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R. N. Gibson

and

Margaret Barnes

The Dunstaffnage Marine Laboratory Oban, Argyll, Scotland

R. J. A. Atkinson

University Marine Biological Station Millport, Isle of Cumbrae, Scotland

Founded by Harold Barnes



LIFE-HISTORY PATTERNS IN SERPULIMORPH POLYCHAETES: ECOLOGICAL AND EVOLUTIONARY PERSPECTIVES

ELENA K. KUPRIYANOVA¹, EIJIROH NISHI², HARRY A. TEN HOVE³ & ALEXANDER V. RZHAVSKY⁴

¹ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, Australia e-mail: Lena.Kupriyanova@flinders.edu.au

(the corresponding author)

² Manazuru Marine Laboratory for Science Education, Yokohama National University, Iwa, Manazuru, Kanagawa 259–0202, Japan

³ Instituut voor Biodiversiteit en Ecosysteem Dynamica/Zoölogisch Museum, Universiteit van Amsterdam, Mauritskade 61, NL-1090 GT Amsterdam, The Netherlands

⁴ A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Leninskij Prospekt 33, Moscow, 117071, Russia

Abstract The paper summarises information on the life history of tubeworms (Serpulidae and Spirorbidae). Topics reviewed are sexuality patterns, asexual reproduction, gamete attributes, fecundity, spawning and fertilisation, larval development and morphology, larval ecology and behaviour (including larval swimming, feeding, photoresponse, and defences), brooding, settlement and metamorphosis, longevity and mortality. Gonochorism, simultaneous and sequential hermaphroditism are found in the group, the last pattern being apparently under-reported. Asexual reproduction commonly leads to the formation of colonies. The egg size range is $40-200 \,\mu\text{m}$ in serpulids and 80-230 µm in spirorbids. The sperms with spherical and with elongated heads correspond, respectively, to broadcasting and brooding. Variability of brooding methods in serpulids has been grossly under-reported and even exceeds that of spirorbids. Development is similar in feeding and non-feeding larvae and the developmental events are easily reproducible in the laboratory until the onset of competency, after which larvae require specific cues to proceed with settlement and metamorphosis. Settlement is affected by both non-specific and substratum-specific cues (conspecifics, microbial film, other organisms). Initial rapid juvenile growth slows down at later life stages. The growth rates are affected both by factors acting after the settlement and those experienced during the larval stage. Maturation is reached at a certain body size and depends on the factors controlling growth. Longevity varies from several months in small serpulids and spirorbids to 35 yr in the largest serpulids. Mortality is highest during the early embryonic and juvenile stages. The egg-size distribution in serpulimorph polychaetes is bimodal but the modes do not correspond to feeding and non-feeding development and egg sizes of species with feeding and non-feeding larvae partially overlap. This pattern may be explained by high interspecific variability in the organic content of eggs and/or facultative larval feeding of some serpulids. Planktonic development is strongly correlated with larval feeding, and planktonic lecitotrophy is rare. The potential selective advantage of larval feeding is in the flexibility of the duration of the competent stage that increases the possibility to locate suitable substrata. As in other groups, small body size correlates with simultaneous hermaphroditism, brooding,

and non-feeding development. Broader generalisations require better knowledge of the life history of a greater number of species. Integration of phylogenetic analyses into life-history studies should help to clarify the direction of life-history transitions in this group and determine whether phylogenetic constraints can account for the observed life-history patterns.

Introduction

Phylogenetic position and taxonomic problems in the group

The serpulimorph polychaetes constitute a discrete group of sedentary worms, which secrete calcareous tubes. Traditionally, they constituted the family Serpulidae and have been divided into three subfamilies: Spirorbinae, Serpulinae and Filograninae (e.g. Fauvel 1927, Rioja 1931). Pillai (1970) elevated the Spirorbinae to family status. Ten Hove (1984) and Fitzhugh (1989) questioned this division of serpulimorph polychaetes into Serpulidae (with subfamilies Serpulinae and Filograninae) and Spirorbidae. They suggested, based on cladistic analyses, that the Spirorbidae are more closely related to the Serpulinae than to the Filograninae and assigning a rank of family to this group makes the Serpulidae sensu stricto a paraphyletic group. Smith (1991) also concludes that family rank of the Spirorbidae is not justified. It is also not clear if Filograninae are monophyletic (ten Hove 1984, Kupriyanova & Jirkov 1997).

Being aware of these phylogenetic considerations, we maintain here the separation of the serpulimorph polychaetes into the families Serpulidae and Spirorbidae for practical reasons. First, confusion may exist whether the family Serpulidae includes Spirorbinae or not, since some authors (e.g. A. Rzhavsky, P. Knight-Jones and E. W. Knight-Jones, pers. comm.) continue to use family rank for spirorbids. Second, an elaborated taxonomic system below the family level in the Spirorbidae needs to be revisited if the rank of the group is to be lowered to subfamily and such a revision is clearly out of scope of the current review.

A major problem in writing a literature survey of experimental and ecological studies in serpulimorph polychaetes is their confused taxonomy. For example, many earlier fouling studies from all over the world mention *Hydroides norvegicus*. However, this is a strictly boreal species, extending into deeper waters in the Mediterranean. In (sub)tropical waters the fouling species is generally H. elegans (Zibrowius 1973, ten Hove 1974), although in tropical waters a few similar species may also occur incidentally. Frequently used in earlier experimental studies is "H. uncinatus", which was shown to be a "dustbin" of about 13 species (Zibrowius 1971). The often quoted work of Sentz-Braconnot (1964) on "Hydroides norvegica" with an operculum in the shape of a double funnel and "Serpula concharum" with a single funnel most probably only dealt with the single species Hydroides elegans. Studies on the regeneration of opercula in *H. elegans* by Cresp (1964) have shown that if the peduncle (opercular stalk) is cut proximally, the regenerating operculum will form a single funnel only; a distal caesura will regenerate the normal double funnel. Even the well known Pomatoceros triqueter should be regarded with some suspicion: Zibrowius (1968) demonstrated that the "P. triqueter" of earlier authors contains two valid species, P. triqueter and P. lamarckii; this was confirmed by electrophoretic studies by Ekaratne et al. (1982). Most, but maybe not all, of Straughan's (1972a,b) studies on the ecology of *Ficopomatus* were not based upon *F. enigmaticus*, but on the related tropical form *F. uschakovi*. "Spirorbis spirillum" reported in numerous ecological studies more likely refers to *Circeis armoricana*, whereas the data on "Spirorbis granulata" may refer to Bushiella (Jugaria) granulatus, B. (Jugaria) similis, B. (Jugaria) quadrangularis or some other Bushiella species. In many cases it is still unclear which species were studied.

This review takes advantage of the taxonomic research on the group that has been conducted in the past few decades. Only the taxonomic names that are currently considered valid are used in the review. We have compiled an addendum (p. 72) that contains all species names appearing in the text as well as their correspondence to invalid names or misidentifications that appear in original publications.

Importance of life-history research in serpulimorph polychaetes

Secretion of calcareous tubes make serpulimorph polychaetes important and troublesome members of fouling communities (e.g. Mohan & Aruna 1994). Studies of larval development and settlement therefore have practical importance and constitute a major part of serpulimorph life-history research. Spirorbid larvae with very short planktonic stage are especially convenient subjects of settlement studies. Planktotrophic larvae of serpulids, in contrast with larvae of most polychaetes, can be easily obtained and reared in the laboratory. "Nothing is easier than the rearing of Serpulids in the laboratory and especially is this the case with regard to *Pomatoceros*" (Fuchs 1911, most probably referring to *P. lamarckii*). Consequently, serpulids have served as objects of classical descriptive studies of embryology and early development since the mid-nineteenth century (see review in Segrove 1941). Also, their larvae have often been used as "typical polychaete larvae" in various recent question-orientated ecological, ultrastructural, life-history and evolutionary studies. As a result, life history of serpulimorph polychaetes has been studied very unevenly. Reproduction, development and settlement of a few common and fouling species are fairly well known but information on the life history of most species is lacking.

The objective of this paper is to put together available up-to-date information derived from various studies in order to elucidate the diversity of life-history patterns in this group. We also consider this information in the light of current hypotheses of life-history evolution in marine invertebrates and discuss possible evolutionary mechanisms shaping life history in the group.

Sexuality patterns

Gonochorism and sequential hermaphroditism

The sexes were traditionally considered to be almost exclusively separate in the Serpulidae, Johnson (1908) for instance lists, with some Spirorbidae, only the genus *Salmacina* as hermaphroditic. However, studies on the biology of the most common and commercially important fouling species eventually revealed protandric hermaphroditism with a very short intermediate stage in some species (*Hydroides elegans*: Ranzoli 1962; *Pomatoceros triqueter*: Føyn & Gjøen 1950, 1954; *Ficopomatus uschakovi*: Straughan 1968, 1972a,b; *F. enigmaticus*: Dixon 1981). Individuals producing both eggs and sperm can be found also in populations of *Galeolaria caespitosa* and *G. hystrix* (Kupriyanova unpubl.), suggesting sequential herma-phroditism in these species.

Sequential hermaphroditism causes biased sex ratios and difference in size between sexes (Straughan 1972a, Dixon 1981, Castric-Fey 1984). In *Ficopomatus uschakovi* about 40% of worms were males during the peak of the reproductive season (Straughan 1972a). The male : female sex ratio was 1 : 5 in *Pomatoceros triqueter* (Cragg 1939). Although the overall sex ratio was reported to be 1 : 1 in both *P. triqueter* and *P. lamarckii*, very young worms were male and old worms were female (Castric-Fey 1984). The male to female ratio of juvenile *Hydroides elegans* varied from 1 : 4 to 3 : 1 (Qiu & Qian 1998). However, in the apparently gonochoristic *Pomatoleios kraussi* the sex ratio was 1 : 2 in the peak of the reproductive season and even during other months (Nishi 1996).

There is a growing perception among polychaete biologists that hermaphroditism is significantly under-reported in the family and that sequential hermaphroditism may be the rule rather than an exception for serpulids. The difficulty arises from the fact that simple examination is sufficient to determine simultaneous hermaphroditism but special population-level studies are required to distinguish between true gonochorism and sequential hermaphroditism.

Simultaneous hermaphroditism

Simultaneous hermaphroditism is less common in serpulids and it seems to develop as a result of slower protandrous transition in small species such as *Rhodopsis pusilla* and species of the *Filograna/Salmacina* complex. In *Salmacina dysteri* colonies, simultaneous hermaphrodite specimens coexist with male and female specimens (Japan: Nishi & Nishihira 1993, 1994) (Fig. 1B–D). In *Salmacina* and *Filograna*, male segments are usually or mainly in anterior segments and female ones are usually or mainly in posterior ones (UK, Italy, *Salmacina dysteri*: Huxley 1855, Vannini 1965). However, Claparède (1870) explicitly states the reverse for *S. aedificatrix* from Naples but this trend does not apply for all individuals. Few segments contained both male and female gametes in *S. dysteri* (Japan: Nishi & Yamasu 1992b, Nishi & Nishihira 1993). Protandrous *S. incrustans* retains the capacity to produce male gametes after emergence of female gametes (Vannini 1950). *Spirobranchus polycerus* sensu stricto is also a simultaneous hermaphrodite (Marsden 1992), although the two-horned sympatric form (var. *augeneri*, ten Hove 1970), of supposedly the same species, is apparently gonochoristic.

In contrast to serpulids, all known spirorbids are simultaneous hermaphrodites. Their anterior abdominal segments contain eggs and the posterior segments contain male gametes (e.g. Bergan 1953, Potswald 1967a,b, King et al. 1969) (Fig. 1B). However, because sperm appear to develop faster than oocytes, juvenile worms may function as males before they can also function as females (Potswald 1981). The number of female and male chaetigerous segments varied between 2–4 and 6–31, respectively (e.g. *Circeis* cf. *armoricana*, *Spirorbis spirorbis*, and *Bushiella* sp.: Bergan 1953; *Simplaria potswaldi*: Potswald 1967a,b; *Spirorbis spirorbis*: King et al. 1969; *Neodexiospira brasiliensis*: Rzhavsky & Britayev 1984) (Fig. 1). Stagni (1959, 1961) also reported the presence of female germ cells in the achaetigerous region of *Janua pagenstecheri*.



Figure 1 Simultaneous hermaphroditism in serpulids and spirorbids. A: *Spirorbis spirorbis*, schematic representation of female and male segments (after King et al. 1969 with permission of Cambridge University Press), e – eggs in female segments, s – sperm in male segments; B: *Salmacina dysteri*, histological section, hermaphrodite segment; C: *S. dysteri*, histological section, female segments; D: *S. dysteri*, histological section, male segments (after Nishi & Nishihira 1993). B–D, no scale given in original publications.

Bergan (1953) found that in most specimens of *Circeis* cf. *armoricana* there were one or two segments where the right (concave) half was female, while the left (convex) half was male. These segments were situated between the completely female segments and the completely male ones. Similar lateral asymmetry in sex differentiation was found in one specimen of *Simplaria potswaldi* (Potswald 1967b). According to Bergan (1953), with exception of this asymmetry, spirorbid segments never contain both mature eggs and sperm, although Potswald (1967b) found two individuals of *S. potswaldi* that had oocytes and sperm developing together in the second abdominal segment, between a purely female and male segment.

Asexual reproduction

Asexual reproduction has been most extensively studied in the genera *Filograna* and *Salmacina*. In these taxa the parental animal divides into two, a process that leads to the

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Figure 2 Asexual reproduction of *Salmacina dysteri* (scanning electron microphotograph). The asexual bud (bu) and parental worm (st) both have extended branchial crowns (br) (Nishi unpubl.). Scale: 1 mm.

formation of colonies. Before the real separation takes place, the new cephalic region forms in the middle part of the parental specimen by transformation of abdominal segments into thoracic ones (morphallaxis) (e.g. Malaquin 1895, 1911, Benham 1927, Faulkner 1929, Vannini 1950, 1965, Ranzoli 1955, Vannini & Ranzoli 1962, Nishi & Yamasu 1992b, Nishi & Nishihira 1994) (Fig. 2).

Filogranula gracilis reproduces asexually by transverse fission in the middle of the abdomen (ten Hove 1979b). Scissiparity results in chains of individuals with the greater part of each tube growing along the substratum. However, its youngest part is generally free and erect, causing the mouth to lie at some distance from the substratum. Very thin tubes of new individuals bud at the mouths of established tubes and descend to the substratum, where they gradually attain the appearance and-dimensions of mature tubes.

In Josephella marenzelleri asexual reproduction leads to a network of branching tubes (George 1974). The same holds for *Rhodopsis pusilla* (Ben-Eliahu & ten Hove 1989, Nishi & Yamasu 1992a). Scissiparity was inferred from a few branching tubes in at least three species of *Spiraserpula*. In *S. snellii* one tube revealed two specimens: a parent and a schizont closely pressed to its posterior end (Pillai & ten Hove 1994), which proves asexual reproduction.

Ben-Eliahu & Dafni (1979) give no evidence of asexual reproduction in *Filogranella*, but ten Hove (pers. comm.) found three very evidently branching tubes of *Filogranella elatensis* from the Seychelles, which is indicative of asexual reproduction.

Gametes

Gamete production and development

Gonads and other gamete-producing organs

True gonads are absent in some serpulids (e.g. *Hydroides dianthus, Ficopomatus enigmaticus*) in either sex and the germ cells are produced by a germinal epithelium associated with the ring blood vessels in the intersegmental septa (Schenk 1875, Vuillemin 1965, Dixon 1981). Rullier (1955) described these gonadial tissues as zones of proliferation. Di Grande & Sabelli (1973) described their structure and the connections with blood vessels. Similar structures are present in other species of the Serpulidae (Clark & Olive 1973). Genital organs other than ovaries or testes in the Polychaeta have been reviewed by Westheide (1988).

Distinct gonads have been described in *Salmacina/Filograna* complex (Malaquin 1925, Faulkner 1929) and in *Pomatoceros triqueter* (Thomas 1940, Jyssum 1957). Developing gametes are released into the coelom. In both sexes there is a lack of synchrony in the way gametes are produced, with all but the pre-spawning mature and recently spawned individuals containing gametocytes in different stages of development. If spawning is artificially induced in laboratory conditions, a mixture of mature and immature oocytes is sometimes expelled (Kupriyanova unpubl.). It is unknown, however, whether immature oocytes are also released during natural spawning events.

Stagni (1961) reported that the female germ cells of the spirorbid *Janua pagenstecheri* are localised around the walls of the ventral blood vessel in the achaetigerous region and around ring vessels and the ventral vessel in abdominal segments 1 and 2. Oocytes are released into the coelom only at the beginning of vitellogenesis. Male germ cells are connected with the same vessels in other abdominal segments. They may separate from the vessel walls and float into the coelom where they actively multiply.

In several species of spirorbids (*Simplaria potswaldi*, *Protolaeospira eximia*, *Circeis spirillum* and *Paradexiospira* (*Spirorbides*) vitrea), Potswald (1967b) described the gonad as a discrete organ composed of clumps of primordial germ cells. These cells are arranged in two retroperitoneal rows along the middle of the ventral nerve cord and running the length of the abdominal segments. Both female and male gametes differentiate simultaneously in the same individual (Potswald 1967b).

Chromosome numbers, including those known in the Serpulidae and Spirorbidae have been reviewed by Christensen (1980) and Vitturi et al. (1984). The diploid chromosome numbers in serpulids normally range from 20 to 28, although there are two records of 14 in *Serpula vernicularis* as opposed to one record of 28 (Vitturi et al. 1984). Spirorbids have a diploid chromosome count of 20 (Dasgupta & Austin 1960, Table 1).

