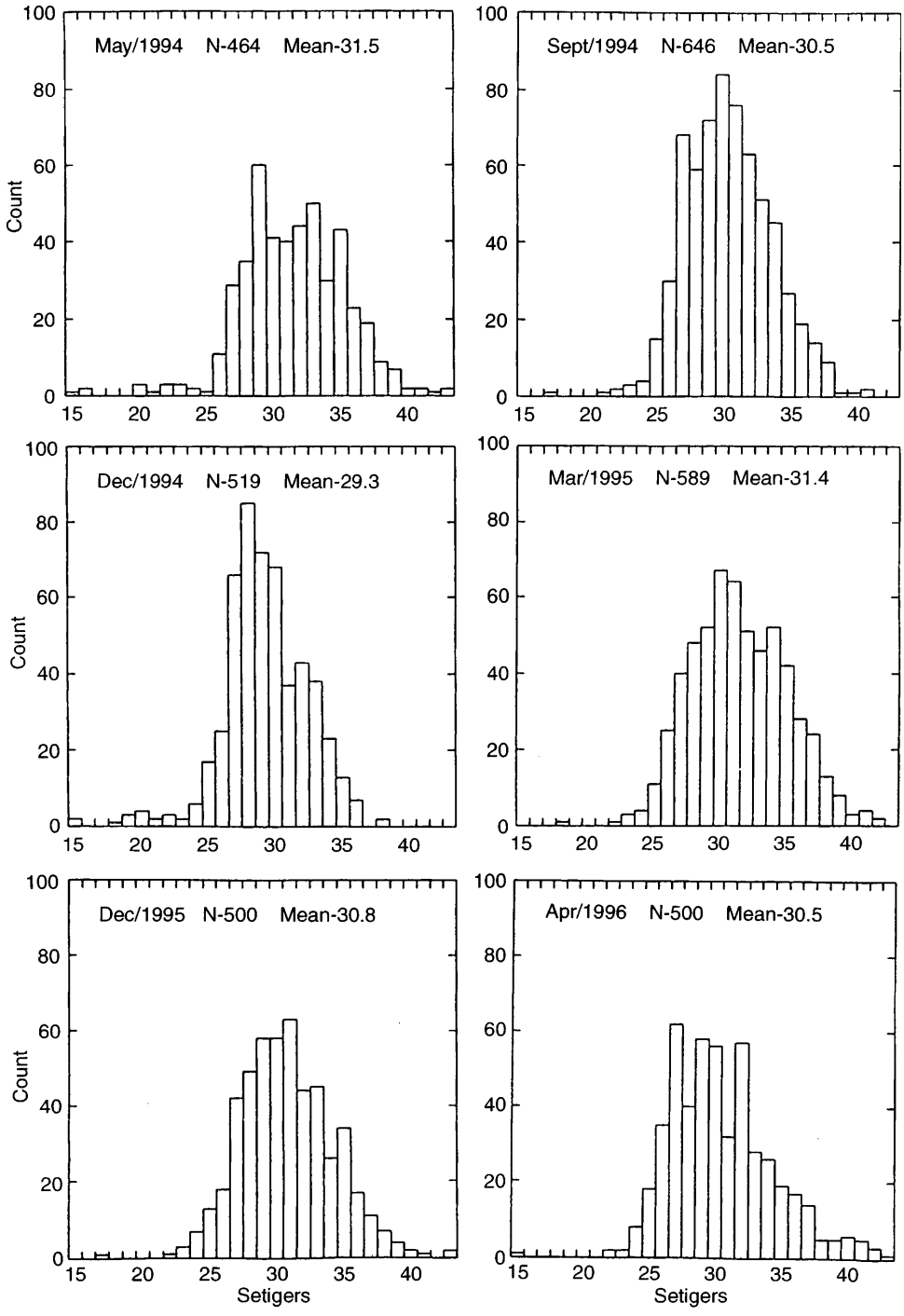

Fig. 2 *Dipolydora armata.* Size–frequency distributions

mouth along the ciliated grooves of the palps was readily observable. The guts of adult worms examined ($N = 25$) all contained homogenous, dark-brown material in which occasional plant cells were visible. These observations are consistent with a diet derived from suspended particulate matter. Fecal rods were 0.4 to 1.0 mm in length and 0.1 to 0.15 mm wide in adult worms. Rods contained fine, sedimentary particles (greatest dimension 5 to 10 μm) together with unidentifiable, fine-grained brown material, diatom tests, spines and arthropod skeleton fragments.

Reproduction

Dipolydora armata reproduces sexually. Individuals with regenerated head or tail sections, at various stages of development, were observed in samples (1 to 2%) however, and thus autotomy may be regarded as a potential form of asexual reproduction as reported for other spionids (Blake 1996). Males were difficult to discern in preserved material, but females could be readily distinguished externally by the presence in the genital segments of paired ovaries containing oocytes.