Oogenesis and spermatogenesis

Cytological events and ultrastructural details of oogenesis have been studied in *Pomatoceros* (Jyssum 1957), *Hydroides norvegicus* (Nordback 1956), *Spirorbis spirorbis* (King et al. 1969, Potswald 1969, 1972), *Simplaria potswaldi, Paradexiospira (Spirorbides) vitrea, Circeis spirillum* and *Protolaeospira eximia* (Potswald 1967b). Spermatogenesis has been studied

Species	n	2n	Locality	Reference
Ditrupa arietina	10	20	Oslofjord, Norway	Olsen 1970
Ficopomatus enigmaticus		26	Swansea, Milford, UK	Dasgupta & Austin 1960
Filograna implexa	13		Plymouth, UK (mix of <i>Filograna</i> and <i>Salmacina</i>)	Faulkner 1929
F. implexa		20	Off E. Anglesey, UK	Dasgupta & Austin 1960
F. implexa		44	Espegrend, Norway	Samstad 1971
Hydroides elegans	13	26	Swansea, Queen's Dock, UK;	Dasgupta & Austin 1960,
			Palermo, Italy	Vitturi et al. 1984
H. norvegicus		22	Oslofjord, Norway	Nordback 1956
Placostegus tridentatus	10	20	Oslofjord, Norway	Olsen 1970
Pomatoceros triqueter		26	Menai Straits, UK; may have been <i>P. lamarckii</i>	Dasgupta & Austin 1960
P. triqueter	12	24	Oslofjord, Norway	Jyssum 1957, Olsen 1970
Serpula vermicularis	7		5	Makino 1951
S. vermicularis		14	? Mediterranean	Soulier 1906, Dasgupta & Austin 1960
S. vermicularis		28	Oslofjord, Norway	Samstad 1971
Spirorbis spirorbis		20	Menai Straits, UK? Denmark	Dasgupta & Austin 1960, Christensen 1980
S. corallinae		20	Menai Straits, Rhosneigr, UK	Dasgupta & Austin 1960
S. tridentatus		20	Menai Straits, Holyhead, UK	Dasgupta & Austin 1960
Janua pagenstecheri		20	Menai Straits, Holyhead, UK	Dasgupta & Austin 1960
Circeis spirillum		20	Off Puffin Island, UK	Dasgupta & Austin 1960

Table 1Chromosome numbers of serpulids and spirorbids.

in Chitinopoma serrula (Franzén 1982, Franzén & Rice 1988), Hydroides norvegicus, Placostegus tridentatus, Protula globifera and Serpula vermicularis (Franzén 1956), Hydroides diramphus (Mona et al. 1994), Simplaria potswaldi (Potswald 1966, 1967a,b), Paradexiospira (Spirorbides) vitrea, Circeis spirillum and Protolaeospira eximia (Potswald 1967b), Janua pagenstecheri (Stagni 1959, 1961), and Spirorbis spirorbis (Picard 1980). These details are not considered here. Both oogenesis and spermatogenesis of the Polychaeta are discussed in a broader context by Eckelbarger (1983, 1988) and Franzén & Rice (1988).

In the spirorbid *Circeis armoricana* from the Sea of Japan two to three generations of oocytes develop simultaneously. The gonads of a specimen that has just started incubation of a brood usually contain oocytes up to 50 μ m in diameter. These oocytes mature by the time the development of the brood is completed. The specimen starts a new brood soon after the previous brood is released from the brooding structure (Ivin et al. 1990).

Fecundity

Little information is available on the number of gametes produced by free-spawning serpulids (Table 2). The available data indicate that female fecundity may vary by an order of magnitude within a species. The average number of mature ova expelled by a female of *Hydroides dianthus* is reported to vary from 3600 (Toonen & Pawlik 1994) to 30 000 (Leone 1970),

Species	Body size, mm*	Sex†	Sperm type	Sperm storage	Egg size, µm	Fecundity (eggs per female)	Egg fate	Larval nutrition	Dev. time, days	Metam size, µm	<i>T</i> °C	References
FAMILY SERPULIDAE												
Chitinopoma arndti							BR					Zibrowius 1983
C. rzhavskii	40						BR					Rzhavsky unpubl.
C. serrula	20		EL		180-200	20	BR	NF		200		Dons 1933, Thorson 1946, Franzén 1982
Crucigera irregularis	60				90		FS	F			12	Strathmann 1987
C. zygophora	110	GH			70		FS	F			12	Strathmann 1987
Ficopomatus enigmaticus	44	PR			60		FS	F	20-25	160	12.5	Morris et al. 1980, Dixon 1981
F. miamiensis	11				46-50		FS	F	14	150	26	Lacalli 1976
F. uschakovi	12						FS	F				Hill 1967
Filograna/Salmacina complex	5	SM	CDU	YES	180-200		BR	NF	7			Rullier 1960, Nelson- Smith 1971, Vannini 1975, Wu & Chen 1979, Nishi 1992b, 1993, Nishi & Yamasu 1992b, Nishi Nishihira 1993, Rouse 1996
Floriprotis sabiuraensis	20		SPH				BR					Uchida 1978, Bailey- Brock 1985
Galeolaria caespitosa	15	PR	SPH	No	60–64	500-20 000	FS	F	10–19	230	25	Andrews & Anderson 1962, Grant 1981, O'Donnel pers.com., Kupriyanova unpubl.
G. hystrix	25	PR	SPH		60	40 000	FS	F	20	200	20	Kupriyanova unpubl.

Table 2Descriptive table of literature on reproduction and development of serpulimorph polychaetes. PR – protandric hermaphrodite, SM – simultaneous
hermaphrodite, GH – gonochoristic, FS – free spawning, BR – brooding (type of brooding is specified in the text), F – feeding (planktotrophic) larva,
NF – non-feeding (lecithotrophic) larva, EL – sperm with elongated head, SPH – sperm with spherical head.

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Species	Body size, mm*	Sex†	Sperm type	Sperm storage	Egg size, μm	Fecundity (eggs per female)	Egg fate	Larval nutrition	Dev. time, days	Metam size, μm	<i>T</i> °C	References
Hydroides dianthus	25		SPH	No	45	600-80 000	FS	F	5	150	24	Colwin & Colwin 1961a, Zuraw & Leone 1968, Scheltema et al. 1981
H. elegans	25	PR		No	45-53		FS	F	5–9	150-250	25	Carpizo-Ituarte & Hadfield 1998, Franzén 1956, 1970, Matsuo & Yoshioshi 1983
H. ezoensis	25		SPH	No	45-63		FS	F	8-10	230	21	Matsuo & Ko 1981, Miura & Kajihara 1981
H. fusicola	25		SPH	No	67		FS	F	10		21	Matsuo & Yoshioshi
Marifugia cavatica Microprotula ovicallata	12 5				80		FS BR	NF				Matjasic & Sket 1966 Uchida 1978
Metavermilia cf.							BR					ten Hove unpubl.
Paraprotis dendrova	9				80	40	BR	NF	5	120-210	24	Nishi 1992a, Nishi & Yamasu 1992c
Paraprotula apomatoides							BR					Uchida 1978
Placostegus tridentatus	30		SPH					F				Franzén 1956, 1970
Pomatoceros triqueter	20	PR			60-80		FS	F	21	180	18	Segrove 1941, Føyn & Gjøen 1954, Dorresteijn & Luetjens 1994
P. terranovae	20				60		FS	F				Kupriyanova unpubl.
Pomatoleios kraussii	25		SPH	No	60-65		FS	F	17	250	24	Crisp 1974, Sawada 1984

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Pomatostegus actinoceras	55						FS					Nishi 1993
Protula sp. 1					85		FS	NF			26	Tampi 1960
Protula sp. 2					86		FS	NF	4		25	Pernet pers. comm.
P. globifera	37		SPH									Franzén 1956, 1970
P. palliata			SPH		80	10 000-13 000	FS	F	21	300	20	Kupriyanova unpubl.
P. tubularia	50						BR	NF		120		Salensky 1882
Pseudochitinopom a occidentalis	15			No	60	2500	FS	F				Hess 1993, Kupriyanova unpubl.
Pseudovermilia sp.	15						BR					ten Hove unpubl.
Rhodopsis pusilla	3		EL		78–90	1	BR	NF	8	250	24	Ben-Eliahu & ten Hove 1989, Nishi & Yamasu 1992a
Salmacina amphidentata							BR	NF				Nishi unpubl.
S. dysteri	3 `		EL		120–150	26	BR	NF	5	300	26	Franzén 1956, 1958, 1970, Rullier 1960, Nishi & Yamasu 1992b, Nishi & Nishihira 1993
Salmacina sp.	3		EL				BR	NF				Rouse 1996
S. tribranchiata	5					14	BR	NF				MacGinnitie & MacGinnitie 1949, Nishi unpubl.
Semivermilia cf. uchidai							BR					ten Hove unpubl.
Serpula columbiana	60				65		FS	F	50	300	12	Young & Chia 1982, Strathmann 1987
Serpula sp.			SPH				(FS)	(F)				Jamieson & Rouse 1989
S. uschakovi	120						FS	F				Kupriyanova unpubl.
S. vermicularis	70		SPH				FS	F				Franzén 1956, 1970
Spirobranchus corniculatus	70		SPH	No	80		FS	F	10	500	29	Smith 1984a, 1985
S. giganteus	90			No	83		FS	F				Allen 1957
S. polycerus sensu stricto	40	SM			65		FS	F			26	Lacalli 1976, Marsden 1992

Species	Body size, mm*	Sex†	Sperm type	Sperm storage	Egg size, µm	Fecundity (eggs per female)	Egg fate	Larval nutrition	Dev. time, days	Metam size, µm	<i>T</i> °C	References
S. tetraceros Vermiliopsis infundibulum– glandigera complex EAMILY SPRORPHDAE	10	GH			60		FS FS	F		360	28	Gaikwad 1988 Nishi 1993
Spirorbinae												
Spirorbis bifurcatus	1.75	(SM)				Up to 24	BR	(NF)				Knight-Jones 1978
S. corallinae	2.5	SM			100–150	20	BR	NF		250-350		de Silva & Knight-Jones 1962, Knight-Jones & Knight-Jones 1977
S. cuneatus	2	SM					BR	NF		250		Gee 1964
S. (Velorbis) gesae	2	(SM)				About 15‡	BR	(NF)				Knight-Jones & Knight-Jones 1995
S. inornatus	3.5	SM		Yes	150-230		BR	(NF)		300		L'Hardy & Quievreux 1964, Gee 1967, Picard 1980
S. infundibulum	2	(SM)			125–128	1–5	BR	(NF)				Harris & Knight-Jones 1964
S. rothlisbergi	2	(SM)				Up to 70	BR	(NF)				Knight-Jones 1978
S. rupestris	4.5	SM		Yes	110-180	Up to 35	BR	NF		400		Gee & Knight-Jones 1962, Picard 1980
S. spatulatus	2	(SM)				Up to 50	BR	(NF)				Knight-Jones 1978
S. spirorbis	4	SM	EL	Yes	110-190	1–90 (usually 10–60)	BR	NF	14	360	11.5	Daly 1978a,b
S. spirorbis									20-23			Knight-Jones 1951, Franzén 1956, 1970, de Silva & Knight-Jones 1962, Daly & Golding 1977, Picard 1980

Table 2continued

S. strigatus	1.5	(SM)				Up to 9	(BR)	(NF)				Knight-Jones 1978
S. tridentatus	3.5	SM	EL	Yes	110-180	Up to 50	BR	NF		280-350		Franzén 1956, 1970, de Silva & Knight-Jones 1962, Picard 1980
Circeinae												
Circeis armoricana	3.5	SM		Yes	6–295	6–295	BR					Picard 1980, Al-Ogily & Knight-Jones 1981, Rzhavsky & Britayev 1988, Ivin 1998
C. cf. armoricana A		SM			140×95	10-80	BR	NF	5	260		Okuda 1946
C. cf. armoricana B		(SM)				12–36	BR	NF		250		Sveshnikov 1978
C. oshurkovi	1.3	SM				10-12	BR	(NF)				Rzhavsky 1998, unpubl.
C. paguri	1.5	SM					BR	NF				Knight-Jones & Knight-Jones 1977, Al-Ogily & Knight- Jones 1981
Circeis sp.		SM	EL				BR					Franzén 1956, 1970
Paradexiospira (Spirorbides) vitrea	2	SM	EL	Yes		4–65 (24.7, 0.03) n = 57	BR	NF		250-350		Franzén 1956, 1970, Quievreux 1962, Uchida 1971, Picard 1980, Hess 1993
Januinae												
Janua pagenstecheri	1.3	SM	EL	Yes	120-150	7–25	BR	NF	About 15	200	10	Franzén 1956, 1970, Kiseleva 1957, Knight-Jones et al. 1974 - Bicard 1980
Neodexiospira	2.8	SM			140×1	40	BR			370		Okuda 1946
alveolata	210	BILL			60	10	BR			570		ORdau 1910
N. brasilensis	2.5	SM				2–60 (occasionally about 100)	BR	(NF)	About 15			Knight-Jones et al. 1975, Fauchald 1983, Rzhavsky & Britayev 1984
N. cf. brasiliensis		(SM)			95–99		BR	NF		320		Abe 1943
N. foraminosa		SM			80		BR	(NF)	7	150	25	Nishi & Yamasu 1992d

Species	Body size, mm*	Sex†	Sperm type	Sperm storage	Egg size, μm	Fecundity (eggs per female)	Egg fate	Larval nutrition	Dev. time, days	Metam size, μm	<i>T</i> °C	References
N. formosa	1‡	(SM)			-	8-12	BR	(NF)				Knight-Jones 1972, Knight-Jones et al. 1974
N. kavi	1.5	(SM)				9–19	BR	(NF)				Knight-Jones 1972
N. lamellosa	1‡	(SM)				About 8	BR	(NF)				Knight-Jones et al. 1974
N. pseudocorrugata	1	(SM)				About 8	BR	NF		220		Harris 1968, Knight- Jones et al. 1974
N. steueri	1.5‡	(SM)				1–14	BR	(NF)				Knight-Jones 1972, Knight-Jones et al. 1974
Pillaiospira trifurcata	1‡	(SM)				6-8	BR	(NF)				Knight-Jones 1973
Paralaeospirinae												
Paralaeospira levinseni	2.5	(SM)				5-40	BR	(NF)				Knight-Jones & Walker 1972, Vine 1977
P. malardi		SM		Yes			BR	(NF)		300		Quievreux 1962, Picard 1980
<i>P. parallela</i> Romanchellinae	2	(SM)				About 10	BR	(NF)				Vine 1977
Eulaeospira convexis	0.9	(SM)				Up to 20	BR	(NF)				Knight-Jones et al. 1974
Helicosiphon platyspira	5	(SM)				About 90	BR	(NF)				Knight-Jones 1978
H. biscoensis	21 (tube length)	(SM)				About 200	BR	(NF)				Knight-Jones et al. 1973
Metalaeospira clasmani	2.8	(SM)				30 (one spec.)	BR	(NF)				Vine 1977

Table 2continued

M. pixelli	3.0‡	(SM)				>200, probably up to 300‡	BR	(NF)		Knight-Jones & Knight-Jones 1994
M. tenuis	2.5	(SM)				Up to 13	BR	(NF)		Knight-Jones 1973
Protolaeospira (P.) eximia		SM				$20-106\ 58.7$ (22.3) n = 50	BR	(NF)		Hess 1993
P. (P.) pedalis	2‡	(SM)				About 50‡	BR	(NF)		Knight-Jones & Knight-Jones 1994
P. (P.) striata	3	SM	Y	es		About 30‡	BR	NF	300	Picard 1980, Oujevreux 1963
P. (P.) tricostalis	1.5‡	(SM)				Up to 17	BR	(NF)		Knight-Jones 1973
P. (P.) triflabellis	4	(SM)				About 200	BR	(NF)		Knight-Jones 1973
P. (Dextralia) stalagmia	6	(SM)				>200	BR	(NF)		Knight-Jones & Walker 1972
Romanchella pustulata	4	SM			100-160	165–270	BR	NF	210	Canete & Ambler 1990, Knight-Jones 1978
R. quadricostalis	2 ±	(SM)				Up to 25	BR	(NF)		Knight-Jones 1973
R. scoresbyi	1.5	(SM)				Up to 16	BR	(NF)		Harris 1969
R. solea	2	(SM)				Up to 20	BR	(NF)		Vine 1977
Pileolariinae						-		× /		
Bushiella (B.) abnormis		SM				20-107 (60, 19.2) n = 82	BR			Hess 1993
B. (Jugaria) atlantica		(SM)				Up to 3	BR	(NF)		Knight-Jones 1978
B. (Jugaria) granulata	2	SM				5-12	BR	(NF)		Rzhavsky unpubl.
B. (Jugaria) kofiadii	2.5	SM				Up to 25	BR	(NF)		Rzhavsky unpubl.
B. (Jugaria) quadrangularis	3	SM				Up to 30	BR	(NF)		Rzhavsky unpubl.
Bushiella sp.		SM E	EL				BR	(NF)		Franzén 1956, 1970
B. (Jugaria) similis	2.5	SM				8-17	BR	(NF)		Rzhavsky unpubl.
Nidificaria nidica	1.2	(SM)				2-4	BR	(NF)		Knight-Jones 1978
N. palliata	2	(SM)				20	BR	(NF)		Knight-Jones 1978

-

Species	Body size, mm*	Sex†	Sperm type	Sperm storage	Egg size, μm	Fecundity (eggs per female)	Egg fate	Larval nutrition	Dev. time, days	Metam size, µm	T°C	References
Pileolaria berkeleyana sensu lato		SM				4-56 13.9 (7.25) n = 71	BR					Hess 1993
P. sp. 1 (connexa)	1.5	(SM)				8-12	BR	(NF)				Rzhavsky & Knight- Jones 2001
P. daijonesi	2 evoluted‡	(SM)				About 10	BR	(NF)				Knight-Jones 1972
P. dakarensis	1.2	(SM)				About 5	BR	(NF)				Knight-Jones 1978
P. sp. 2 (invultuosa)	2	(SM)				About 20	BR	(NF)				Rzhavsky & Knight- Jones 2001
P. lateralis	1.5	(SM)				About 15 [±]	BR	(NF)				Knight-Jones 1978
P. marginata	2	(SM)				Up to 16	BR	(NF)				Knight-Jones 1978
P. militaris	2	SM	EL		About 230	9–14	BR	NF		390		Franzén 1958, 1970, Kiseleva 1957
P. pseudoclavus	1	(SM)				3‡	BR	(NF)				Vine 1972
P. spinifer	2	(SM)				Up to 12	BR	(NF)				Knight-Jones 1978
P. tiarata	1.5	(SM)				Up to 10	BR	(NF)				Knight-Jones 1978
Protoleodora uschakovi	5					Up to 150	BR	(NF)				Knight-Jones 1984, Rzhavsky unpubl.
Simplaria potswaldi	3	SM				About 30	BR	NF	42	320	10	Knight-Jones 1978, Potswald 1978
S. pseudomilitaris	1.3‡	(SM)				8–20	BR	(NF)				Knight-Jones et al. 1974
Vinearia zibrowii	0.7	(SM)				24	BR	(NF)				Knight-Jones 1978

Table 2continued

* Note that in serpulids the body length without a tube is reported, while in spirorbids it is the coil diameter of the tube that is used as a measure of body size, unless indicated otherwise. † Since all known spirorbids are simultaneous hermaphrodites and characterised by non-feeding development, data in parentheses (SM), (NF) are used when sexual pattern and larval feeding were not explicitly stated in cited publications.

‡ Estimated from figure.

whereas Zuraw & Leone (1968) report a range of 600–180 000. Average female fecundity of *Pseudochitinopoma occidentalis* was reported to be about 2500 (Hess 1993) and that of *Hydroides elegans* ranged from 1100 to 9050 oocytes per female (Qiu & Qian 1998). Similarly, the fecundity of *Ficopomatus enigmaticus* is reported to vary between 1000–10 000 (Kinoshita & Hirano 1977).

Fecundity of brooding serpulid species may be as low as one embryo per brood chamber in *Rhodopsis pusilla* (Nishi & Yamasu 1992a) and does not exceed 50 embryos in *Paraprotis dendrova* (Nishi & Yamasu 1992c) (Table 2). The maximum number of eggs per segment in *Salmacina dysteri* was six and it was on average 26 in a whole worm (Japan: Nishi & Nishihira 1993).

In contrast to the fecundity of serpulids, the fecundity of brooding spirorbids is well documented (Table 2). It is slightly higher than that of brooding serpulids but also shows significant variability among species. The lowest fecundity (not more than five embryos per brood) was reported for *Nidificaria nidica*, *Spirorbis infundibulum*, *Bushiella (Jugaria) atlantica*, *Pileolaria dakarensis* and the highest (>200 embryos per brood) was reported for *Romanchella pustulata*, *Metalaeospira pixelli*, and *Protolaeospira (Dextralia) stalagmia*.

Even less is known about male fecundity in both spirorbids and serpulids. The estimated number of sperm released by *Hydroides dianthus* is 62 millions (Leone 1970). The maximum number of 7600 sperms per segment was reported for *Salmacina dysteri* (Japan: Nishi & Nishihira 1993).

Factors affecting gamete maturation and fecundity

Temperature Later stages of gametogenesis in *Ficopomatus enigmaticus* require an increase in water temperature (Dixon 1981). The rate of gamete maturation in *Spirorbis rupestris* was slow at 5°C but was more rapid at higher temperatures (Gee 1967). *Hydroides dianthus* responds to artificially elevated temperatures in the winter by developing gametes out of season. Worms subjected to a temperature approximating that of the natural environment during the normal reproductive period developed normal ripe gametes in 10 days (Turner & Hanks 1960). On the other hand, according to Leone (1970), gamete production (fecundity) in this species decreased at temperatures abnormally high for this species (26–30°C). Average fecundity of *H. elegans* was unaffected by temperature within the range of 15–30°C (Qiu & Qian 1998).

Salinity Low salinity reduces gamete production in serpulids. The average fecundity in *H. dianthus* decreased from 34 000 at a salinity of 35 to 28 000 at 25 and to 13 000 at 15. Average fecundity of *H. dianthus* and *H. elegans* was similar at salinities \geq 25 but was lower at the lowest survival salinity of 15–20 (Leone 1970, Qiu & Qian 1998).

Food The type of food affects the number of sperm released in *H. dianthus*: more sperm were obtained in the worms fed an algal mixture than in those fed a single species (Leone 1970) but the number of eggs did not appear to be significantly affected by the different food types.

Chemical stimulation of gamete maturation Certain chemicals affect gamete maturation. Hörstadius (1923) found that increased concentrations of $CaCl_2$ in calcium-free sea water promoted maturation of *Pomatoceros*. Maturation of oocytes in this species was also promoted by the absence of potassium in artificial sea water and the addition of increasing levels of potassium chloride had an increasingly inhibitory effect. Ashton (1959) found that oocytes of *Hydroides* could be activated by trypsin or chymotrypsin in the absence of calcium.

Body size Adult body size is the major factor determining fecundity in many invertebrates, including serpulimorph polychaetes. Larger maximum body size correlates with higher maximum fecundity in spirorbids, where such data are available (see Fig. 14, p. 69). Observed significant intraspecific variability is determined by the environmental conditions during the reproductive season, individual age, nutritional status, or a combination of factors. Daly (1978a) showed that the number of eggs per brood of a Northumberland population of *Spirorbis spirorbis* positively correlated with individual size (and age) and, for a given size, declined steadily during the breeding season. Fecundity of *Neodexiospira brasiliensis* from the Sea of Japan also correlates with the size of animals but does not change during the reproductive season (Rzhavsky & Britayev 1984). The average fecundity of *Circeis armoricana* increased from 79 in January to 160.8 in June, but only the maximum fecundity observed in April–May positively correlated with body size (Ivin 1998).

Gamete morphology and composition

The eggs

Mature egg sizes show a wide range of variation (Table 2, Fig. 3). Egg size in serpulids range from $45-50 \ \mu\text{m}$ in *Ficopomatus miamiensis* (Lacalli 1976) and *Hydroides ezoensis* (Miura & Kajihara 1981, 1984) to $180-200 \ \mu\text{m}$ in *Chitinopoma serrula* (Dons 1933). Egg size in spirorbids ranges from $80 \ \mu\text{m}$ in *Neodexiospira foraminosa* (Nishi & Yamasu 1992d) to 230 \ \mu\text{m} in *Pileolaria militaris* (Kiseleva 1957, see also Table 2). Many authors report some range for serpulid egg sizes which, at least partly, may be due to measuring at different moments in the cycle (see below). No detailed studies on natural intraspecific variability of egg size are available.

The unfertilised oocytes of free-spawners are negatively buoyant. When released, they are lens-shaped (double-concave) in *Serpula columbiana* (Strathmann 1987), biconvex in *Pomatoceros triqueter* (von Drasche 1884, Kuhl 1941), cup shaped to irregular in *Ficopomatus enigmaticus* (Fischer-Piette 1937, Vuillemin 1965) or somewhat polygonal and crumpled in appearance in *Galeolaria caespitosa* and *Hydroides ezoensis* (Andrews & Anderson 1962, Grant 1981, Miura & Kajihara 1981). All become spherical after contact with sea water. The colour of oocytes ranges from pale pink or yellowish (*Pomatoleios kraussi:* Crisp 1977; *Galeolaria caespitosa:* Marsden & Anderson 1981) to deep red-violet in *Pomatoceros triqueter* (Segrove 1941, Kuhl 1941). The egg coat (chorion) is approximately 2 µm thick and sometimes has a reticulate patterned surface (*Spirobranchus corniculatus:* Smith 1984a; *Galeolaria caespitosa:* Grant 1981; *G. hystrix:* Kupriyanova unpubl.; *Spirobranchus polycerus:* Lacalli 1976). The development of an extracellular coat in oocytes of *Galeolaria caespitosa* is described by Grant & Crossley (1980).

There are few reliable observations on shape and size of freshly spawned unfertilised eggs of spirorbids. Quite often the eggs (= unfertilised oocytes) are confused with embryos at early developmental stages or, more often, developing embryos in brooding structures are



Figure 3 Eggs of serpulids and spirorbids. A: *Hydroides elegans* 50 μm (after Wisely 1958 by permission of CSIRO Australia); B: *Galeolaria hystrix*, 60 μm (Kupriyanova unpubl.); C: *Pomatoceros triqueter*, 75 μm (after Segrove 1941); D: *Rhodopsis pusilla*, 90 μm (after Nishi & Yamasu 1992a); E: *Salmacina dysteri*, 150 μm (after Nishi & Yamasu 1992b); F: *Spirobranchus giganteus*, 80 μm after Smith 1984a); G: *Dexiospira foraminosa*, 80 μm (after Nishi & Yamasu 1992d); H: *Protula* sp. 80 μm (after Tampi 1960).



Figure 4 Sperm morphology of serpulimorph polychaetes. Broadcasting species, A: *Serpula* sp. (after Jamieson & Rouse 1989 with permission of Cambridge University Press); B: *Pomatoleios kraussi* (after Jamieson & Rouse 1989); C: *Spirobranchus giganteus corniculatus* (after Nishi 1992b); D: *Galeolaria caespitosa* (after Grant 1981 with permission of Springer-Verlag, redrawn from SEM photo); E: *Hydroides elegans* (after Nishi 1992b). Brooding species, F: *Paraprotis dendrova* (from Nishi & Yamasu 1992b); G: *Salmacina* sp. (after Rouse 1996 with permission of Springer-Verlag); H: *Chitinopoma serrula* (after Franzén 1982 with permission of Balaban Publishers); I: *Spirorbis spirorbis* (after Franzén 1956 with permission); J: *Bushiella* sp. (after Franzén 1956); K: *Pileolaria militaris* (after Franzén 1958 with permission); L: *Janua pagenstecheri* (after Franzén 1958). A, B, G, H redrawn from TEM photograph. Scale, A–C and E: 2 μm; D and F: 1 μm; G and H: 2 μm; I–L: 5 μm.

mistakenly termed "eggs" (e.g. Sveshnikov 1978). Eggs and embryos of spirorbids are brown, green, yellow, red, or pale. Knight-Jones & Knight-Jones (1977) mentioned various colours (brownish orange, orange brown, reddish brown, salmon pink, etc.) of ovaries but most likely they referred to the colour of ripe oocytes in the coelomic cavity of genital segments.

There are almost no data on the biochemical composition and energetic content of serpulid and spirorbid eggs. One published estimate of egg energy content in a serpulid is that of Strathmann & Vedder (1977) for *Serpula columbiana* from Friday Harbor, WA, USA. Based on significant overlap in egg size of species with feeding and non-feeding larvae (see Table 2), one should expect a significant variation in energetic content for eggs of similar size from distantly related species.

The sperm

Sperms that are characterised by a spherical to conical head were already described in 1870 for *Hydroides elegans* (Claparède 1870). Such sperm, with a midpiece containing spherical mitochondria and a flagellum, are known for *Pomatoleios kraussi*, *Spirobranchus corniculatus* (Nishi 1992b), *Protula globifera*, *Placostegus tridentatus*, *Serpula vermicularis*, *Hydroides norvegicus* (Franzén 1956), *H. dianthus* (Colwin & Colwin 1961a), *H. ezoensis*, *H. fusicola* and *H. elegans* (Matsuo & Yoshioshi 1983, Nishi 1992b), *Floriprotis sabiuraensis* (Uchida 1978) and *Galeolaria caespitosa* (Grant 1981) (Fig. 4A–E).

Sperm with an an elongated head and midpiece are known for brooding species, such as *Salmacina dysteri* (Sweden) and *Chitinopoma serrula* (Franzén 1956, 1958, 1982), *Rhodopsis pusilla* and *Paraprotis dendrova* (Nishi & Yamasu 1992a,c) (Fig. 4F–L). Spirorbidae also (Table 2) have elongated sperm, although Franzén (1958) recognises three and Potswald (1967b) two different morphological types within the general elongated sperm type. Differences in sperm morphology are considered to reflect different modes of fertilisation or sperm transfer (Franzén 1956, 1982, Sawada 1984). Jamieson & Rouse (1989) distinguished ect-aquasperm for broadcast spawning species and ent-aquasperm that is released into water at some stage but is stored by the female prior to fertilisation (see p. 000).

Spawning and fertilisation

Morphological changes accompanying spawning

According to Vuillemin (1965), in *Ficopomatus enigmaticus* and *Hydroides elegans*, maturation is accompanied by "epitoky", significant morphological changes (mainly an increase in pigmentation) in the abdomen. Such a phenomenon has not been reported since 1965. It is strange that she found many regenerating abdomens both in *Hydroides* and *Ficopomatus*, indicative of autotomy. However, she explicitly states that she never observed autotomised abdominal parts being passed out of the tube, which one would expect of real epitoky (concurrent with swarming). Nevertheless, her photographs indeed are very suggestive for regeneration and thus autotomy. Dixon (1977) states: "Following spawning the gonadial tissues undergo a short resting phase during which the spent adults resemble juvenile worms, except for their larger size." He, however, does not mention a sharp contrast between unspent and spent segments, which could be an alternative explanation for Vuillemin's regenerating specimens. One wonders if spawning may result in such a damage that the animal sheds part of the spent abdomen.

Frequency of spawning and length of the breeding seasons

Serpulimorph polychaetes are referred to as iteroparous, polytelic, or multiannual with respect to the frequency of reproduction. All these terms are used to describe species that spawn several times in a lifetime.

Serpulids spawn more or less continuously during an extended reproductive season. For example, the reproductive period of Spirobranchus giganteus in Puerto Rico lasted from March through October (Allen 1957). Spawning of S. polycerus from the West Indies was also observed during the summer months (Lewis 1960, Marsden 1960) but Lacalli (1976) found ripe gametes in this species from mid-October to late May in Barbados. The greatest proportion of ripe adults of S. corniculatus was found in Australia in summer between October and January (Smith 1984a). Crucigera irregularis, C. zygophora and Serpula columbiana spawn from April to September in Puget Sound, Washington State, USA (Strathmann 1987). Spawning of Ficopomatus enigmaticus in southeastern England commences in June and continues through October (Dixon 1981). The breeding season of Japanese Hydroides ezoensis lasts from late May to September and is longer than that of sympatric Pomatoleios kraussi (Miura & Kajihara 1984). Nishi (1996) reported that the reproductive season of *P. kraussi* in Japan lasts from April to December, although worms with eggs can be found all year around (Nishi unpubl.). It was possible to find a few ripe individuals of Galeolaria caespitosa at any time of the year but the most successful fertilisations were achieved with worms collected in spring (from early September) and summer (M. A. O'Donnell pers. comm.). Tropical populations of Ficopomatus uschakovi have a longer breeding season than populations of their temperate relative F. enigmaticus (Dixon 1981).

The data on spawning of spirorbids exist only for populations from the Northern Hemisphere and mainly for arctic and/or boreal species. Commencement of spawning is inferred from the presence of brooded embryos. Some spirorbids (*Spirorbis spirorbis, S. tridentatus, S. rupestris, Janua pagenstecheri*) spawn between April–May and October–November (Garbarini 1933, 1936a, Bergan 1953, de Silva 1967, Gee 1967, Daly 1978a), except for *Spirorbis corallinae*, which stop spawning by the end of July (de Silva 1967). The breeding season of the spirorbid *Circeis paguri* in southern UK lasts from February to August (Al-Ogily & Knight-Jones 1981).

Other spirorbids spawn all year round, although the proportion of spawning individuals decreases significantly during the winter. These are *Simplaria potswaldi* (Potswald 1967b), *Spirorbis rothlisbergi* (Rothlisberg 1974), *Circeis spirillum* (Potswald 1967b), *Neodexiospira* cf. *brasiliensis* (Abe 1943), *Bushiella* sp. (Bergan 1953), *Neodexiospira alveolata* (Rzhavsky & Britayev 1984, Radashevsky pers. comm.) and *Pileolaria berkeleyana* sensu lato (Thorp 1991). The proportion of *Circeis armoricana* with broods increased from 9.4% in February to 96.7% in June then gradually decreased to 2.5% in December (Ivin 1997).

While special studies on breeding periods for tropical, subantarctic and Antarctic spirorbids are lacking, occasional observations (Rzhavsky unpubl.) and data in faunistic papers (e.g. Vine 1977) suggest that tropical and subtropical species spawn continuously all year round, whereas the peak of breeding of antarctic/austral species occurs during austral summer (December–March).

The breeding periods for a species may vary geographically. For example, *Circeis armoricana* from the Kamchatka coast probably stops breeding by the end of September (Rzhavsky & Britayev 1988), whereas it breeds throughout the year in the Sea of Japan (Ivin et al. 1990, Ivin 1998) and possibly on the Norwegian coast (Bergan 1953). *Paradexiospira (Spirorbides) vitrea* from the Pacific coast of USA (Potswald 1967b) and from Kamchatka (Rzhavsky unpubl.) brood throughout the entire year. However, Bergan (1953) states that the Norwegian population of this species only broods from October to November and never in the summer months, which seems quite unlikely.