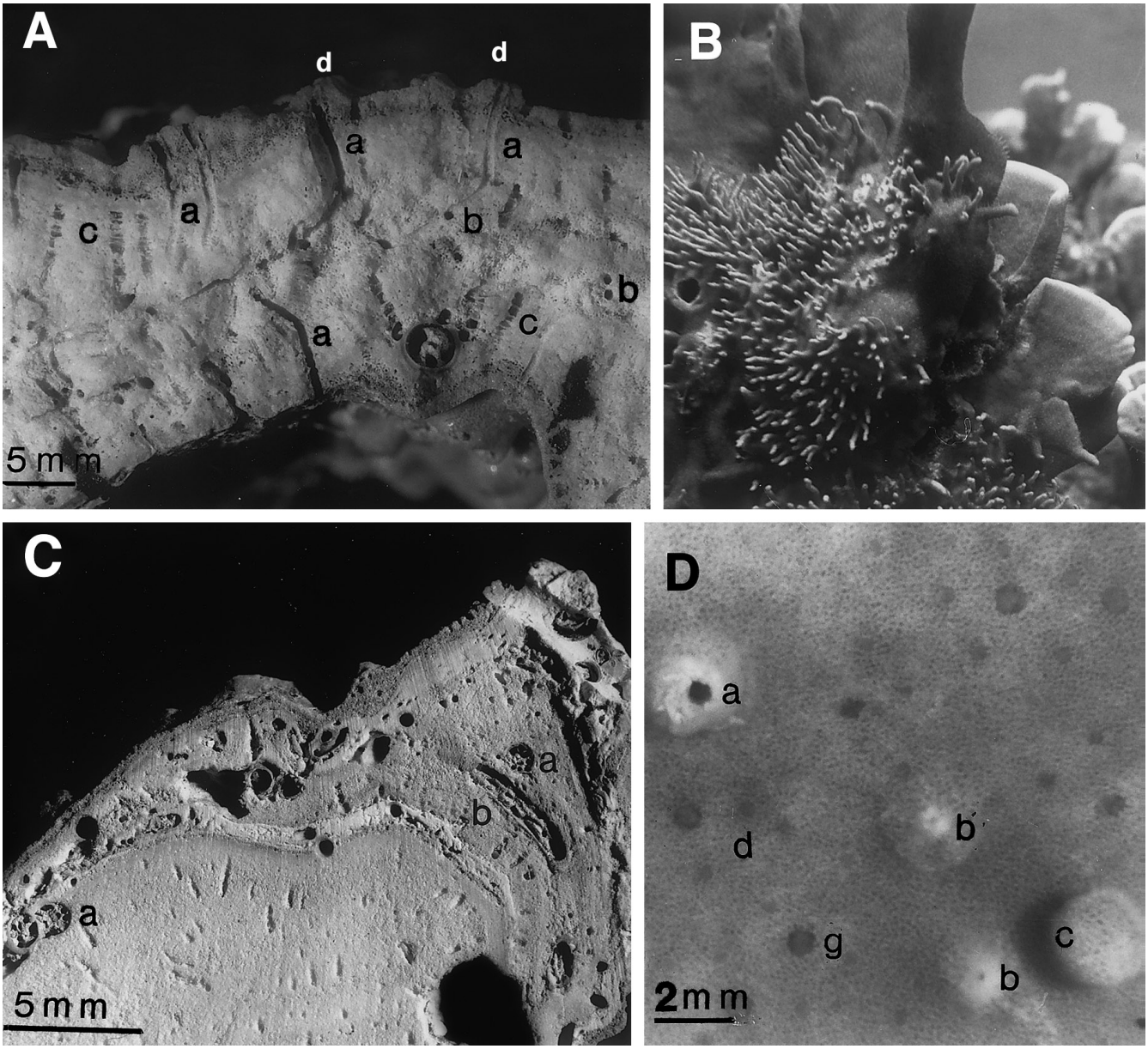

Fig. 3 **A** Cross-section of branch of *Millepora complanata* showing burrows of *Dipolydora armata* (*a* longitudinal section of burrow; *b* cross-section of burrow; *c* longitudinal section of gastrozooid tube with tabulae; *d* raised skeletal mound of tube opening formed by growth of millepore). **B** Underwater photograph of branches of *M. complanata* showing cluster of elongate burrow spines. **C** Cross-section of *M. complanata* branch showing aggregations of tubes of *D. armata* in cavities (*a* cross-section of *Spirobranchus polycerus* tube with burrows of *D. armata*; *b* longitudinal section of *S. polycerus* tube with burrows of *D. armata*). **D** Surface of *M. complanata* branch showing stages in the "break-through" of tube openings of *D. armata* (*a* tube opening; *b* skeletal mound with partial tube opening; *c* skeletal mound with no tube opening; *d* dactylopore; *g* gastropore)

Genital segments were restricted to the central region of the body between the 12th and 24th setigers. The mean number of setigers of mature females (ripening and ripe gonads) from all decalcified branch samples was 33.56 ± 0.44 SE. Male worms produce small, oval spermatophores (Fig. 4A) which were attached by a stalk to the capillary setae, or occasionally to the body wall, on the genital segments of the females. Spermatophores were 40 to 50 μm in length, about 10 μm in diameter at the widest dimension, with a stalk 20 to 30 μm in length. Eggs were of uniform size, 102.35 μm ± 0.88 SE ($N = 25$) in diameter and were deposited in brood sacs or capsules. Egg capsules were of a simple type of transparent, hollow cylinder, 1 to 2.5 mm long, attached to the wall of the parent tube by several thin stalks and occurring singly or accompanying an adult worm. This type of capsule has been illustrated and described in detail for *Dipolydora quadrilobata* by Blake (1969) and for *D. giardi* by Day and Blake (1979). The number of eggs deposited in each capsule varied between 50 and 100 depending upon the length of the sac.

In *Dipolydora armata* all the eggs in a capsule do not develop into larvae. Nurse eggs serve as food for the

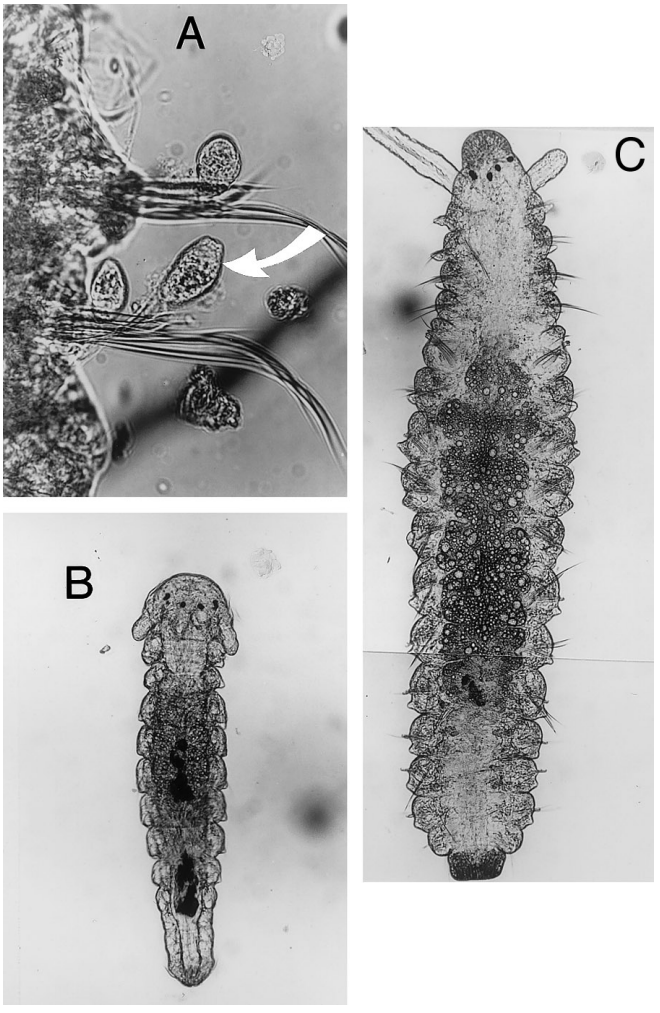

Fig. 4 *Dipolydora armata*. Photomicrographs of **A** spermatophores (50 μm long) attached to setae of female worm (indicated by arrow), **B** nine-segment larva (1000 μm long) and **C** sixteen-segment larva (1500 μm long)

developing larvae as reported in other adelphophagous species (Simon 1967; Blake 1969; Blake and Woodwick 1975; Blake and Kudenov 1981). Nurse eggs appeared identical to the viable oocytes before cleavage (Gibson 1997); they were white in colour and similar in appearance to those described by Blake and Kudenov 1981). A wide size range of larvae, varying from asetigerous individuals up to larvae of 18 segments, were found with nurse eggs in capsules, but there was a small range of larval size per brood. Eighty-two percent of the sacs examined contained larvae of ten setigers or less (Table 1). In general, all larvae examined within individual capsules were of similar size, i.e. within a size class of Table 1. Larvae of all sizes, from 3 to 4 segments up to 18 setigers and juveniles were released from coral branches into seawater in the laboratory. Early, asetigerous stages, characterized by a single pair of pigmented eye spots, were observed moving about within the egg capsules. Larvae tended to be confined towards

Table 1 *Dipolydora armata*. Size–frequency distribution of larvae (in parentheses percentage of total egg sacs) in egg sacs

	Larva size class:				
	3–6 segments	7–10 segments	11–14 segments	15–18 segments	>18 segments
No. egg sacs (%)	9 (21)	26 (61)	4 (9)	4 (9)	0

Table 2 *Dipolydora armata*. Comparison of mean number and size of larvae with number of nurse eggs in egg sacs

No. nurse eggs per sac	Mean no. larvae (±SE)	Mean no. setigers (±SE)	No. sacs examined
25–50	3 (0.61)	6.7 (0.90)	10
15–24	4 (1.05)	7.3 (1.02)	10
8–14	7 (1.21)	6.8 (0.77)	15
0–7	5 (0.95)	9.4 (0.75)	15

one end of the capsules rather than being scattered throughout.

Table 2 shows a comparison of the mean number and size of *Dipolydora armata* larvae with the number of nurse eggs in capsules in a random sample of five decalcified millepore branches. The number of larvae per capsule was not affected by the number of nurse eggs (regression; $F = 0.22$, $r^2 = 0.09$, $p = 0.39$, not significant). However, the mean number of segments per larva was less in capsules containing 25 to 50 eggs than in capsules with 0 to 7 eggs by *t*-test for two-sample means ($t = 3.61$, $p < 0.05$), thus confirming that nurse eggs are consumed by developing larvae.

Seasonal variation in reproductive activity of adults sampled from decalcified branches is examined in Table 3. A one-way analysis of variance indicated that there were significant monthly differences in the number of ripe females (ovaries with developing and mature oocytes) ($F_{4.17} = 2.60$, $p = 0.05$). A post hoc Tukey's HSD-test for differences of means showed that December (1994 and 1995) means were significantly lower than those of the other 3 months (at $p = 0.05$ level). Females carrying spermatophores were present throughout the year but there was no apparent seasonal trend in relative percentages. Similarly, egg sacs containing eggs and developing larvae were present in burrows in all samples but there was no apparent seasonal trend in the percentages of worms with capsules.

Larval development

Early larvae (*Fig. 5A, B*)

Unsegmented, single-segment and two-segment larvae were observed moving about within egg capsules but could not swim well if released artificially from their capsules. They are rounded and fat in shape due to their large yolk mass. Unsegmented larvae have two eye spots, one on either side of the head. Two-segment lar-

Table 3 Seasonal variation in reproductive activity of *Dipolydora armata* burrowing in *Millepora complanata*

	Sample date:					
	5 May 1994	16 Sep 1994	4 Dec 1994	18 Mar 1995	10 Dec 1995	25 Apr 1996
% ripe females	19	12	05	16	05	15
% females with spermatophores	16	26	20	32	35	33
No. egg sacs in sample	28	10	11	15	5	5
No. worms in sample	360	489	534	214	558	500

vae have two pairs of eyes which are also borne laterally. Early larvae have developed both prototrochs and telotrochs situated laterally. A mouth has begun to form as a short ciliated depression. No larval bristles were observed on these stages. Unsegmented larvae measure 140 to 160 μm in length and two-segment stages are about 200 μm long.