Factors affecting spawning

Environmental physical factors

Spawning in polychaetes is influenced by environmental factors such as temperature, day length and lunar cycles (Clark 1979). Temperature seems to be one of the major exogenous factors controlling the timing of reproduction of serpulids and spirorbids because the peaks of the reproductive seasons generally coincide with warmer months. *Spirorbis spirorbis* spawned in Roscoff every 14 days throughout the whole year as long as water temperature remained at 11–18°C (Garbarini 1936a). However, this is not always the case for some spirorbids.

De Silva (1967) observed that the sea temperature was higher when breeding of *S. spirorbis* ceased than it was when brooding commenced. Probably, change in temperature may be more important than the absolute level, or the decline in breeding during autumn is related more to a reduction in food supply (de Silva 1967). The time when breeding begins in a *S. spirorbis* population in Northumberland, England varies little from year to year but is apparently not triggered by an environmental temperature rise (Daly 1978a). Abe (1943) found that *Neodexiospira* cf. *brasiliensis* in Japan breeds throughout the year at temperatures as low as $5-6^{\circ}$ C in winter and as high as 32° C in summer.

Spawning synchronisation

Given the semi-continuous or continuous nature of their spawning, serpulids apparently synchronise gamete release with their closest neighbours and pheromones probably coordinate gamete release, as has been demonstrated for other polychaetes (Hardege & Bentley 1997, Hardege et al. 1998). However, the degree of this synchronisation and its mechanisms are not known.

Since spawning events are very difficult to observe in brooding species, synchronisation of spawning in spirorbids is often inferred from the synchronous release of competent larvae. Distinct synchronisation of spawning was reported for *Spirorbis spirorbis* (Garbarini 1933, 1936a, Knight-Jones 1951, de Silva 1967, Gee 1967), *S. rothlisbergi* (Rothlisberg 1974) and not so obviously for *S. corallinae* (de Silva 1967). These species have 2-wk

periods of larval development that correlate with lunar cycles. Daly (1978b) also found synchronisation in spawning and release of embryos of *S. spirorbis* from Northumberland, England but it cannot be synchronised with lunar or tidal cycles since the larval development takes about 20-23 days. The synchrony within the population in both spawning and larval release increases later in the breeding season, even though the events are not synchronised with any obvious environmental variable (Daly 1978b). Such synchrony of spawning and larval release may be under an endogenous control. Daly (1978b) suggested that a factor causing epidemic spawning might also improve the synchrony of spawning within the population.

For populations of *S. spirorbis* from Norway synchronisation of spawning is very local, that is, specimens from the same *Fucus* breed synchronously but synchronisation with breeding of specimens from the neighbouring tidal pool is absent (Bergan 1953). Complete lack of spawning synchronisation has been demonstrated for some species (Bergan 1953, Gee 1967, Potswald 1967b).

Ecology of fertilisation

External fertilisation in broadcast spawning species

The gametes of broadcast-spawners (e.g. genera *Hydroides*, *Serpula*, *Crucigera*, *Galeolaria*, *Pomatoceros* and *Spirobranchus*, see Table 2, p. 9) are released through nephridiopores and are delivered to the tube orifice with the help of ciliary beating in the faecal groove. In *Spirobranchus corniculatus* gametes are released via the right side of the branchial crown and are ejected in a stream extending several centimetres above the worm (Smith 1985). Natural spawning events are rarely observed in serpulids but gamete release is stimulated by breaking the tubes and artificial fertilisation is easy to achieve in the laboratory.

The rates of gamete transport and mixing, as well as fertilisation success and factors affecting it, have not been studied in natural populations nor in the laboratory. In free-spawning invertebrates contact of gametes is highly dependent on the proximity of conspecifics, the hydrological conditions at the time of spawning and the quantity of gametes released (a function of the size of adults and the overall population density). Successful fertilisation may be further influenced by the egg-sperm contact time, the age of gametes and sperm swimming velocity (Chia & Barker 1996). Qian & Pechenik (1998) state that fertilisation is successful over a remarkably broad range of sperm concentration in *Hydroides elegans* and usually more than 95% of eggs were fertilised within 15 min after the eggs and the sperm were mixed.

Fertilisation in brooding species

Little is known about the fertilisation biology in small-bodied brooding serpulids and spirorbids. In spirorbids artificial fertilisation is difficult to achieve: none of the attempts to fertilise eggs of *Simplaria potswaldi* (Potswald 1968) artificially was successful. No data are available on fertilisation success and the assumption that the fertilisation rate for brooding species is high may not be correct and evidence for this is needed.

Gee & Williams (1965) reported that in *Spirorbis spirorbis* eggs and sperm are shed through the nephridioducts and fertilisation occurs externally to the body but inside the tube.

Broadcasting of sperm was previously assumed to be a common fertilisation mechanism for all brooding tube-dwellers. However, discovery of a spermatheca in spirorbids (Daly & Golding 1977, Picard 1980) and one serpulid (Rouse 1996, see below) suggests that fertilisation is more complex in some, if not most, brooding species.

S. spirorbis stores sperm in single spermatheca located at the base of the branchial crown (Daly & Golding 1977, Picard 1980). It has been proposed that sperm is released into the sea, collected by other individuals and stored in the spermatheca. Sperm leaves the spermatheca at the time of spawning and fertilises eggs within the animal tube. Fertilisation probably also takes place in the tube of the operculum-brooding spirorbids and fertilised embryos are transferred later to the opercular incubating chamber.

Picard (1980) states that among spirorbids spermathecae were found in *S. spirorbis*, *S. in*ornatus, *S. rupestris*, *S. tridentatus*, Janua pagenstecheri, Paradexiospira vitrea, Circeis armoricana, Protolaeospira striata, and Paralaeospira malardi, but he does not give any details.

Spermathecae of *Salmacina*, the only serpulid species so far known to store sperm, are different from those of spirorbids. Females of *Salmacina* sp. store sperm in paired spermathecae situated in the base of the branchial crown (Belize: Rouse 1996).

Self-fertilisation

Electrophoretic evidence and laboratory experiments with isolated individuals showed that spirorbids are capable of self-fertilisation (*Simplaria potswaldi*: Potswald 1964; *Spirorbis spirorbis* and *Janua pagenstecheri*: Gee & Williams 1965; *Neodexiospira brasiliensis* and *Simplaria pseudomilitaris*: Beckwitt 1982). Self-fertilisation in the laboratory does not occur as readily as cross-fertilisation and it is believed to be facultative and not obligatory in spirorbids (Potswald 1964, 1968, Gee & Williams 1965, Beckwitt 1982). Many embryos of *Spirorbis borealis* and *Janua pagenstecheri* resulting from self-fertilisation develop slowly or are not viable; some, however, are capable of hatching and metamorphosing (Gee & Williams 1965). Self-fertilisation could not be demonstrated in the hermaphrodite serpulid *Salmacina* (Japan: Nishi & Nishihara 1993).

Cytological aspects of fertilisation

The ultrastructural details of cytological processes taking place during fertilisation in serpulids and spirorbids have been addressed by a number of authors and were placed in a wider context by Franklin (1970). A classic series of studies on the ultrastructure of sperm-egg interaction in *Hydroides dianthus* by Colwin & Colwin (1961a,b,c) addressed the functional significance of the acrosome reaction, and the sequence of events during the fusion of the gamete membrane. The fertilisation reaction has been studied in *Pomatoceros triqueter* (Cragg 1939, Kuhl 1941, Monroy 1948, 1954, Ap Gwynn & Jones 1971, 1972, Ap Gwynn et al. 1971), *Hydroides elegans* and *H. norvegicus* (Monroy 1954, Nordback 1956), *Ficopomatus enigmaticus* (Rullier 1955, Sichel 1965), *Galeolaria caespitosa* (Grant & Dwarte 1980) and *Spirorbis spirorbis* (Babbage & King 1970).

In most polychaetes the oocytes are arrested in the prophase of the first meiotic division and fertilisation is a physiological trigger that activates the oocyte maturation. The egg starts precleavage development and resumes meiosis. In some tube dwellers, the oocytes resume meiosis before fertilisation. The oocytes in these species undergo "prematuration", that is, they progress from prophase I to metaphase I after release from the female. Apparently, serpulid eggs that are spawned when the female is removed from the tube, undergo spontaneous prematuration, similar to that reported for the sabellariid *Sabellaria alveolata* (Peaucellier 1997).

Development

Overview of embryological and developmental studies

The embryonic development of serpulids has been studied extensively, especially at the turn of the century. Shearer (1911) summarised early embryological data from the literature published mostly prior to 1910 and provided a detailed description of development of *Hydroides dianthus* through the early trochophore stage (see Rouse 1999 for a (re)definition of the trochophore concept). More recent studies on serpulid embryonic development include the work of Vuillemin (1965, 1968) on *Ficopomatus enigmaticus* and Groepler (1984, 1985) on *Pomatoceros triqueter*.

Most of the accounts that have followed serpulid larval development from fertilisation to settlement include a brief description of pre-trochophore development, including some description of cleavage and gastrulation (*P. triqueter*: Segrove 1941; *Hydroides elegans*: Wisely 1958, Sentz-Braconnot 1964; *Spirobranchus polycerus*: Marsden 1960; *Galeolaria caespitosa*: Andrews & Anderson 1962, Grant 1981; *Marifugia cavatica*: Matjasic & Sket 1966; *Pomatoleios kraussi*: Crisp 1977; *Hydroides ezoensis*: Miura & Kajihara 1981; *Spirobranchus corniculatus*: Smith 1984a; *Pomatoceros triqueter*: Dorresteijn & Luetjens 1994). Tampi (1960) gave a brief description of development of *Protula* sp. up to the threechaetiger stage. Very short accounts of larval development in *Spirobranchus corniculatus* were given by White (1976) and in *S. giganteus* by Allen (1957) and Lewis (1960). Formation of larval segments is described in *Protula tubularia* by Soulier (1917) and in *Hydroides dianthus* by Ivanoff (1928). An overview of early development in polychaetes, including *Pomatoceros triqueter*, is given by Dorresteijn & Fischer (1988).

A number of studies addressed various aspects of ultrastructural larval morphology. Lacalli (1984) provided a very detailed study of the nervous system in *Spirobranchus polycerus* trochophore (48-h old to metatrochopohore). Structure and development of the apical organ in this species on the basis of ultrastructural surveys and three-dimensional reconstructions was described by Lacalli (1981). The ultrastructure of the eyespot in *S. corniculatus* was described by Smith (1984b) and in *Serpula columbiana* and *Spirobranchus giganteus* by Marsden & Hsieh (1987). Pemerl (1965) and Wessing & Polenz (1974) studied the ultrastructure of protonephridia in *Serpula columbiana* and *Pomatoceros triqueter*, respectively. Uschakova (1989) described the nervous system of some unidentified spirorbid larva (probably *Spirorbis spirorbis*) from the White Sea.

Development of feeding larvae

Developmental events in genera such as Ficopomatus, Galeolaria, Hydroides, Pomatoceros, Pomatoleios, Serpula and Spirobranchus, which have small eggs and planktotrophic larvae,



Figure 5 Development of serpulids with planktotrophic larvae. *Hydroides elegans* (after Wisely 1958 by permission of CSIRO Australia). A: egg, B: 2-cell stage; C: 4-cell stage; D: 8-cell stage; E: early trochophore, apical view; F: the same, lateral view; G: later metatrochophore, lateral view; H: 3-chaetiger competent stage, dorsal view; I: larva starting to metamorphose. Scale, A–I: 50 µm.

are very similar (Fig. 5). After fertilisation, the negatively buoyant eggs sink to the bottom, where they undergo cleavage up to the blastula stage. The first cleavage occurs after 1–1.5 h after fertilisation at 20–25°C (Wisely 1958, Andrews & Anderson 1962, Smith 1984a) but it takes 2.5 h at 15°C and almost 4 h at 10–11°C (Strathmann 1987). See Table 2, p. 9 for the comparative timing of planktotrophic development.

All cleavages of the blastomeres up to the morula stage are synchronous, holoblastic, and equal. Blastulae are uniformly ciliated and move about the culture dish (Smith 1984a). The blastula develops into a larva with a prototroch consisting of a single ring of cilia. The prototroch separates a rounded episphere from conical hyposphere. The simple gut opens with the mouth below the prototroch and the anus exiting on the opposite side above the anal vesicle. The anal vesicle is a large transparent functionally enigmatic sac located posteriorly in feeding serpulid larvae. The apical plate and the apical tuft of long rigid cilia become distinct. Cilia on the hyposphere are organised into the neurotroch, which runs from the ventral posterior surface to the mouth.

Later, the prototroch develops three main ciliary bands: the upper and lower with shorter cilia and the middle with much longer cilia (Smith 1984a, Grant 1981). A metatroch is developed at this stage. Between the prototroch and metatroch is a band of short feeding cilia.

On the right side of the episphere, a cluster of red pigment cells forms an ocellus. The ventral longitudinal muscle and metatroch circular muscle form and protonephridia become visible. The trochophore continues to grow but does not undergo any significant changes. Next, the larva develops the left ocellus identical to the right one. After this stage the growth is mostly confined to the hyposphere and the larva elongates and develops three chaetigerous segments. Before the settlement a small fourth trunk segment is delineated and paired branchial rudiments appear posterior to the metatroch.

Development of non-feeding larvae

Serpulid larvae

The only non-feeding planktonic development reported for the Serpulidae is that of *Protula* sp. by Tampi (1960). The early stages of development are characterised by the presence of a large number of oil globules. The development is very similar to that of feeding larvae but the active gut is still not formed by the 3-chaetiger stage. Non-feeding development in *Protula* sp. from Florida observed by Pernet (pers. comm.) was similar to that described by Tampi (1960).

Development of non-feeding serpulid embryos that takes place within a brooding structure has been less well studied than that of planktotrophic larvae. Short accounts of development of non-feeding larvae of serpulids are given for *Salmacina dysteri* (Nishi & Yamasu 1992b), *Paraprotis dendrova* (Nishi & Yamasu 1992c), and *Rhodopsis pusilla* (Nishi & Yamasu 1992a). Apparently, the developmental events and general larval morphology are very similar for brooded and planktonic serpulid larvae (Fig. 6).

R. pusilla develops to a trochophore with a prototroch consisting of three rows of ciliary bands that at first lacks the apical tuft. The trochophore develops into a one-chaetiger larva and then into a three-chaetiger larva with neurotroch, metatroch and two ocelli. *Paraprotis dendrova* eggs develop into slowly rotating trochophores with a long apical tuft. The early trochophore of *Salmacina dysteri* bears a prototroch, a short apical tuft and a pair of brownish red ocelli. The later trochophore stage has a well-developed neurotroch and the prototroch differentiates into three separate ciliary rings: a middle ring with longer cilia and anterior and posterior rings with short cilia. Hatching and settlement in all three species take place at the three-chaetiger stage, when larvae possess an apical tuft, a neurotroch and two ocelli.

Spirorbid larvae

The description of developmental events inside the spirorbid brooding structures is very fragmentary (e.g. Schively 1897, Abe 1943, Kiseleva 1957). Early embryology has been described only by Salensky (1883) for *Pileolaria* cf. *militaris*. Development from the early trochophore to swimming competent larvae (Fig. 7) was described in more or less detail for *P*. cf. *militaris* by Salensky (1883), for *Spirorbis* sp. by Fewkes (1885), for *Circeis* cf. *armoricana* and *Neodexiospira alveolata* by Okuda (1946), for *N. pseudocorrugata* by



Figure 6 Development of serpulids with lecithotrophic larvae. Brooded larvae: *Salmacina dysteri*, development inside the adult tube, A: egg; B: 2-cell stage; C: late stage of cleavage; D and E: early trochophore; F: 3-chaetigerous competent larva (after Nishi & Yamasu 1992d). Planktonic larvae: *Protula* sp., G: egg; H: 2-cell stage; I: 4-cell stage; J: 16-cell stage; K: spherical ciliated larva; L: early trochophore; M: later trochophore; N: 3-chaetiger competent stage; O: larva starting to metamorphose (after Tampi 1960). Scale, A–C: 0.15 mm; D–F: 0.1 mm; G–O: 50 µm.

Casanova (1954), and for *Neodexiospira* sp., *Circeis* cf. *armoricana* and *Spirorbis spirorbis* by Sveshnikov (1967, 1978). The most detailed description is given by Okuda (1946).

Like serpulid trochophores, early spirorbid trochophores are subdivided into a small episphere and a large hyposphere by a prototroch. The prototroch of the early spirorbid consists of two bands of cilia (the upper from long and the lower from short cilia). Apical cilia and ocelli may be present or absent at the early stage. A functional mouth and anus are always absent, although the future location of the mouth can be recognised by an oval depression (Okuda 1946).

In metatrochophores the collar forms ventrally under the prototroch; the apical cilia and eyes spots are always present. A neurotroch consisting of transverse rows of cilia appears mid-ventrally. At this stage the prototroch may consist of two rows (the upper long and the lower short cilia), or three rows (the upper short, middle long, and lower short cilia), as in serpulids. In the late stages of metatrochophore development the mouth opens, and branchial and opercular buds develop. The terminal part of the anal segment is covered with short cilia and may bear, in addition, two very long stiff cilia. Some species develop very distinct white primary shell glands (see below).