The earliest larvae released from coral branches in the laboratory were three-segment stages. Prior to the release of larvae, the adults extended the prostomium from the burrow opening, palps waved about excitedly and larvae emerged from the space between the burrow lining and the prostomium. Three-segment larvae range between 200 and 300 μm in length and can swim actively. They are strongly positively phototropic and swarm at the water surface, towards the lighted side of glass bowls. Two pairs of prominent eyes are present, situated near the mid-line. The inner pair are nearly circular and the outer pair kidney shaped. The prototroch and telotroch are well developed. The prototroch extends ventrally nearly to the mouth and dorsally as far as the inner pair of eyes. The mouth is enlarged and deepened. Body segments are distinct and there is a large, central, orange yolk mass. No larval setae were observed but large setal sacs are present on the first segment. There are lateral spiny processes and a few faint pigment spots on the tip of the pygidium.

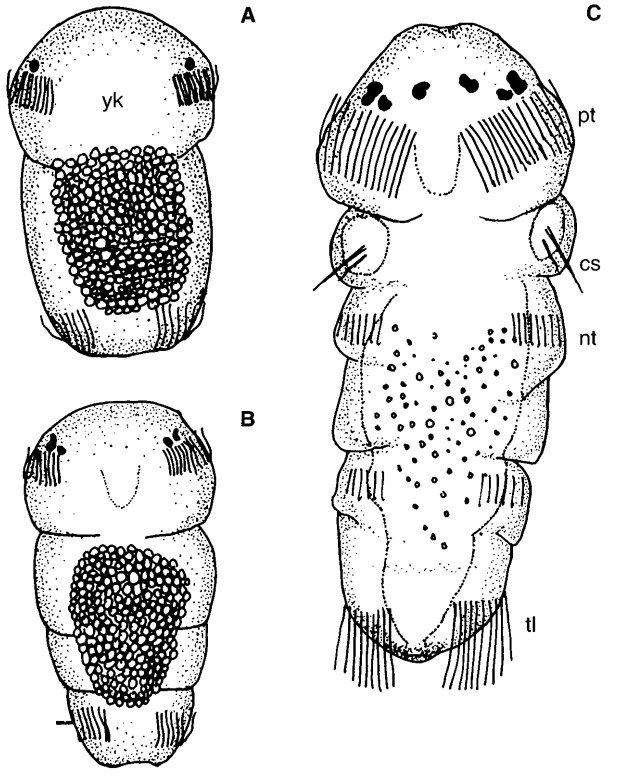

Fig. 5 *Dipolydora armata.* **A** Unsegmented larva (150 μm long), **B** dorsal view of two-segment larva (200 μm long) and **C** dorsal view of four-segment larva (450 μm long) (*cs* capillary spine; *nt* nototroch; *pt* prototroch; *tl* telotroch; *yk* yolk mass)

Four-segment larvae (*Fig. 5C*)

This stage measures 400 to 460 μm in length and is about 150 μm in width. Like the previous stage, four-segment larvae released in the laboratory showed strongly positive phototaxic responses. There are six eyes nearly in line: an outer pair is elongated in shape and below is a small rounded pair. The innermost pair near the midline are also rounded but are slightly larger. Four-segment larvae can swim strongly and both the prototroch and the telotroch are well developed. Nototrochs are present on the second and fourth segments in dorsal view and consist of two patches along the lateral edges of the segments. Gastrotrochs are present ventrally on the third segment. The gut is clearly visible and in most larvae is partially full of bright-orange yolk droplets. Additional darker grained material in the gut suggests that the larvae have already begun to feed on nurse eggs as did the early larvae of *Dipolydora quadrilobata* (Blake 1969). There is a prominent ciliated vestibule in the mouth region. Provisional larval setae are lacking as in the earlier stages but setal sacs are present on the first two segments. A pair of small, capillary setae project from the sacs of the first larval segment. Distinct lateral swellings indicate the developing parapodial lobes. Dark pigment dots surround the distal edge of the pygidium.

Six-segment larvae

Six-segment larvae measure between 600 and 700 μm in length, are about 180 μm wide and are more fusiform in shape than previous stages. The first and second segments are narrower than segments three and four. Developing palps are present and may extend as far as the second segment. The eyes are slightly darker and further apart than in the previous stage. Setal sacs are present

on the first three segments: segments two to five inclusive bear two pairs of short, unequal setae and the first segment bears two pairs of longer capillary setae. The parapodial lobes each bear a single stout spine.

Nine-segment larvae (*Figs. 4B, 6A*)

Nine-segment larvae measure about 1000 μm in length and 250 μm in width. There are three pairs of eyes, a round central pair, a large kidney shaped pair situated laterally and, below the latter, a third pair of small rounded spots. There are prominent palps which are variable in length and may extend as far as the fifth segment. Larvae swim in a directional manner by means of the cilia of the prototroch and telotroch but can also move in a serpentine fashion by undulations of the body. They are positively phototropic and may adhere firmly to the substratum by the pygidium. The gut is well defined and contains orange yolk droplets as well as other dark material.

This is the earliest stage bearing capillary setae on all segments and thus may be termed a nine-setiger larva. Parapodia are prominent and bear capillary noto- and neurosetae on each of the nine segments. Segments one and two each bear two capillaries per ramus, segments three to six bear three capillaries and segments seven, eight and nine again bear two capillaries each. The major modified spines of the fifth segment were not observed in this stage. Nototrochs are present on the third to ninth segments, and neurotrochs were present on segments three, five and seven. The distal end of the pygidium is deeply pigmented and bears a pair of stout protuberances.

Twelve-segment larvae (*Fig. 6B*)

Larvae with 12 setigers vary in length from 1300 to 1500 μm and are about 500 μm wide. This stage is distinguished by the development of the modified spines on the fifth segment and by an increase in the number of neurosetae and notosetae on all segments. The number of pairs of major spines of segment five varies from one to three per fascicle, and they are frequently of unequal length. The first two segments bear sets of two and three notosetae, respectively; the following segments bear sets of five setae. Neurosetae are slightly shorter than the notosetae and are borne in groups of five between the third and tenth setigers. Hooded, hooked setae occur posterior to the seventh segment. Larvae of 12 to 15 segments were observed to crawl about on the bottom of dishes in the laboratory but could also swim strongly by means of undulations of the body.

Sixteen-segment larvae (*Figs. 4C, 7A, B, C*)

Larvae with 16 segments are 1400 to 2000 μm in length and 400 to 600 μm in width. The palps are large, bear a

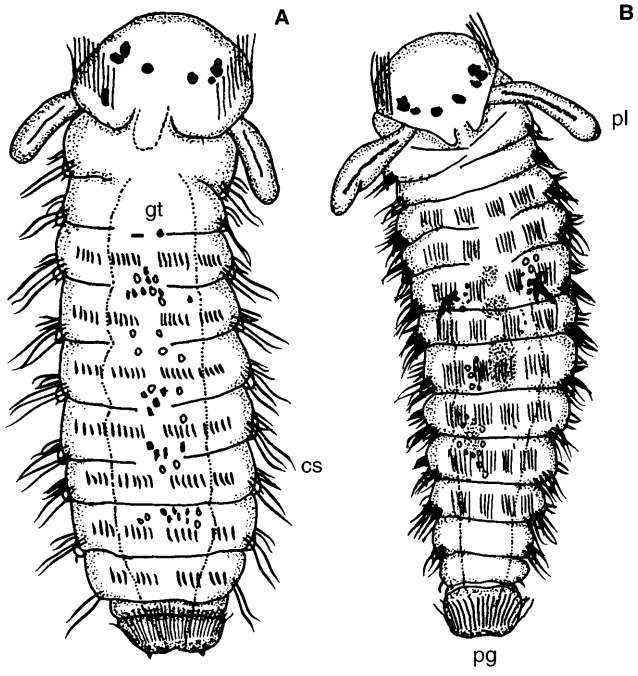

Fig. 6 *Dipolydora armata.* **A** Dorsal view of nine-segment larva (1000 μm long) and **B** dorsal view of twelve-segment larva (1300 μm long) (*cs* capillary setae; *gt* gut; *pg* pygidium; *pl* palp)

ciliated groove and may extend as far posteriorly as the fifth segment. The prostomium is elongated and there are usually only two pairs of eyes. The fifth setiger carries two pairs of major spines (Fig. 7C) which are similar to the adult modified spines described by Blake (1996). The lateral edges of the segments are lined with red pigment. Notosetae and neurosetae are all longer than in the previous stage. Larvae of 16 setigers were frequently observed crawling about on the glass surface of culture bowls and to initiate burrowing in detritus on the bottom. They adhered firmly to the substratum when disturbed.

Twenty-segment larvae

Larvae with 20 segments were released with larger juveniles and adults from coral branches cultured in glass finger-bowls. This stage appears to be in the process of metamorphosis. Twenty-segment larvae are 3500 to 4000 μm long, are strong swimmers but also actively crawl about on the substratum. The palps are bulky and may extend as far as the tenth segment. There are two pairs of indistinct eye spots. External branchiae have not formed but are present as developing buds in pink or rose sacs in segments seven to eleven.

Twenty-two-segment juvenile (*Fig. 8*)

The morphological features which distinguish a twenty-two-segment juvenile from a twenty-segment larva

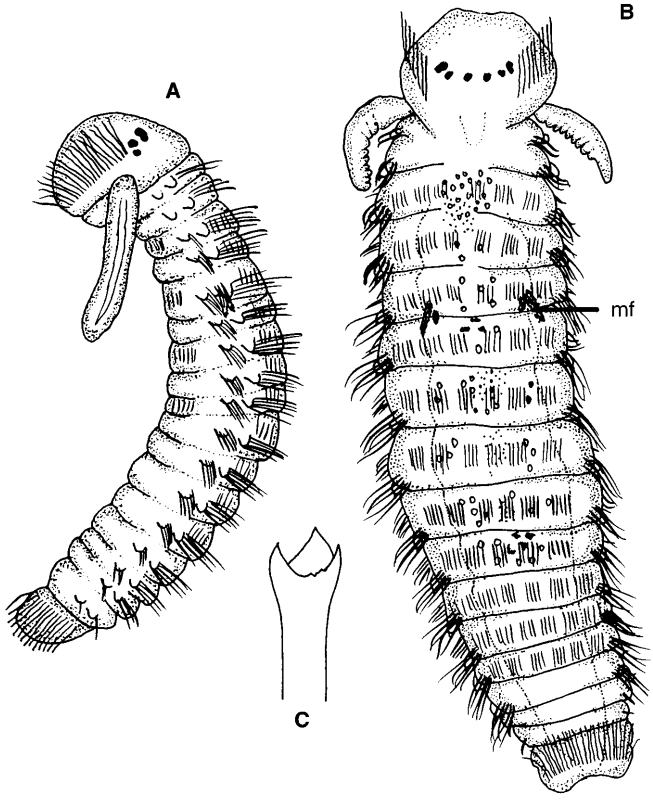

Fig. 7 *Dipolydora armata.* **A** Lateral view of sixteen-segment larva (1500 μm long), **B** dorsal view of sixteen-segment larva (1700 μm long), and **C** modified spine of fifth segment (*mf* modified spine)