A competent spirorbid larva released from the brooding chamber has three chaetigers and a terminal segment, bands of locomotory cilia (prototroch, metatroch and neurotroch), apical cilia, eyespots, branchial and opercular buds and a large collar which is wider ventrally than



Figure 7 Development of spirorbid larvae. *Circeis* cf. *armoricana*, A: trochophores, ventral view; B and C: early metatrochophores, lateral and ventral views; D–F: late metatrochophores, dorsal, lateral, and ventral views; G: pre-release larva ventral view; H: swimming larva (no primary shell glands) lateral view (after Okuda 1946). *Janua pagenstecheri*, I and J: swimming larva with two primary shell glands, ventral and lateral views (after Höglund 1951). *Spirorbis tridentatus*, K and L: swimming larva with a single shell gland, ventral and lateral views; psg – primary shell glands (after Höglund 1951); M: sagittal section of competent larvae, midgut and hindgut are not connected (after Nott 1973). Scale, A–F: 50 µm; G–H: 100 µm; I–M: no scale was given in the original publication.

dorsally. The mouth (stomodeum) is open ventrally, between prototroch and collar, but the stomach is not functional and is filled with yolk. The anus is also open and surrounded by cilia; some species also have two additional stiff long cilia. Stiff long cilia may also be present apically on the head, on the branchial rudiments and collar. Species differ in the number of larval eyespots (1–5 pairs) whose size and shape can change during development from trochophores to competent larvae. Based on illustrations presented in various publications, the neurotroch, as a rule, contains four ciliary rows but this number may vary slightly among species.

Comparative morphology of feeding and non-feeding larvae

The morphology and development of feeding and non-feeding serpulid larvae are extremely similar. The latter contain more yolk, and as a result, are opaque and have under-developed stomachs. However, some features apparently distinguish serpulid and spirorbid larvae. The prominent collar that develops by the early metatrochophore stage and unfolds during spirorbid metamorphosis is such a feature. Another striking feature is the presence of various larval glands. Nott (1973) and Potswald (1978) describe a complex of thoracic gland cells that do not persist after metamorphosis. A pair of ventral subcollar glands secretes the adult tube. Dorsal collar glands are unicellular glands on either side of the mid-dorsal line. In some larvae the hindgut serves as a large white sac known as the "attachment gland" (Knight-Jones 1951) or the "primary shell gland" (Höglund 1951). The latter author recognised three morphological types of spirorbid larvae: (a) lacking a primary shell gland (Circeinae, Romanchellinae and Paralaeospirinae), (b) with one abdominal shell gland (Spirorbinae, Pileolariinae) and (c) with two primary shell glands (Januinae) (Fig. 7H, I, J, K, L). The structure of the last type is not well understood. The glands are located on the ventral side of the thorax and are retained in juveniles for a short time. Finally, serpulid larvae have a pair of large eyes, whereas spirorbid larvae may have several pairs of eyes that are similar to each other or differ significantly in size and shape.

The order of some developmental events also differs for serpulid and spirorbid larvae. In serpulids the collar and branchial buds develop in late demersal larvae after the collapse of the prototroch and before tube construction starts, whereas development of the operculum begins later, at the juvenile stage. In contrast, competent spirorbid larvae with branchial and opercular buds retain the prototroch that serves as a means of locomotion during their short planktonic stage.

The anal vesicle is large and unpaired in the feeding larvae of *Hydroides*, *Pomatoceros*, and *Spirobranchus* (e.g. Hatschek 1885, Shearer 1911, Segrove 1941, Lacalli 1984): it is small and paired in the non-feeding larvae of *Protula* and spirorbids (Salensky 1883, Meyer 1888). In the latter aspect non-feeding larvae resemble those of sabellids (Wilson 1936).

Factors affecting larval development

The development time of the pelagic feeding stage in serpulids and that of the brooded stage in spirorbids is, like most other reproductive and developmental processes, profoundly affected by temperature (Table 2, p. 9). The duration and success of planktotrophic development also depends on salinity, food availability and external metabolites of other invertebrates.

Temperature

Generally, development time increases with decreasing temperatures, e.g. 7 h at 30°C, and 15 h at 20°C for *Ficopomatus enigmaticus* (Vuillemin 1958). Although the planktonic stage in *Pomatoceros lamarckii* is 3 wk in laboratory conditions at 18°C, it varies from about 2 months in early spring to 8–15 days in June and 20 days in August (South Brittanny: Castric-Fey 1984). Larval development of *Serpula columbiana* takes up to 50 days (the longest developmental period recorded in the laboratory) at 12°C at Friday Harbor, Washington State, USA (Young & Chia 1982, Strathmann 1987); *Hydroides dianthus* and *H. elegans* develop to metamorphosis in only 5 days at 24–35°C (Scheltema et al. 1981, Carpizo-Ituarte & Hadfield 1998).

The brooding period of *Pileolaria berkeleyana* sensu lato increases with decreasing temperature from about 10 days at 25°C to about 37 days at 10°C (Thorp 1991). The reported variation in the time of brooding in *Spirorbis spirorbis* from 14 to 23 days (Garbarini 1933, 1936a, Knight-Jones 1951, de Silva 1967, Gee 1967, Daly 1978b) apparently results from different temperature conditions.

Although low temperature (15°C) led to longer duration of development of *Hydroides elegans*, it did not affect survival from newly-released oocyte to trochophore stages and temperature does not seem to be a limiting factor for early development of this species (Qiu & Qian 1997). On the other hand, Crisp (1977) demonstrated that suboptimal temperatures had a significant effect on both duration of development and survival in *Pomatoleios kraussi*. At low temperatures of 15–21°C the development to metamorphosis was not completed and at 15°C it did not proceed beyond the gastrula stage. At 23–25°C *P. kraussi* developed to metamorphosis in 17–18 days, while it took only 7–13 days to reach that stage at 27°C. At 30°C, the development was even faster, the advanced trochophore stage being reached in 4 days but metamorphosis was never observed.

Salinity

Salinity is another important factor affecting larval survival and development. Although *Galeolaria caespitosa* is able to survive dilutions down to 60% sea water, its reproduction is inhibited at concentrations below 80% sea water. Early development proceeded regularly in normal and 80% sea water but no development occurred in oocytes released into 60% sea water (Tait et al. 1984). Lyster (1965) showed that *Pomatoceros triqueter* larvae survive well in a salinity of 20, can tolerate salinities down to only 10 but can survive in such media for only a few hours. Lowered salinity lengthened the duration of development of *Hydroides elegans* and reduced its survival (Qiu & Qian 1997).

Resistance to salinity stress is reduced when the larvae are simultaneously exposed to temperature stress. The temperature at which the maximum salinity tolerance was displayed for *Pomatoceros* larvae was 14°C (Lyster 1965).

Food

Both food concentration and diet composition affect larval planktotrophic development. Low food concentration lengthened the duration of development from trochophore to newlysettled juvenile and reduced survival and settlement of *Hydroides elegans* (Qiu & Qian 1997). Paulay et al. (1985) demonstrated that larvae of *Serpula columbiana* grew signific-

antly faster with enhanced rations than in natural sea water and suggested that natural food supplies may commonly limit growth and development of larvae.

A diet of cultured algae gave less variability through the metatrochophore stage of *Spirobranchus* but poor success at settlement, whereas a diet of wild algae from the field resulted in a more variable development but more robust larvae (Lacalli 1984).

Other invertebrates

External metabolites released by some marine animals can make the surrounding environment either suitable or unsuitable for other organisms. Conditioning of water by adult *Hydroides elegans* promotes normal development of larvae and is more beneficial than natural sea water. Conditioning by *Mytilus* delays development and that by *Balanus* accelerates the development to such an extent that abnormalities may result (Srinivasagam 1966). The early development of *Hydroides elegans* can be affected if the eggs and sperms are treated with the extract of hemichordate *Ptychodera flava* (Whitin & Azariah 1982).

Pollutants

Effects of pollutants vary with the type of pollution. Larval development in *Pomatoceros triqueter* was significantly suppressed in trial water from the titanium dioxide dump site in the North Sea: only about 33–34% of larvae developed normally in the polluted water (Klöckner et al. 1985). However, larval development of *Galeolaria caespitosa* was not greatly affected by exposure to the polluted water from Port Kembla Harbour, Australia (Moran & Grant 1993).

Light

Although light does not affect larval development itself, it may serve as a cue for timing of larval release. The only observation of this type is given by Knight-Jones (1953), who observed that *Spirorbis spirorbis* released larvae in the early morning. Larval release could be induced by exposure to light following a period of darkness.

Larval ecology and behaviour

Larval swimming

Swimming behaviour

Swimming behaviour of larvae has been described for *Spirobranchus spinosus*, *S. polycerus* (Lacalli 1984) and *S. corniculatus* (Smith 1985). The larvae are propelled by the strong and continuous beat of the prototroch cilia and normally swim in a clockwise spiral with the apical tuft directed forward. As they swim, the trochophore also rotate on their axis, their axis of rotation precessing with a period matching that of the rotation. They swim in tight spirals when the angle of precession is small and tumble in broad arcs when it is large.

At younger stages (e.g. the 24-h stage in *S. polycerus*) contact with obstacles results in immediate rebound without change to the prototrochal beat. In older trochophores (48 h and older in *S. polycerus*), collisions are followed by a brief pause accompanied by an apparent alteration to the ciliary beat but only rarely do the cilia stop altogether. The metatrochophore exhibits somewhat more effective and frequent arrests, and its swimming is more erratic as a consequence.

The metatroch beats with variable speed, exhibiting periodic and sudden arrests. After an arrest, its cilia usually resume beating after a few seconds but longer periods of quiescence were observed. Metatrochal arrests were not correlated with any of the other ciliary or muscular activities of the oral apparatus. Cilia of the food groove and neurotroch beat continuously and at a constant speed. Food groove cilia beat towards the mouth and neurotroch cilia away from it (Lacalli 1984).

The body of swimming competent spirorbid larvae (Knight-Jones 1951: *Spirorbis spirorbis*) rotates clockwise on its axis. Sveshnikov (1978) reported that larvae of *Circeis* cf. *armoricana* swim in a straight line, not in spirals, like serpulid larvae. Höglund (1951) observed that spirorbid larvae typically swam forward in a long winding course, all the time turning on their longitudinal axis. Sometimes larvae even turn somersaults with the abdomen bent towards the ventral side. After turning several times in this way larvae then proceed on their winding course. It should be noted that planktonic spirorbid larvae correspond to the presettlement stage of serpulid larvae, therefore, serpulid and spirorbid swimming should be compared with caution.

Swimming mechanism

Marsden & Hassessian (1986) found that swimming cilia of *Spirobranchus giganteus* arrest on exposure to EDTA, Ba(OH)₂, lanthanum chloride, trifluoperazine and Ca²⁺-free sea water, i.e. under conditions that interfere with the supply of external Ca²⁺. They concluded that there is a Ca²⁺-dependent, catecholaminergic excitation of the swimming cilia of the *S. giganteus* larva, involving β receptors and probably neurally mediated. This conclusion agrees well with the description of basal neurite-like processes in the prototroch and neurotroch that serve as a nervous system of *Galeolaria caespitosa* larvae (Marsden 1982). Other cilia on the larval body are insensitive to agents affecting the activity of swimming cilia.

Swimming velocity

Swimming speeds in serpulids increase with increasing size of trochophores. A 1-day-old trochophore of *Spirobranchus giganteus* can attain the speed of at least 1.7 m h⁻¹. By its second day the trochophore has doubled its speed to 3.4 m h⁻¹. A 5-day metatrochophore swims at about 5 m h⁻¹ and some late metatrochophores can achieve speeds in excess of 7 m h⁻¹ (Smith 1985). Marsden (1984) reports that 1–4-day larvae of *S. polycerus* had horizontal swimming speeds of 0.4–3.5 mm s⁻¹ (1.44–12.6 m h⁻¹). Competent larvae of *Spirorbis* show comparable swimming speeds of about 3 mm s⁻¹ (10.8 m h⁻¹, Knight-Jones 1951).

The typical swimming speeds seem to be sufficient to enable serpulid larvae to control their vertical position in the coastal water column whereas horizontally, the larvae of most serpulids are distributed by sea currents. Even a short planktonic stage of about 10 min may result in dispersal up to 270 m in larvae of *Circeis* cf. *armoricanus* (Dirnberger 1993).

Factors affecting larval swimming

Hydrostatic pressure Marsden (1994a) documented the effect of changes in hydrostatic pressure on the vertical swimming of larvae of *Spirobranchus polycerus* and demonstrated a cyclical change in geotactic response mediated by changes in hydrostatic pressure. One-day larvae usually swim up or down more frequently than horizontally. They respond to an increase in hydrostatic pressure with an increase in the percentage of larvae moving downward and to a decrease in pressure with an increase in the percentage moving upward. *S. polycerus* larvae move downward not by sinking passively but by swimming actively.

Temperature Bolton & Havenhand (1997) investigated the relative physiological and viscosity-induced effects of water temperature at 25° C and 15° C on the swimming and sinking velocity of larvae of *Galeolaria caespitosa*. Both physiological and viscosity components of water temperature influenced the swimming velocity of the larvae but the influence of water viscosity did not change significantly over the course of larval development. The sinking velocity of *G. caespitosa* larvae was proportionally reduced with a temperature-induced increase in water viscosity. The metabolic costs of swimming required to counteract this sinking were similar at 25° C and 15° C but the metabolic costs of swimming a given distance were slightly higher at 15° C (Bolton & Havenhand 1997).

Photoresponse

Variability of photoresponses

Serpulid larvae show a wide range of interspecific variations of light responses that can change during the course of development. Trochophores of *Serpula columbiana* (Young & Chia 1982), *Hydroides ezoensis* and *Pomatoleios kraussi* (Miura & Kajihara 1984) show a strong positive photoresponse, whereas later metatrochophores become photonegative. *Spirobranchus corniculatus* and *S. giganteus* display only positive photoresponses (Marsden 1984, 1986, Smith 1985). The non-ocellate trochophores of *S. corniculatus* swim randomly until they develop the first ocellus (Smith 1985) and after that become positively phototactic for the rest of the planktonic stage. A positive photoresponse was reported for the demersal larvae of *Galeolaria caespitosa* but responses at other stages of this species were not described except for a tendency for settling larvae to congregate on light coloured surfaces (Marsden & Andersen 1981). *Pomatoceros lamarckii* (Segrove 1941), *Hydroides dianthus* (Zeleny 1905), and *H. elegans* (Wisely 1958) are reported to settle in the most illuminated regions of the culturing containers.

Crisp (1977) found no consistent photoresponse for swimming larvae of *Pomatoleios kraussi*. Settling larvae of *Pomatoceros triqueter* were found to be negatively phototactic (Klöckner 1976). Planktotrophic larvae of *Spirobranchus polycerus* were photonegative or photoneutral at the age of 16 h to 22 h and photopositive or photoneutral at 72 h to 350 h. During the 22- to 72-h interval, larvae may be photonegative, photoneutral or photopositive.

Some spirorbid larvae are able to change their photoresponse during their short planktonic life, which probably may explain some confusion existing in the literature. Newly released *Spirorbis spirorbis* larvae are photopositive, then become alternatively photopositive and photonegative, until finally entering the completely photonegative stage (Knight-Jones
1953, Williams 1964). However, according to Doyle (1974), larvae of this species are photonegative from the beginning of their planktonic life, whereas de Silva (1962) claimed that they are photopositive when settling. Larvae of *Circeis* cf. *armoricana* are photopositive upon release but turn photonegative within minutes (Dirnberger 1993). Larvae of *Spirorbis rupestris* and *S. tridentatus* are photonegative from release (de Silva 1962, Gee & Knight-Jones 1962), whereas larvae of *Neodexiospira alveolata* are photopositive (Okuda 1946).

Correlates of photoresponse

Photoresponse is reported to be structurally correlated with the pigment cup orientation of larval ocelli. For example, in *Spirobranchus polycerus* (Lacalli 1984) and *Serpula columbiana* (Marsden 1984) the eyecup is directed anteriorly, whereas in *Spirobranchus giganteus* the direction is posterodorsal (Marsden 1984). The receptor cell of larval ocelli in photonegative *S. polycerus* larvae is shaded from below (Lacalli 1988). In *S. giganteus* direct movement towards a light source takes place when the microvilli of the eyespot are largely shaded by the pigmented cup (Marsden 1984, Marsden & Hsieh 1987).

Level of irradiance and duration of exposure influence the strength of the photopositive response. Larvae of *S. polycerus* were indifferent to wavelengths longer than 590 nm (Marsden 1990). *Spirobranchus* trochophores respond positively to white light at levels of illumination from 1 to 2168×10^{14} quanta cm⁻² s⁻¹ and this response is increased by dark adaptation (Marsden 1986).

The photoresponse also depends on the origin of the population. Doyle (1974) showed that larvae of *Spirorbis spirorbis* from specimens taken from a tidal pool were more photonegative than those obtained outside the pool.

Larval feeding

Distribution of larval feeding in the group

Feeding pelagic larvae are common in serpulid species such as *Crucigera zygophora*, *Ficopomatus enigmaticus*, *F. miamiensis*, *Galeolaria caespitosa*, *Hydroides dianthus*, *H. elegans*, *H. ezoensis*, *H. norvegicus*, *Pomatoceros triqueter*, *Pomatoleios kraussi*, *Serpula columbiana*, *Spirobranchus giganteus*, *S. polycerus*. Larvae commence feeding from within 10–14 h after fertilisation in *H. elegans* (Finley 1971) to 48 h in *Protula palliata* (Kupriyanova unpubl.). The difference probably correlates with egg size. Non-feeding planktonic larvae have only been reported for *Protula* spp. (Tampi 1960, Pernet pers. comm.). According to Salensky (1882) and LoBianco (1888) larvae of *P. tubularia* develop (apparently without feeding) in a gelatinous mass outside the tube mouth (see also p. 43). Most small bodied species of serpulids (*Chitinopoma serrula*, *Filograna salmacina* spp., *Microprotula ovicellata*, *Paraprotis dendrova*, *Rhodopsis pusilla*) and all the Spirorbidae have non-feeding lecithotrophic development concurrent with some form of brooding.