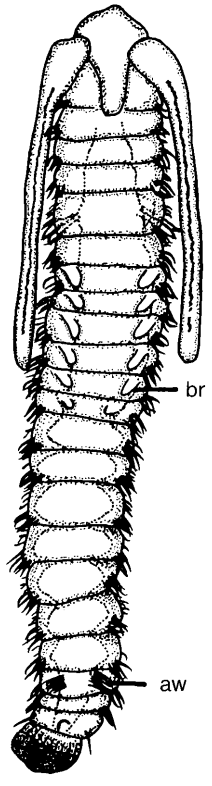

Fig. 8 *Dipolydora armata.* Dorsal view of twenty-two-segment juvenile (4000 μm long) (*aw* awl-like spines; *br* branchia)

consist of changes in the shape of the prostomium, loss of eye spots, loss of the prototroch and teletroch, appearance of branchiae on segments seven to twelve and the appearance of awl-like spines on the 20th segment. The prostomium and peristomium are elongated and there are long, grooved palps. The first segment bears three or four short notopodial setae. Segments two to four bear sets of three to six long, notopodial setae and three shorter, fine neuropodial setae. The fifth segment usually has two pairs (occasionally one pair) of stout, hooked major spines. These spines have a complex structure and are clothed with fine bristles. The sixth segment has five or six long, notopodial setae and four or five shorter, neuropodial setae. Hooded, neuropodial setae appear on segment seven. Sets of two hooded setae are borne on segments seven to ten and on segments thirteen to twenty. Segments ten to twelve bear sets of three, bidentate hooded setae each. Hooded hooks of this species have a smooth, curved shaft without a constriction or manubrium, a reduced angle between teeth and a wide angle between main fang and shaft. Segment twenty bears clusters of five or six awl-like setae and a single long, fine seta. Segments twenty-one and twenty-two each bear a set of long, fine setae and single, small, partly formed hooded setae. Segments seven to eleven bear sets of six or seven long, unequal notopodial setae and these decrease posteriorly to two or three per set on segment nineteen. Posterior to segment twenty-two there is a short region of several developing but undifferentiated future segments. The pygidium is strongly pigmented and resembles the adult pygidium which is cuff-like with numerous bacillary glands.

Discussion and conclusion

Although several polydorid species commonly burrow into calcareous substrata (Blake and Evans 1973; Blake 1996) there are a number of features of the *Dipolydora armata–Millepora complanata* relationship which distinguish it from other spionid associations. There is a complex, interconnecting branching system of burrows bored by *D. armata* throughout the coenosteum of the host millepore. Enlargement of the burrow system occurs within the coenosteum and is indicated by the appearance of rounded mounds on the coral surface, above presumptive openings. Larger cavities, excavated by other burrowers, are also utilized by aggregations or clusters of worms. In other shell-boring spionids, excavated burrows are frequently shallow, U-shaped with a pair of openings, and each is occupied by a single individual (Blake and Evans 1973; Zottoli and Carriker 1974). *Polydora alloporis*, which lives in the hydrozoan *Allopora californica*, also excavates deep burrows but retains paired branch openings (Light 1970).

The spine-like growth of skeletal and soft tissue of *Millepora complanata* around the elevated burrow openings is also a distinctive feature of worm–coral interaction. Spine-like growths are initiated from the

convex mounds which develop on the coral surface prior to the break-through of worms from meandering burrows beneath. Following the appearance of new burrow openings it might be expected that in some circumstances growth of coral tissue could smother worms and cover burrow openings. The burrow openings are densest near the proximal ends of the branches, between creases and in crevices in the coralla or where there are areas of exposed skeleton. The lack of burrow openings near the branch tips suggests difficulty in larval settlement and recruitment there, amongst the stinging zooids. Thus settlement on millepore branches may be constrained by the density of zooids. Intense burrowing activity at the bases of the coral branches would be expected to contribute to weakening of the skeleton as was reported by Hutchings and Bamber (1985).

It was observed that neither dactylozooids nor gastrozooids were present in the immediate vicinity of burrow openings or on spines. Zooid density was previously reported to vary spatially on millepore colonies and to be lowest along the rapidly growing edges of branches (Lewis 1992). The lack of zooids around burrow openings may be due to continuous, rapid growth of coral tissue, there and along spines. Therefore, where densities of openings are high and spines elongate, the number of gastrozooids will be reduced as will the potential feeding surface of the millepore. Protection of worms from grazers such as fish may also be lessened where numbers of dactylozooids are reduced.

From examination of the size–frequency histograms of *Dipolydora armata* (Fig. 2) there is no apparent evidence of more than one size cohort in any of the population samples. The presence of larvae and juveniles in all samples suggests that breeding and recruitment occur throughout the year. The unimodal size structure of the population and the lack of apparent seasonal differences in mean size also suggests that the worms reach adult size and that life-cycles can be completed in a single year. In other spionids, reproduction tends to have a seasonal periodicity (Simon 1967; Blake 1969, 1996; Blake and Kudenov 1981; Bochert and Bick 1995) related to the temperature of the water. Spawning frequently occurs during the spring of the year although there may be more than one peak of activity (Simon 1967; Santos 1994). At Barbados, mean monthly water temperatures in the vicinity of the reefs vary seasonally only by a few degrees between 26.5 and 29.2 °C, and there are only modest seasonal changes in salinity and water-quality parameters (Tomascik and Sander 1985). In the case of the beach-dwelling spionid *Scolelepis squamata* in Barbados, Richards (1970) reported protracted reproductive activity with four distinct, seasonal spawning peaks. Although the population of *D. armata* was not sampled frequently enough to distinguish distinct spawning peaks, an extended breeding season also appears to be the case in this species as well.

The analysis of the size distribution of the larvae of *Dipolydora armata* in brood pouches (Table 1) shows that only 18% of sacs contained larvae of between 11 and 18 setigers. This suggests that larvae of 11 setigers and larger emerge from the egg capsules and become planktonic. Larvae of *D. armata* may thus have a late, short pelagic life as reported for other adelphophagous species by Hannerz (1956), Simon (1967) and Blake (1969). However, there is evidence from size–frequency distributions of worms in the host branch samples (Fig. 2) that larvae of 15 to 20 setigers and juveniles of 20 to 25 setigers live free within adult burrows and may remain and complete their entire development within the host colony. It seems unlikely that allochthonous larvae could settle and invade burrow openings occupied by active adult worms.

It appears therefore that in *Dipolydora armata* alternative strategies of production of planktonic larvae and of benthic juveniles may occur. Blake and Kudenov (1981) reported a plasticity of larval development in *Boccardia proboscidea* but that two distinct larval forms co-occurred in the same capsule. Gibson (1997) described three developmental morphs in one population of the same species. In *D. armata* larval development may lead to planktonic dispersal or to retention and metamorphosis within the colony burrow of juvenile stages, but only one larval morph has been observed. Although one would expect that the trophic mode might be regulated by the number of nurse eggs available for food (Gibson 1997), there was no evidence of a correlation between the number of larvae and eggs in egg sacs in *D. armata*. Other factors such as the degree of crowding in the burrows may control larval release and retention.

The larvae of *Dipolydora armata* differ in a number of aspects of their setation from other non-planktonic larvae of the same genus described by Blake (1969) and from non-planktonic *Spio setosa* (Simon 1967). Larval bristles or provisional setae, which are characteristic of planktonic larvae, are entirely missing in *D. armata*, as they are in non-planktonic larvae of *D. quadrilobata*. Larval setae are present in the non-planktonic larvae of *S. setosa* however. Adult setae are present in *D. armata* from six-segment larvae onwards and are longer and more prominent than in the same stages in *D. quadrilobata*. Because the setae of *D. armata* are stouter and shorter than the fine, long provisional larval bristles found in other species, they would have less importance for flotation or as swimming appendages than the latter, but might be expected to be used in the adult fashion for locomotion and holding in a burrow. Thus large, adult setae would have functional value in brooded, non-planktonic larvae developing entirely within adult burrows.

Although the production of spermatophores in spionids is not uncommon (Simon 1967; Rice 1978), the capsule-like spermatophores produced by *Dipolydora armata* appear to be unique. From Table 3 it is evident that females carrying spermatophores are present throughout the year. Adult females commonly carry two or three each but up to a dozen spermatophores per female were observed. Juvenile stages with 20 to 25 setigers also carried spermatophores. Possession of sperm-

atophores would allow long-term seasonal production of larvae because sperm could be stored until females mature and obviate the need for synchronous spawning. Possession of spermatophores would also be advantageous for successful fertilization in an aggregated or "nested" population within the host coral branch.

In conclusion, there are several features of reproduction and larval development in *Dipolydora armata* which appear to be of adaptive significance and favour its association with the host coral *Millepora complanata*. There is evidence from the presence of larvae living free in the burrows that larval development and metamorphosis are completed within the host but that some larvae may exhibit a planktonic phase. The possession of spermatophores and a protracted breeding cycle would both favour successful fertilization in a population retained within the host skeleton. Complete larval development within the host would lessen settlement mortality in the population (but also modify dispersal potential). Lack of provisional larval setae and the presence of functional adult setae from early larval stages onwards should allow movement and dispersal within the burrow system in the host and thus favour recruitment.

Acknowledgements This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada. I am grateful to Dr. W. Hunte for the use of facilities at the Bellairs Research Institute of McGill University and to Dr. J.A. Blake for his helpful comments on the manuscript.

References

Bellamy N, Risk MJ (1982) Coral gas: oxygen production in *Millepora* on the Great Barrier Reef. Science, NY 215: 1618–1619

Blake JA (1969) Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae). Ophelia 7: 1–63

Blake JA (1996) Chapter 4. Family Spionidae Grube, 1850. In: Blake JA, Hilbig B, Scott PH (eds) Taxonomic atlas of the Santa Maria Basin and western Santa Barbara Channel. Vol. 6. Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae. Santa Barbara Museum of Natural History, Santa Barbara, pp 81–223

Blake JA, Evans JW (1973) *Polydora* and related genera as borers in mollusk shells and other calcareous substrates. Veliger 15: 235–249

Blake JA, Kudenov JD (1981) Larval development, larval nutrition and growth for two *Boccardia* species (Polychaeta: Spionidae) from Victoria, Australia. Mar Ecol Prog Ser 6: 175–182

Blake JA, Woodwick KH (1975) Reproduction and larval development of *Pseudopolydora paucibranchiata* (Okuda) and *Pseudopolydora kempi* (Southern) (Polychaeta: Spionidae). Biol Bull mar biol Lab, Woods Hole 149: 109–127

Bochert R, Bick A (1995) Reproduction and larval development of *Marenzelleria viridis* (Polychaeta: Spionidae). Mar Biol 123: 763–773

Dauer DM (1994) Functional ciliary groups of the feeding palps of spionid polychaetes. In: Dauvin J-C, Laubier L, Reish L (eds) Actes de la 4eme Conference internationale des Polychaetes. Mém Mus natn Hist nat 162: 81–84

Dauer DM, Maybury CA, Ewing RM (1981) Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. J exp mar Biol Ecol 54: 21–38

Day RL, Blake JA (1979) Reproduction and larval development of *Polydora giardi* Mesnil (Polychaeta: Spionidae). Biol Bull mar biol Lab, Woods Hole 156: 20–30