Larval feeding mechanism

Suspension feeding by serpulid larvae is achieved by use of the opposed band system of the trochophore (Strathmann et al. 1972). The long cilia of the preoral band (prototroch) generate

the major current used in feeding and locomotion, whereas the postoral band (metatroch) is used in feeding and rejection and the food groove in transport of particles. Both preoral and postoral bands are essential for clearance. The opposed beat of cilia of the preoral and postoral bands results in increased movement of the preoral cilia relative to the water in the latter half of their effective stroke. Most of the clearance of particles from water occurs at this point. Trochophores are able to continue swimming without feeding. If the metatroch and cilia of the food groove stop beating, particles are not collected behind the prototroch but are carried posteriorly with water (Strathmann et al. 1972).

Feeding rates

The feeding rates of serpulid trochophores have not been studied in much detail. Bolton & Havenhand (1998) fed 3- and 10- μ m diameter polymer spheres to 1-day-old larvae of *Galeolaria caespitosa*. The overall rate of ingestion per 20 min varied from 4 to 20 for 3- μ m spheres and from 2 to 11 for 10- μ m spheres. Reduction by 10°C in the water temperature resulted in a 60% decline in the number of microspheres ingested.

Preferred type of food

Normally unicellular planktonic algae serve as food for both serpulid larvae and adults. There are no special field or laboratory studies documenting either the composition of the natural diet or examining the preferential selection of algal species by trochophores. Larval serpulid cultures have been successfully raised on naked flagellages *Isochrysis galbana* (Crisp 1977, Marsden 1987, Connaugton et al. 1994, Qiu & Qian 1997), diatoms *Chaetoceros* sp. (Connaugton et al. 1994), flagellates *Dunaliella salina* (Lacalli 1984), *D. primolecta* and *D. tertiolecta* (Marsden & Anderson 1981), *Nannochloris atomus* (Andrews & Anderson 1962), *Tetraselmis suecica* (Crisp 1977) or a mixture of flagellates *Dunaliella tertiolecta* and *Isochrysis galbana* and diatoms *Thalassiosira pseudonana* (Scheltema et al. 1981).

Bacterivory

Some invertebrate larvae can meet part of their metabolic needs through bacterivory (e.g. Rivkin et al. 1986 for asteroids). In laboratory experiments, *Hydroides elegans* larvae from Hong Kong were able to survive, grow, develop to competence and metamorphose into healthy early juveniles solely on a diet of bacteria. Recruitment of *H. elegans* occurs throughout the year, suggesting that spawning and successful larval development may be independent of phytoplankton availability, and that larvae largely rely on alternate food sources such as bacteria (Gosselin & Qian 1997a). Larvae of *Ficopomatus miamiensis*, unlike typical serpulid trochophores normally feeding on phytoplankton, lack a metatroch, which is attributed to their ability to use a bacterial surface film as a food source (Lacalli 1976).

Larval defences

Defence mechanisms of larvae can be classified as morphological, behavioural or chemical (Young & Chia 1987). Some polychaete larvae have chaetae that can be erected to a larger or lesser degree and might serve as a potential mechanical defence against predation.

Pennington & Chia (1984) suggested that larval chaetae increase the effective size of the larvae, reduce the chances that predators will contact the larval tissues, and possibly pierce the predator. However, trochophores of the sabellariid *Neosabellaria cementarium*, whose larvae have large chaetae with many teeth, are not preyed upon by the "suction feeding" ascidian *Styela gibbsii* any less than trochophores of *Serpula columbiana*, a species with no apparent structural defences (Cowden et al. 1984, Young & Chia 1987).

While nothing is known about the potential behavioural mechanisms of serpulid larvae, chemical defence has been shown for trochophores of *Hydroides dianthus* that release a water-soluble compound that inhibits feeding in weakfish (*Cynoscion regalis*) larvae (Connaughton et al. 1994).

Parental care of eggs and young

Spirorbid brooding methods

All spirorbids incubate their embryos (Fig. 8). Two major types of incubation are in the opercular brood-chamber or in their tube. However, tube incubation methods vary markedly according to the methods of embryo anchorage within the tube (Knight-Jones et al. 1972, Knight-Jones & Fordy 1978, Rzhavsky 1991, Knight-Jones & Knight-Jones 1994).

Figure 8 (opposite) Brooding methods in Spirorbidae. Tube incubation, A: Paralaeospira levinseni, Paralaeospirinae. Embryo string is free in the tube (after Knight-Jones & Walker 1972 with permission of British Antarctic Society); B: Spirorbis spirorbis, Spirorbinae. Egg string is attached to the tube by a posterior filament (after Knight-Jones et al. 1972 with permission of Springer-Verlag); C: Paradexiospira (Spirorbides) vitrea, Circeinae. Embryos adhere to each other and directly to the tube wall (after Knight-Jones et al. 1972); D: Romanchella scoresbyi, Romanchellinae. Embryo sac attached anteriorly to thoracic funnel-like stalk (after Knight-Jones et al. 1972); E: Metalaeospira tenuis, Romanchellinae. Embryo sac attached anteriorly to epithelial oviducal funnel, fully developed egg-string attached to the thorax; F: Metalaeospira tenuis, Romanchellinae. Embryo sac attached anteriorly to epithelial oviducal funnel, forming smaller egg-string attached to the abdominal faecal groove (after Knight-Jones 1973 with permission). Opercular incubation, Pileolariinae. Embryo brooded inside the brood chamber formed by invagination of an opercular ampula; G: Nidificaria palliata, brood chamber resembles an open cup (after Knight-Jones & Knight-Jones 1991 with permission); H: Pileolaria spinifer, brood chamber is a completely closed ampula, the primary opercular plate is shed (after Knight-Jones 1978 with permission of Academic Press); I: Bushiella (Jugaria) kofiadii, brood chamber is a completely closed ampula fused with primary opercular plate (after Rzhavsky 1988 with permission); Januinae – cuticular brood chambers are formed distally by the calcified opercular plate outside the opercular ampula; J: Neodexiospira brasiliensis, specimen in a process of separation of the primary brood chamber (distal, empty) with talon from the secondary brood chamber without talon (proximal, with embryos); K: primary mature brood chamber with a talon (after Knight-Jones et al. 1979); L: secondary brood chamber without a talon (after Knight-Jones et al. 1975 with permission of Academic Press). Scale, A: 0.25 mm, B-J: 0.5 mm, K and L: 0.2 mm.

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Tube brooding

In the Paralaeospirinae (genus *Paralaeospira*) embryos are not attached to the body or the tube (Fig. 8A). In the Spirorbinae (genus *Spirorbis*) embryos form an egg string attached to the tube by a posterior filament (Fig. 8B). Embryos adhere to each other and directly to the tube wall in the Circeinae (*Circeis* and *Paradexiospira*, Fig. 8C). They are attached anteriorly to a specialised thoracic funnel-like stalk or epithelial oviducal funnel in the Romanchellinae (*Protolaeospira*, Helicosiphon, Romanchella, Metalaeospira and Eulaeospira, Fig. 8D–F).



The last brooding method has also been reported as "embryos directly attached to the body" (e.g. Knight-Jones et al. 1972).

Opercular brooding

Opercular incubation is found in more than a half of approximately 140 known species of the Spirorbidae. About one-fifth of opercular brooders belong to the Januinae and the remainder to the Pileolariinae (Bailey 1969, Knight-Jones & Fordy 1978, Knight-Jones & Thorp 1984, Rzhavsky 1991). How embryos enter the brood chamber has never been observed and this problem has caused numerous discussions (Vuillemin 1965, Potswald 1968, 1977, Bailey 1969, Thorp 1975, Thorp & Segrove 1975, Knight-Jones & Thorp 1984).

The brood chambers of the Pileolariinae (genera *Amplicaria, Pileolaria, Nidificaria, Vinearia, Simplaria, Protoleodora* and *Bushiella*) are very different but all of them are formed by invagination of the opercular ampulla (Thorp 1975, Thorp & Segrove 1975, Knight-Jones & Thorp 1984). The chamber may look like an open cup (e.g. *Vinearia* and *Nidificaria*, Fig. 8G) or a completely closed ampulla (e.g. *Pileolaria* or *Bushiella*) with an opercular pore that is used for the entry of embryos (eggs?) and the exit of larvae (Potswald 1968, 1977, Thorp 1975). Such a brood chamber may be used for a number of broods. The primary calcified non-brooding operculum is usually shed after the brood chamber is formed (e.g. *Pileolaria*, Fig. 8H). Alternatively, it may be fused to the brooding chamber and serve as additional protection for the embryos (*Bushiella*, Fig. 8I). Formation of the brooding operculum is initiated as animals approach maturity. When breeding activity ceases, the brooding organ may again be replaced by a non-brooding operculum, which may also be replaced later by a new brood chamber (Thorp 1989, Rzhavsky & Knight-Jones 2000).

Brood chambers in the Januinae (genera *Neodexiospira, Janua, Pillaiospira, Leodora*) are formed distally by the calcified opercular plate outside of the opercular ampula (Fig. 8J–L). The distal part of the first brooding chamber is the distal plate of the primary non-brooding operculum. In the next generations of brood chambers, the distal part of a new brood chamber is the basal part of the previous brood chamber. Every brood chamber is used for only one brood and it has to be shed to liberate larvae (Knight-Jones & Thorp 1984). How embryos enter the brood chamber is still unclear, because the Januinae with mature brood chambers do not have any pores similar to those of the Pileolarii-nae. Numerous perforations in brood chambers are too small for the embryos and apparently serve to facilitate embryonic respiration (Knight-Jones & Thorp 1984). Vuillemin (1965) observed in *Neodexiospira pseudocorrugata* what she calls an egg canal within the opercular stalk and suggested that eggs (embryos?) reach the brood chamber via the stalk route.

Thorp & Segrove (1975) initially reported that at some stage of the opercular moult *Janua pagenstecheri* develops an apparently temporary pore through which the eggs enter the brood chamber. Later Knight-Jones & Thorp (1984) proposed that the embryos enter through a split between the base and the lateral wall of the brood chamber that closes to retain the embryos in the chamber. They also considered as a plausible possibility Vuillemin's suggestion that embryos enter the chamber through the opercular stalk, although such a route implies fertilisation inside the body cavity in the Januinae, which seems to be quite unlikely in our opinion.

Serpulid brooding methods

Although brooding was previously considered an exception among serpulids, several new brooding taxa have been recently reported for serpulids and it has become obvious that the variety of brooding methods even exceeds that of spirorbids.

Tube brooding

Tube incubation, probably, the simplest and most primitive type of incubation is well known for species of *Filograna/Salmacina* complex (Fig. 9A). These animals brood embryos on the compressed abdomen (Faulkner 1929, Nishi & Nishihira 1993, Nishi et al. 1996). According to ten Hove (unpubl. obs.), *Semivermilia* aff. *uchidai* from the Seychelles produced eggs and at least two swimming trochophores when its tube broke open.

Uchida (1978) mentions that *Paraprotula apomatoides* spawns inside the tube and that hatched larvae are spherical trochophores approximately 90 μ m in diameter but he does not say how long the larvae stay inside the tube or whether when released they are early trochophores or competent three-chaetiger larvae.

Brooding in tube ovicells

This type of brooding is more common in serpulids but the number of embryos incubated, the shape and the position of these ovicells vary among species. *Chitinopoma serrula*, *C. arndti* and *C. rzhavskii* produce pouches with twin chambers at the orifice of the tube, each containing 10–20 larvae (Fig. 9B) (Dons 1933, Thorson 1946, Zibrowius 1969, 1983, Rzhavsky unpubl.).

Ovicells of *Microprotula ovicellata* start as tube peristomes and then narrow down to a diameter barely wider than that of the usual tube. Thus, the ovicells resemble swellings encircling the distal part of the tube (Uchida 1978) (Fig. 9C). After the worm completes building the upper narrow part of the ovicell, it spawns about 10–15 eggs and covers the space between the upper margin of the ovicell and the inner tube with the collar. The tube stops growing during incubation. After the larvae are released, the worm continues growing the inner tube up over the distal margin of the ovicell.

Brooding in ovicells by *Rhodopsis pusilla* was originally proposed by Ben-Eliahu & ten Hove (1989) and then later described by Nishi & Yamasu (1992a) (Fig. 9D). The ovicells in this species do not encircle the tube but rather resemble wide inverted pouches arranged one by one along the length of the tube. Each ovicell contains a single egg.

At least 3 out of 17 specimens of *Filogranula* sp. from the Seychelles showed 1-3 ovicells near the tube mouth. These are balloon-shaped, slightly oval, and associated with one of the keels of the tube.

Pseudovermilia cf. occidentalis from Bonaire broods larvae in a scalloped tube peristome; one of the spoon-shaped leaflets in a three-leafed orifice was filled with developing embryos. Another specimen with large spoon-shaped leaflets near the orifice was found on Curaçao (Fig. 9E). *P. conchata* has been named after these cupped leaflets (ten Hove 1975: plate VIIIe) and similar structures are found on tubes of *Pseudochitinopoma occidentalis* (ten Hove unpubl.), although it is unclear if they are also used for brooding. Such scooped tube parts might indicate retention of early embryos for a short time. A tube of *Pseudovermilia* cf. *pacifica* from the Seychelles shows a beautiful cup- to dome-shaped ovicell over the entrance of the tube, deeper than that figured for *Pseudovermilia* cf. occidentalis (ten Hove unpubl.).



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Brooding inside the branchial crown

Paraprotis dendrova embryos are brooded inside the branchial crown on a long and slightly spiral appendage with branches growing from the mouth parts (Nishi 1992a, 1993, Nishi & Yamasu 1992c) (Fig 9F). *Metavermilia* cf. *ovata* from the Seychelles has developing embryos inside the base of its branchiae (ten Hove unpubl.) (Fig. 9G).

Brooding in pockets of the thoracic membranes

Such incubation of eggs is only known for *Floriprotis sabiuraensis* (Uchida 1978, Bailey-Brock 1985). A pair of pockets, one on each side of the inner surface of the thoracic membrane, is located between the second and the third thoracic segments. The pockets are rectangular with the opening directed forward.

Brooding in gelatinous masses

It is strange that the explicit record of *Protula tubularia* brooding eggs until the threechaetiger stage in a gelatinous mass near the tube mouth (Salensky 1882, LoBianco 1888, 1909) – a common method in sabellids and other tubicolous or burrowing polychaetes (Strathmann 1987) – is not mentioned in the subsequent extensive literature on this common species. However, this type of brooding in *Protula* has recently also been observed independently by R. Sanfilippo (material from the BIOICE project on benthic fauna around Iceland, deposited at the Marine Invertebrate Icelandic Institute and Museum of Natural History of Reykjavik) and D. Martin (pers. comm.) (Fig. 9H).

Erroneous records of serpulid brooding

The presumed brooding by *Serpula vasifera*, as mentioned by Schroeder & Hermans (1975), is an erroneous quote from Augener (1914). He stated that he, contrary to Haswell (1884, 1885), had not been able to find embryos of a commensal or parasitic isopod in the tube of *S. vasifera*.

The record of opercular brooding in *Ficopomatus enigmaticus* by McIntosh (1924) was demonstrated to be erroneous by McIntosh (1926). The single, but very explicit record by Fischer-Piette (1937) of *F. enigmaticus* brooding its larvae in the tube is uncorroborated in the subsequent very extensive literature on this species (over 300 records) and refuted by Dixon (1977). Hoagland & Robertson (1988) give Gravier (1923, cited by Thorson 1936) as

Figure 9 (opposite) Brooding methods in serpulids. Brooding inside the tube, A: *Salmacina dysteri*, two larvae in the tube near the parental abdomen. Histological section, la – larvae, ab – abdomen, t – tube (after Nishi & Yamasu 1992d with permission of Shokabu Publishing). Brooding in ovicells outside the tube, B: *Chitinopoma serrula*, paired ovicells at the tube orifice (after Dons 1930); C: *Microprotula ovicellata*, ovicells encircling the distal part of the tube (after Uchida 1978); D: *Rhodopsis pusilla*, single ovicells located along the tube, SEM photographs (after Nishi & Yamasu 1992a); E: *Pseudovermilia occidentalis*, spoon-shaped leaflets (ten Hove unpubl.). Brooding inside the branchial crown, F: *Paraprotis dendrova*, eggs and embryos on spiral branchial rudiment, SEM photographs (after Nishi & Yamasu 1992b); G: *Metavermilia* cf. *ovata*, embryos inside the base of branchia (ten Hove unpubl.). Brooding in gelatinous masses outside the tube, H: *Protula tubularia* (Sanfilippo unpubl.). Scale, A: no scale was given in the original publication; B and C: 1 mm; D and E: 0.5 mm; F: 0.2 mm; H: 5 mm; G: 1 mm.

the primary source for the observation of ovovipiparity (a form of brooding) in *Pomatoceros triqueter*. However, Gravier refers to Saint-Joseph (1894: 359) who claims to have found embryos without any organisation except an eyespot in the abdomen of the female. This observation has not been confirmed in the very extensive literature (over 500 records) on *P. triqueter*.

Length of metamorphic competence stage and delaying of metamorphosis

The three-chaetiger stage in serpulimorph polychaetes marks the onset of metamorphic competence in larvae. In planktonic serpulid larvae the competence coincides with the transition to the demersal stage and with changes in larval behaviour, while in brooded larvae it is marked by the release from the brooding structure and the beginning of a short pelagic swimming stage.