Dean D, Blake JA (1966) Life history of *Boccardia hamata* (Webster). Biol Bull mar biol Lab, Woods Hole 130: 316–330

Foster BA (1987) Barnacle ecology and adaption. In: Southward AJ (ed) Barnacle biology. Balkema, Rotterdam, pp 113–133

Foster NM (1971) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. Stud Fauna Curaçao 36 (129): 1–183

Gibson GD (1997) Variable development in the spionid *Boccardia proboscidea* (Polychaeta) is linked to nurse egg production and larval trophic mode. Invert Biol 116: 213–226

Gudmundsson H (1985) Life history patterns of polychaete species of the family Spionidae. J mar biol Ass UK 65: 93–111

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

Hoagland KE, Robertson R (1988) An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? Biol Bull mar biol Lab, Woods Hole 174: 109–125

Hutchings PA (1983) Cryptofaunal communities of coral reefs. In: Barnes DJ (ed) Perspectives on coral reefs. Brian Clouston, Manuka, Australia, pp 200–208

Hutchings PA, Bamber L (1985) Variability of bioerosion rates at Lizard Island, Great Barrier Reef: preliminary attempts to explain these rates and their significance. In: Gabrié C et al. (eds) Proc 5th int Coral Reef Congr. Vol. 2. Antenne Museum – EPHE, Moorea, French Polynesia, pp 333–338

Levin LA (1984) Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. Ecology 65: 1185–1200

Levin LA, Caswell H, DePatra K, Creed EL (1987) Demographic consequences of larval development mode: planktotrophy vs. lecithotrophy in *Streblospio benedicti*. Ecology 68: 1877–1886

Levin LA, Creed EL (1986) Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic and lecithotrophic development. Mar Biol 92: 103–113

Levin LA, Huggett DV (1990) Implications of alternative reproductive modes for seasonality and demography in an estuarine polychaete. Ecology 71: 2191–2208

Lewis JB (1992) Recruitment, growth and mortality of a coral-inhabiting barnacle *Megabalanus stultus* (Darwin) upon the hydrocoral *Millepora complanata* Lamarck. J exp mar Biol Ecol 162: 51–64

Light WJ (1970) *Polydora alloporis*, new species, a commensal spionid (Annelida, Polychaeta) from a hydrocoral off central California. Proc Calif Acad Sci 37: 459–472

Lunz RJ (1940) The annelid worm, *Polydora*, as an oyster pest. Science, NY 92: p 310

Marsden JR (1992) Reproductive isolation in two forms of the serpulid polychaete, *Spirobranchus polycerus* (Schmarda) in Barbados. Bull mar Sci 51: 14–18

Medcoff JC (1946) The mud-blister worm, *Polydora*, in Canadian oysters. J Fish Res Bd Can 6: 498–504

Moyse J (1971) Settlement and growth pattern of the parasitic barnacle *Pyrgoma anglicum*. In: Crisp DJ (ed) Proc 4th Eur mar Biol Symp. Cambridge University Press, Cambridge, pp 125–141

Okuda S (1937) Spioniform polychaetes from Japan. J Fac Sci Hokkaido Univ (Ser VI, Zoology) 5: 217–254

Rice SA (1978) Spermatophores and sperm transfer in spionid polychaetes. Trans Am microsc Soc 97: 160–170

Rice SA, Simon JL (1980) Intraspecific variation in the pollution indicator polychaete *Polydora ligni* (Spionidae). Ophelia 19: 79–115

Richards SL (1970) Spawning and reproductive morphology of *Scolelepis squamata* (Spionidae: Polychaeta). Can J Zool 48: 1369–1379

Santos PJP (1994) Population dynamics and production of *Scolelepis gaucha* (Polychaeta: Spionidae) on the sandy beaches of southern Brazil. Mar Ecol Prog Ser 110: 159–165

Sato-Okoshi W (1994) Life history of the polychaete *Polydora variegata* that bores into the shells of scallops in northern Ja-

pan. In: Dauvin J-C, Laubier L, Reish DJ (eds) Actes de la 4eme Conference internationale des Polychaetes. Mém Mus natn Hist nat 162: 549–558

Simon JL (1967) Reproduction and larval development of *Spio setosa* (Spionidae: Polychaeta). Bull mar Sci 17: 398–431

Simon JL (1968) Occurrence of pelagic larvae in *Spio setosa* Verril, 1873 (Polychaeta, Spionidae). Biol Bull mar biol Lab, Woods Hole 134: 503–515

Te Strake D, Jaap WC, Truby E, Reese R (1988) Fungal filaments in *Millepora complanata* Lamarck, 1816 (Cnidaria: Hydrozoa) after mass expulsion of zooxanthellae. Fla Scient 51: 184–188

Tomascik T, Sander F (1985) Effects of eutrophication on reef-building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. Mar Biol 87: 143–155

Weisberg SB, Ranasinghe JA, Dauer DM, Schaffner LC, Diaz RJ, Frithsen JB (1997) An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. Estuaries 20: 149–158

Woodwick KH (1964) *Polydora* and related genera (Annelida, Polychaeta) from Eniwetok, Majuro and Bikini Atolls, Marshall Islands. Pacif Sci 18: 146–159

Zajac RN (1991a) Population ecology of *Polydora ligni* (Polychaeta: Spionidae). I. Seasonal variation in population characteristics and reproductive activity. Mar Ecol Prog Ser 77: 197–206

Zajac RN (1991b) Population ecology of *Polydora ligni* (Polchaeta: Spionidae). II. Seasonal demography variation and its potential impact on life history evolution. Mar Ecol Prog Ser 77: 207–220

Zottoli RA, Carriker MR (1974) Burrowing morphology, tube formation and microarchitecture of shell dissolution by the spionid polychaete *Polydora websteri*. Mar Biol 27: 307–316