The easy repeatability of serpulid larval development up to a three-chaetiger (competent) stage in laboratory cultures indicates that the developmental events up to this stage are predetermined genetically (Marsden & Anderson 1981). However, after the onset of competency, larvae require a cue (or cues) to proceed with further development. If such cues are temporarily unavailable, the competence period can be significantly protracted and metamorphosis delayed. For example, competent larvae of *Hydroides elegans* will remain swimming in clean water for several weeks if they do not receive an appropriate cue (Bryan et al. 1997, Qian & Pechenik 1998). Exposure to metamorphic cues curtails the competency period, thus resulting in a shorter overall developmental period: larvae of this species can complete development in 5 days.

Settlement and metamorphosis of lecithotrophic spirorbids are similarly affected by the absence of appropriate cues. Under laboratory conditions, larvae of *Spirorbis spirorbis* normally settle after 15 min to 3 h of swimming if suitable substrata are present. Later they become less discriminating in their choice of the substratum. After swimming for about 8 h many larvae fail to settle (Knight-Jones 1951, 1953).

Given that the pelagic stage in spirorbids roughly corresponds to the competence stage, one should expect that the swimming periods would be shortened by availability of suitable settlement cues. Interestingly, the length of the pelagic stage is reported to depend both on the availability of suitable substrata and the degree of permanence of these substrata (Gee 1963a): lack of suitable substrata prolonged the pelagic stage and their presence reduced the pelagic life to differing degrees in four spirorbid species. *S. rupestris*, which inhabits permanent and widely distributed substrata such as bedrock encrusted by *Lithothamnion*, lacks the pelagic stage, whereas *Spirorbis borealis*, which occupies *Fucus serratus*, a comparatively ephemeral and discontinuous substratum, has a pelagic stage. A pelagic stage may also be eliminated in *Spirorbis inornatus* from populations found on the turf alga *Chondrus* (Al-Ogily 1985).

Settlement and metamorphosis

Settlement and metamorphosis are terms that are often used interchangeably and clarification is necessary. For the purpose of the current review, settlement is defined as the ecological transition from a pelagic swimming to an obligate sessile life style. Metamorphosis is a set of morphogenetic events accompanying this transition and making it possible. The metamorphosis in serpulimorph polychaetes begins with the disappearance of the prototroch and is further characterised by differentiation of the branchial crown in the head region the collar and thoracic membrane in the thoracic region, and the pygidium at the tip of the abdomen. Successful attachment and construction of the calcareous tube marks the completion of normal metamorphosis.

In planktonic serpulid larvae, the onset of metamorphosis generally coincides with the shift into demersal life but it is not completed until after settlement. Some initial events of metamorphosis, such as collapse of prototroch, development of branchial buds, pygidial appendages and thoracic membrane rudiments, can be observed even in the absence of settlement (*Galeolaria caespitosa*: Marsden & Andersen 1981).

Other events of metamorphosis, especially tube formation, depend on successful settlement, which itself depends on a number of cues. Lack of such cues may result in failure to complete normal metamorphosis. Bryan et al. (1997) observed several types of abnormal metamorphosis in *Hydroides elegans*: (a) attached, production of branchia but no tube, (b) not attached, production of branchia but no tube, and (c) deformed development involving elongation of larvae and crawling behaviour but no tube or branchia production. Carpizo-Ituarte & Hadfield (1998) reported that some metamorphosed *H. elegans* larvae (i.e. with branchia buds) were unable to secrete primary and secondary tubes but survived up to 2 months in cultures when fed single-celled algae. In the absence of any substrata in clean Petri dishes lacking a microbial film, spirorbid larvae start metamorphosis, settle and build tubes underneath the water surface film but die very soon after (Britayev pers. comm.). In subsequent sections of the review only the events of normal settlement and metamorphosis will be considered.

Settlement behaviour

Settlement behaviour of planktotrophic larvae

Settlement behaviour has been described for planktotrophic larvae of *H. dianthus* (Zeleny 1905), *H. elegans* (Wisely 1958, Ghobashy & Selim 1979a), *Ficopomatus enigmaticus* (Straughan 1968), *Pomatoceros triqueter* (Segrove 1941), *Pomatoleios kraussi* (Crisp 1977) and *Spirobranchus corniculatus* (Smith 1984a).

As metamorphosis starts, the behaviour of planktotrophic serpulid larvae changes from pelagic swimming to a slow exploration of the bottom of the dish. From time to time, metamorphosing larvae of *Pomatoleios* stop their forward crawling and quiver on the spot. Larvae which had been quivering in the same position for many minutes sometime attach to the substratum by mucous threads but this attachment may be temporary (Crisp 1977). The searching demersal larvae of *Spirobranchus* swim over the bottom with the abdomen usually in close contact with the surface. They pause and flex the abdomen from side to side across the substratum. Settlement behaviour is more variable in *Hydroides elegans* (Wisely 1958). Larvae begin to secrete an adhesive substance that trails from the posterior end of their bodies before they reach the fully developed metatrochophore stage. Larvae were seen towing small pieces of bacterial film, detritus, or even smaller larvae through the cultures, often some distance behind them. Apparently, larval feeding is not adversely affected by this

temporary attachment relatively early in development. No evidence of pre-settling searching was observed in this species and the larvae apparently settled at random (Wisely 1958). However, Hadfield et al. (1994) observed that pre-settlement larvae of *H. elegans* spent much time swimming across submerged surfaces, repeatedly contacting these surfaces with their apical tufts.

After the demersal stage, the larvae settle by secreting an abdominal posterior mucous bag. Juveniles originally secrete a mucous tube, covering it later with calcareous matter secreted by the ventral collar surface. During this stage the juvenile *Spirobranchus* partially emerges from its tube and partially rotates within it. The rotation allows the ventral secretory area to produce a complete tube (Smith 1985). The further process of tube-formation in *Pomatoceros triqueter* has been described by Hedley (1958).

Settlement behaviour of lecithotrophic larvae

In spirorbids, settlement behaviour has been described for *Spirorbis spirorbis* by Knight-Jones (1951, 1953), Wisely (1960), Williams (1964), and Nott (1973) and for *S. corallinae* by de Silva & Knight-Jones (1962).

Spirorbid larvae are competent to settle when they are liberated from the brood chamber and the length of the pelagic swimming stage may last up to several hours (Knight-Jones 1951). After the short pelagic stage, *S. spirorbis* larvae enter a searching stage when swimming alternates with slow (about 1 mm s⁻¹) crawling on the ventral side (Knight-Jones 1951). Wisely (1960) rarely observed the alternating swimming-crawling behaviour in *S. spirorbis*; the movements of settling larvae mostly consisted of crawling. Most larvae of *S. spirorbis* arrive at the substratum in a head-on collision but remain attached for <1 s. During this initial attachment, properties of the substratum determine whether larvae will investigate the surface further or resume swimming in search of another substratum. The exploring larvae move on the substratum and, if dislodged by a jet of water, remain attached at some distance by a thread, originating from the terminal segment (Nott 1973). When the larva has selected a settlement site, it remains stationary on the substratum (Nott 1973) or frequently changes the direction of crawling (Knight-Jones 1951, Wisely 1960).

In *Simplaria potswaldi* the contents of the primary shell gland are extruded via the anus in an explosive fashion and the calcareous secretion is moulded by the movements of the larva into a tube capable of housing the entire settled larvae in <5 min (Potswald 1978). In *Spirorbis spirorbis* the initial tube is transparent. The larva rolls from side to side and vigorously moves the extended chaetae so that the secretion is spread to form a transparent covering over the posterior half of the body. Within a minute of the release of secretion from the attachment gland, the animal rolls 180°, together with the mucoid covering, to assume the adult position – i.e. the ventral surface facing upwards and the dorsal one facing the substratum (Nott 1973). *Simplaria potswaldi* does not rotate a full 180° until about 2 h after discharge of the primary shell gland (Potswald 1978).

After initial attachment of the *Spirorbis spirorbis* larvae, the secretion from the ventral collar gland is released onto the uppermost ventral surface and moved posteriorly by the neurotroch action forming a primary mucoid tube. The secretion of the ventral gland does not persist beyond this stage. The collar unfolds revealing the dorsal collar gland, which remains active after metamorphosis and cements the tube to the substratum. Within an hour of settlement calcification starts and 4 h after settlement a calcareous tube encloses the whole animal (Nott 1973).

The initial tube of *Neodexiospira alveolata* is transparent and soft and it covers only the thoracic region of settled larva. A pair of shell glands is now used to form a tube. A day later the tube hardens and elongates covering the juvenile completely (Okuda 1946)

Morphological changes at metamorphosis

Metamorphosis in planktotrophic larvae

The morphological stages of metamorphosis in planktotrophic larvae have been described for *Hydroides elegans* (Wisely 1958, Sentz-Braconnot 1964), *Spirobranchus corniculatus* (Smith 1985), *Pomatoceros triqueter* (Segrove 1941) (Fig. 10A–F) and *Galeolaria caespitosa* (Grant 1981, Marsden & Anderson 1981).

The onset of metamorphosis is preceded by increased contraction of the circular muscles, especially the anterior band, which contracts just below the eyes to constrict a definite head region. The contraction of the prototroch circular muscle decreases the larval diameter whilst increasing its length. The ventral collar rudiment evaginates, forming a ventral fold and at first two separate dorsoventral folds develop behind the metatroch. Usually ventral and lateral collar folds fuse to form the adult collar. The formation of collar folds is described by Meyer (1888), Segrove (1941), Wisely (1958), Grant (1981) and Marsden & Anderson (1981).

The chaetal sacs enlarge and the most anterior pair begins to turn upwards. Uncini appear on the second chaetiger and later on the third. During settlement the head is reduced and the mouth and anus move to occupy their terminal positions. The prototroch, metatroch, and feeding band disappear. The collar folds evaginate completely to form the adult configuration and the anterior pair of chaetae becomes collar chaetae. Stiff ciliary tufts are formed on the branchial rudiments and all subsequently develop pinnules (Smith 1985).

The intraepithelial system of nerves supplying the larval pharynx in trochophores of *Spirobranchus spinosus* is retained through metamorphosis and, with minimal alteration, provides the source of nerves in the juvenile foregut (Lacalli & West 1988). Post-settlement development of the branchial crown and the operculum, as well as the formation of additional thoracic segments have been described in *Ficopomatus enigmaticus* (Vuillemin 1962a,b), *Pomatoceros triqueter* (Segrove 1941), *Hydroides elegans* (Wisely 1958, Sentz-Braconnot 1964) and *Pomatoleios kraussi* (Crisp 1977).

Metamorphosis in lecithotrophic larvae

Post-metamorphic development of the non-feeding larvae of *Protula tubularia* described by Meyer (1888) and *Salmacina dysteri* described by (Nishi & Yamasu 1992d) (Fig. 10) do not differ significantly from that of planktotrophic larvae.

Morphological events associated with settlement and metamorphosis in spirorbids (Fig. 11) have been described by Agassiz (1866), Fewkes (1885), Abe (1943), Okuda (1946), Höglund (1951), Casanova (1954), Nott (1973) and Nott & Parker (1975). A detailed comparative study of metamorphosis, including internal changes, in spirorbids *Simplaria potswaldi*, *Paradexiospira* (S.) *vitrea* and *Circeis* cf. *armoricana* was provided by Potswald (1978).

The opercular and branchial rudiments start to develop at a rapid rate only after formation of the initial tube. The cells producing trochal cilia, the trochoblasts, become detached and



Figure 10 Serpulid metamorphosis. *Pomatoceros triqueter*, A: ventral view of a larva with branchial rudiments; B: dorsal view of a metamorphosed juvenile; C and D: ventral view of a juvenile removed from the tube; E: juvenile in the tube, pinnules form on 4th right filament; F: dorsal view of young worm, pinnules form on second right filament (after Segrove 1941). *Salmacina dysteri*, G: recently settled worm with branchial rudiments; H: juvenile with thin tube; I: juveniles with branchial crowns; J: juvenile with collar setae and 10 chaetigerous segments (after Nishi & Yamasu 1992d). Scale, A–C: 0.1 mm; D: 0.25 mm; E and F: 2 mm; G, H and J: 0.1 mm; I: 0.15 mm.

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Figure 11 Spirorbid metamorphosis. *Spirorbis spirorbis*, A: recently settled larva secreting the tube; B: early juvenile (after Fewkes 1885). *Neodexiospira alveolata*, C: Metamorphosing juvenile in soft transparent tube, the abdomen is naked; D: one day after settlement, the tube covers entire body of the juvenile; E: juvenile completed the metamorphosis (removed from the tube); F: the same, inside the tube. *Circeis* aff. *armoricana*; G: recently metamorphosed juvenile in the tube, adhesive processes are extended (after Okuda 1946). Scale, B: 200 µm; A, C–F: no scale was given in the original publication; G: 320 µm.

are completely sloughed off. *Simplaria potswaldi* larvae do not ingest prototrochal cells (Potswald 1978), as it is thought to be the case in *Spirorbis spirorbis* (Nott 1973). Apical tuft cilia are lost at the time of settlement but the apical cells are retained and apparently incorporated into the brain.

Two hours after formation of the initial tube, the branchial and opercular rudiments in *Simplaria potswaldi* grow to about twice the length they were in fully formed larva and the opercular rudiment is much larger than any of the simple branchial rudiments. The pigmented eyecups migrate to the midline and remain there for a day or two before they disappear. In the midline, ventral to the rapidly developing branchial crown, shrinking of the head results in the appearance of a "proboscis" or snout-like structure. The post-settlement larval abdomen becomes shorter and broader and therefore is not clearly delimited from the thorax as in the free-swimming larvae.

The initial tube is chalky white and opaque in *S. potswaldi* but it is transparent in *Circeis* cf. *armoricana* and *Paradexiospira* (*Spirorbides*) *vitrea* (Potswald 1978). In species of Januinae these tubes are transparent, soft and cover only the thorax (Abe 1943, Okuda 1946). The part of the tube adjacent to the substratum is secreted by the ventral thoracic glands prior to the turning over of the larva to assume the adult position (with the dorsum towards the substratum). Soon after the collar has folded back to enclose the lip of the primary tube, deposition of the secondary tube begins. Calcium secretions originating from the major subcollar glands, as demonstrated by Swan (1950), Hedley (1956a,b), and Nott & Parker (1975), are added to the anterior lip of the tube and moulded into place by the encompassing collar fold. Twenty-four hours after settlement, the anterior end of the tube starts to turn in a direction typical for each species (Potswald 1978).

During further development, the yolk of the midgut breaks down and is absorbed, the anus takes the terminal position, the abdominal shell gland becomes the hindgut, the partition between the midgut and hindgut opens, the "proboscis" is cast off and the branchial rudiments develop into the branchial crown. The ventral prostomial glands, the apical tuft, and various trochs are lost during metamorphosis. By the eleventh day of post-larval development the major features of the adult, with the exception of abdominal or secondary segments, are either present or starting to form in *Simplaria potswaldi*. The gross asymmetry, characteristic of spirorbids, develops as a result of differential growth in the achaetous zone, which corresponds to the larval abdomen. This change from an essentially symmetrical larva to an asymmetrical pre-adult is considered to constitute spirorbid metamorphosis (Potswald 1978).

Interesting changes of the posterior body region during the settlement were observed for *Circeis* cf. *armoricana* by Okuda (1946). According to his observations, the posterior lateral portions of the body are protruded backwards to form a pair of massive foot-like appendages. Each of them terminates posteriorly in a digit-shaped adhesive process, which is attached to the inner wall of the tube and supports the body. When the body is withdrawn into the tube, these foot-like appendages are contracted to the level of the anal region. Such processes are absent in adults and it is unclear for how long they function in juveniles. Okuda (1946) also reports that juveniles of *Neodexiospira alveolata* certainly lack these processes.

Factors affecting settlement and metamorphosis

There is a vast amount of literature on settlement cues for larvae of sessile fouling invertebrates, including serpulids and spirorbids. Settlement and recruitment are complex processes, determined by the interaction of biotic and abiotic factors. These factors can serve as positive or negative cues, which are physical or chemical in nature and they operate at different temporal and spatial scales and various levels of organisation (i.e. ecological– physiological–molecular, see Rodriguez et al. 1993 and Slattery 1997 for reviews). One of the ways to deal with such a complexity of factors is to separate all factors into generic precondition factors and specific settlement cues. The former factors affect a wide range of larvae and act at various stages of development. An optimal combination of such factors ensures that larvae are in condition to respond to specific cues. The settlement cues are species-specific, they act during the settlement periods and affect only the larvae preconditioned to respond to them.

Generic precondition settlement factors

Seasonal settlement Settlement in serpulids and spirorbids living in temperate climates is seasonal and generally the length of the settlement period coincides with the length of reproductive period. In tropical species that reproduce throughout the entire year, settlement also takes place throughout the entire year. However, the intensity of settlement may vary significantly within the reproductive period and may show one or more peaks. The intensity of settlement in the field is usually inferred from the intensity of recruitment on various submerged panels.

Larvae of *Pomatoleios kraussi* settle in Kuwait from March to December with the maximum of abundance in August (Mohammad 1975). In many places (Australia and New Zealand, California, Japan, China) peaks of Hydroides elegans settlement occur in summer and autumn but in Hong Kong settlement of this species peaks in early spring to early summer (Qiu & Qian 1997). Ficopomatus enigmaticus shows two distinct settling peaks, March/April and November/December in Argentina (Schwindt & Iribarne 1998), June/ July and September in the North Adriatic (Bianchi & Morri 1996), May and October in Japan (Okamoto & Watanabe 1997). Sentz-Braconnot (1968) mentions a variable settling pattern in Mediterranean Pomatoceros triqueter over a period of 10 yr, mostly between July and October, often in two peaks. However, she may have been working with two species, P. triqueter and P. lamarckii, and thus the observations are not conclusive. The same holds for Alvariño's (1951) observations on "P. triqueter" from Atlantic Spain, settling in three peaks between May and December. While P. triqueter in northern Helgoland shows a single period of maximal settlement in August/September (Klöckner 1976), Castric-Fey (1983), who distinguished between the two species, mentions settlement all year round but with maxima in April, June, August and October (South Brittany, France). The settling season for seven serpulid taxa in the harbour of Civitavecchia (Mediterranean) is generally 4 months per species (Chimenz Gusso & Rivosecchi Taramelli 1973). Filograna implexa settles throughout the entire year except for May in the northern Adriatic (Igic 1969).

General abiotic factors: temperature, salinity, dissolved oxygen, sedimentation During the settlement season, abiotic factors such as ambient temperature, salinity, dissolved oxygen and light intensity that generally have measurable affects on larval development, behaviour, and survival also affect the intensity of settlement. Settlement of Hydroides elegans occurred when the water temperature was above 20°C and more intensive settlement occurred at stations having a greater concentration of dissolved oxygen (Reish 1961). Dew & Wood (1954) present non-conclusive evidence of the settlement periodicity of H. elegans, which may be related to tides, while Daniel (1958) showed that larvae of this species could not settle in water currents exceeding 0.9–1.2 knots. Settlement of Ficopomatus uschakovi (Hill 1967) took place in a range of salinities from 1 to 33 but the most abundant settlement occured in salinity above 30. *Hydroides dianthus* settled only when the high tide salinity was above 30 and the low tide salinity was 20 or over (Hill 1967). Soldatova & Turpaeva (1960) assumed settlement of *Pomatoceros triqueter* to be a compromise between photopositive attraction to surface waters and a negative reaction to brackish water, resulting in settling intertidally in normal sea water, at depths of 15-20 m under brackish conditions. Increased sedimentation reduced recruitment of Pseudochitinopoma occidentalis (Duggins et al. 1990) and other serpulimorph polychaetes (Vine & Bailey-Brock 1984).

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Photoresponse The larval photoresponse at the time of settlement can affect settlement preferences. A general approach to this phenomenon was given by Thorson (1950). Reduced light intensity negatively affected recruitment of *Pseudochitinopoma occidentalis* (Duggins et al. 1990). Larvae of *Spirorbis tridentatus* tend to be photonegative when settling, which apparently reflects the natural occurrence of this species in dimly lit places (de Silva 1962).

Substratum Physical properties associated with the abiotic substratum, such as its colour and its roughness may be important for settlement preferences (e.g. Wisely 1959, Sentz-Braconnot 1968, Straughan 1969). Spirorbids recruit in greater numbers to bare, dark grey shale boulders than to bare, light yellow sandstone boulders on the same shore (James & Underwood 1994). *Spirorbis rupestris* prefer to settle on rough surfaces rather than on smooth ones (Gee & Knight-Jones 1962, Gee 1965), whereas larvae of *S. spirorbis* clearly avoid roughened surfaces (Crisp & Ryland 1960). Although settling larvae of *Pomatoleios kraussi* adhere much better on artificial substrata with higher surface tension than on those with low tension, colonisation patterns under natural conditions were not influenced by surface tension (Becker 1993).

Specific settlement factors

Larvae of many invertebrates often settle in response to highly specific stimuli. Although some serpulimorphs are notorious opportunistic foulers and are apparently able to colonise any available substratum, many spirorbids and serpulids have very specific habitat requirements. Such substratum-specific settlement usually results from active substratum selection by settling larvae. In the majority of cases the substratum is biogenic and the settlement cues are believed to be chemical in nature. Pawlik (1992) distinguishes three main categories of substratum-specific settlement: associative settlement, settlement on microbial films and gregarious settlement.

Associative settlement According to (Crisp 1974), associative settlement is the specific or enhanced settlement of one species on another. The degree of substratum specificity varies significantly within serpulimorph polychaetes. Members of the *Spirobranchus giganteus* complex are obligate associates of corals and their successful settlement with tube construction occurs only on live corals (Marsden 1987, Hunte et al. 1990, Marsden et al. 1990). Adults of *S. corniculatus* occur commonly on *Acropora prolifera* and much less frequently on *Porites ramosa* (Marsden 1987). The pre-settlement larvae respond positively to waterborne exudates of corals commonly colonised by the worm and are indifferent to exudates of rarely colonised corals (Marsden & Meeuwig 1990).

Spirorbids are commonly found in specific epiphytic associations with various macrophytes and their larvae show remarkable discrimination among algal substrata. Settlement of such organisms can be stimulated by algal extracts. *Spirorbis rupestris* larvae seem reluctant to settle on clean smooth surfaces but settle abundantly if slates are soaked in aqueous extracts of *Lithothamnion polymorphum* (Gee 1965). Larvae of *Spirorbis spirorbis* settle in significantly greater numbers on surfaces treated with extracts of *Fucus serratus*, the typical host alga, than on untreated surfaces (Williams 1964). Photopositive behaviour is curtailed and the duration of the crawling behaviour preceding settlement is shortened as a result of contact with this alga (Williams 1964).

Spirorbids not only select particular algal species for settlement but also tend to differentiate between younger and older parts of the alga. Larvae of *Spirorbis* cf. *inornatus* and Janua pagenstecheri prefer to settle on younger parts of fronds of Laminaria digitata. The youngest part is probably a more stable substratum because the growth of Laminaria occurs near the base of the frond and the old tissue is shed distally (Stebbing 1972). Similarly, *Neodexiospira brasiliensis* and *Circeis* cf. armoricana that co-occur on Zostera marina, Z. asiatica and Phyllospadix iwatensis were observed to be more abundant on younger leaves of all three seagrass species. They were distributed evenly along entire young leaves of all three species but were restricted to the basal portion of old leaves (Hamamoto et al. 1996). Larvae of *Circeis* cf. armoricana tended to settle near the base of growing seagrass blades of *Thalassia testudinum* (Dirnberger 1990, 1993, 1994), apparently searching efficiently for space produced rapidly by the blade growth (Dirnberger 1990).

In contrast, Nelson (1979) reports that *Neodexiospira brasiliensis* tends to be more abundant on older portions of *Zostera* blades, probably because it requires a diatom mat for settling. These data totally contradict the data of Hamamoto et al. (1996, see above) that *Neodexiospira brasilensis* prefer settling on younger parts of *Zostera*. This discrepancy is strange if both authors did study the same spirorbid species.

Algae serve as negative or positive settlement cues for serpulid larvae. Settlement of *Hydroides elegans* larvae was affected by waters conditioned by 12 species of macroalgae. Compounds released by 4 of 12 macroalgae tested immediately killed larvae of *H. elegans* or inhibited their settlement; the remaining eight algal species prevented settlement, had no effect or even stimulated settlement (Walters et al. 1996). Larval settlement of *H. elegans* was also inhibited by brown algal phlorotannins (Lau & Qian 1997).

Many serpulids and spirorbids form epizoic associations with other invertebrates, mostly molluscs, crustaceans, and some bryozoans and hydrozoans (e.g. Stebbing 1972, Stachowitsch 1980, ten Hove 1994a). For spirorbids such relations can be quite specific. For example, *Circeis spirillum* is usually found only on hydrozoans and bryozoans (Knight-Jones & Knight-Jones 1977, Knight-Jones et al. 1979), *Protoleodora uschakovi* settles only on the shells of molluscs and large crustaceans (Rzhavsky unpubl.). *Circeis paguri* is associated with the hermit crab *Eupagurus bernhardus* (Al-Ogily & Knight-Jones 1981) and *Bushiella* (*B.*) *evoluta* is found only on the inner surface of gastropod shells inhabited by hermit crabs. However, it is not known whether active larval habitat selection takes place nor whether extracts from the host species also stimulate settlement in these organisms.

Epizoic relations of serpulids with their hosts are apparently less specific than those of spirorbids. The only example of settlement stimulation of serpulid larvae by an invertebrate host is that demonstrated for *Hydroides elegans*. This species, which inhabits a wide variety of substrata, is also found living on the arboresent bryozoan *Bugula neritina* in Hong Kong and the samples derived from this bryozoan induce metamorphosis in the laboratory (Bryan et al. 1998).

When several hosts are used by a species, preference for specific hosts may vary for different populations within one species and appears to be genetically determined. Larvae of *Spirorbis inornatus* favoured the algal species to which their parents were attached (Knight-Jones et al. 1975). Similarly, larvae of *S. spirorbis* from a tidepool population prefered *Ascophyllum*, while those from an embayment settled much more readily on *Fucus* (Mackay & Doyle 1978). Animals collected from an environmental cline ranging from tidepool-like to embayment-like conditions exhibit a corresponding range in behaviour.

Bio-organic film The presence of a bio-organic film has been long recognised as a prerequisite for larval settlement in many fouling marine invertebrates (e.g. Scheltema 1974).

Micro-organisms have been reported to promote settlement of *Spirorbis spirorbis* (Meadows & Williams 1963), *Hydroides elegans* (Hadfield et al. 1994, Harder & Qian1999), *Serpula* sp. (Keough & Raimondi 1995) and *Neodexiospira brasiliensis* (Kirchman et al. 1982a).

Bacterial films of different age and composition have different effects on larval settlement. Clean surfaces exposed to sea water go through a succession of changes advancing to the development of a complex microbial community (Mitchell & Kirchman 1984) and it is not surprising, therefore, that recruitment of serpulids and spirorbids is affected by the film age and immersion time (Keough & Raimondi 1995). Larvae of *Hydroides elegans* distinguish among the films ranging in age from 1 to 3 days. Larval settlement curves closely parallel population growth curves for bacteria, suggesting that settlement is quantitatively dictated by bacterial density (Hadfield et al. 1994).

Different film-forming species and strains vary in their ability to promote settlement in serpulid and spirorbid larvae. *Spirorbis spirorbis* larvae settle more readily on films developed in the presence of diatoms and their associates than on those developed in the presence of a green flagellate (Meadows & Williams 1963). Larvae of *Neodexiospira brasiliensis* prefer to settle on pure culture films of bacteria isolated from *Ulva lobata* (Kirchman et al. 1982a). Larvae of *Hydroides elegans* settle differentially on different species of bacteria (Lau & Qian 1997). Of a series of bacterial strains isolated from marine biofilms, 13 induced larval settlement, 11 gave moderate or mixed results and 10 others did not stimulate the settlement of *H. elegans* (Unabia & Hadfield 1999).

Changes in the ratio of species in multispecies bacterial films also affected larval settlement. The amount of settlement induced by monospecific strains is usually less than that induced with natural, multispecies films (Unabia & Hadfield 1999). Most of the isolated bacteria that induce settlement in *H. elegans* were motile Gram-negative rods but Grampositive strains were also present. Biofilms killed by treatment with heat, ultraviolet radiation or chemical fixatives were no longer inductive. Soluble, dialysable, heat-stable bacterial products induced settlement and metamorphosis more slowly (Unabia & Hadfield 1999).

Gregarious settlement Many serpulid and spirorbid larvae settle in response to the members of their own species to form conspecific aggregations (*Spirorbis spirorbis, Janua pagenstecheri*: Knight-Jones 1951; *Spirorbis tridentatus* and *S. corallinae*: de Silva 962; *Galeolaria caespitosa*: Andrews & Anderson 1962; *Spirorbis corallinae* and *Janua pagenstecheri*: Stebbing 1972, Ryland 1972; *Neodexiospira pseudocorrugata*: Ghobashy & Selim 1979b; *N. brasiliensis*: Nelson 1979; *Hydroides dianthus*: Scheltema et al. 1981, Toonen & Pawlik 1996; *Pomatoceros triqueter*: Klöckner 1976; *Pomatoleios kraussi*: Crisp 1977).

Such gregarious settlement is thought to rely on chemical cues associated with adults and could not be demonstrated between members of a single cohort of settling larvae of *Hydroides dianthus* (Mullineaux & Garland 1993). Gregarious response is well pronounced at the presettlement period but Marsden (1991) observed preference for adult tubes by planktonic metatrochophores of *Spirobranchus polycerus*.

Still-water laboratory assays demonstrated that the settlement cue was soluble in water and was associated with the body of live adults in *Hydroides dianthus* and *H. elegans* (Toonen & Pawlik 1996, Bryan et al. 1997). Live worms removed from their tubes and amputated tentacular crowns of live worms resulted in a greater settlement response than dead worms, empty tubes or slides with biofilms. A single adult was equally capable of eliciting a gregarious response as were five or 25 conspecifics and newly settled juveniles began to elicit gregarious settlement after approximately 96 h (Toonen & Pawlik 1994, 1996). However, Carpizo-Ituarte & Hadfield (1998) contradict Bryan et al. (1997), hypothesising that the latent response of H. *elegans* to extracts of adult worms is a result of the build-up of bacteria in their test vessels.

Toonen & Pawlik (1994) found that females of *H. dianthus* produced larvae that settled in two different ways: one type colonised uninhabited substrata (founders), whereas the other settled only in response to cues associated with conspecifics (aggregators). There was a distinct subordination of larvae that responded to a biofilmed substratum; once these individuals were removed, the remaining aggregators delayed settlement in the absence of acceptable conspecific-associated clues.

Some authors argue that aggregations may also arise as a result of passive deposition of larvae. Walters et al. (1997) demonstrated that larvae of *H. elegans* did not settle faster or in greater numbers on surfaces already occupied by adults or their tubes. However, in the field in moving water there was significantly more settlement in tube crevices than expected by chance, which probably results from hydrodynamics. The authors concluded that dense aggregations of *H. elegans* found on hard surfaces in bays and estuaries probably result from passive deposition of larvae in crevices beside tubes of conspecific individuals, followed by selective attachment in these locations if the bio-organic film is acceptable (Walters et al. 1997).

Chemical nature of inducers

Conspecific inducers

A new monoacyl glycerol isolated from the methyl alcohol extract of adults acts as a metamorphosis-inducing substance in *H. ezoensis* larvae. However, since acyl glycerols are common primary metabolites, they have been hypothesised to act as the second messengers, not as a primary cue of metamorphosis (Watanabe et al. 1998). Isolation of larval metamorphic inducers from adults of *H. elegans* showed that biologically active fractions were composed of free amino acids. The entire free amino acid composition was found to comprise aspartic acid, glutamic acid, serine, histidine, glycine, arginine, alanine, asparagine, glutamine and taurine. The larval metamorphic response to an artificially prepared sample in identical concentrations of these amino acids was very similar to the response to the natural isolates (Harder & Qian 1999).

Beckmann et al. (1999) tested whether the metamorphic response was caused by direct dissolved free amino acids (DFAA) perception or by induction of DFAA-utilising bacteria. The results of the experiment suggested that the larval response had been exclusively triggered by an inductive bacterial film rather than by direct larval perception of DFAA. If putative signalling compounds serve as a nutrition source for settlement-inducing bacteria, an explicit investigation of the efficacy of chemical metamorphic cues is unreliable (Beckmann et al. 1999).

Artificial induction or inhibition of settlement

Inductors The metamorphic response in *H. elegans* larvae can be induced by ions Cs^+ or K^+ but such a response is much slower than the response to biofilms (Carpizo-Ituarte & Hadfield 1998). Lectines have been shown to mediate the settlement and metamorphosis of *Neodexiospira brasiliensis* larvae (Kirchman et al. 1982b). Settlement by larvae of this species was blocked if the biofilms were first exposed to certain lectines, indicating that larvae settled in response to particular surface polysaccharides or glucoproteins in the bacterial films.

The cyclic nucleotide phosphodiesterase inhibitor isobutyl methylxanthine (IBMX) and non-specific phosphodiesterase inhibitors theophylline and papaverine induced a high percentage of normal metamorphosis in *Hydroides elegans* (Bryan et al. 1997, Holm et al. 1998, Pechenik & Qian 1998, Qian & Pechenik 1998). Gamma-aminobutyric acid (GABA), choline chloride, dihydroxyphenyl L-alanine (L-DOPA), and potassium chloride evoked a low percentage of settlement but abnormal metamorphosis in this species (Bryan et al. 1997). L-DOPA and D-DOPA were shown to induce larval metamorphosis in *Hydroides ezoensis*, *Pomatoleios kraussi*, and *Ficopomatus enigmaticus*. Other neuroactive molecules, epinephrine and norepinephrine, also induced larval metamorphosis in *Hydroides ezoensis* and *Pomatoleios kraussi* (Okamoto et al. 1995, 1998).

Inhibitors Polyaromatic hydrocarbons (PAHs), the main toxic components of crude oil polluting the marine environment, have an adverse effect on the settlement of *Hydroides elegans* larvae (Paul et al. 1998). Six cuporous oxide antifouling paints resulted in both post-attachment mortality and pre-attachment mortality of larva of *Neodexiospira lamellosa* and *Eulaeospira convexis* (Wisely 1964). Glucose blocks the settlement and metamorphosis of *Neodexiospira brasiliensis* larvae (Kirchman et al. 1982b).

Larval settlement may be inhibited directly, or through compounds that regulate the growth of bacteria, which in turn affects larval settlement. Settlement of *Hydroides elegans* is inhibited by brown algal phlorotannins and two related compounds, tannic acid and phloroglucinol. Phlorotannins, tannic acid and phloroglucinol were inhibitory to *H. elegans* larval settlement and to the growth of certain marine bacteria that induced high levels of *H. elegans* larval settlement. However, some of the bacteria that induced low levels of larval settlement were resistant to these compounds (Lau & Qian 1997). Adenylate cyclase activator forskolin inhibited responses of larvae of *H. elegans* to inductive bacterial bio-films (Holm et al. 1998).

Signalling pathways involved in metamorphosis

Studies of the response of *H. elegans* larvae to neuropharmacological agents demonstrated that neither the G-protein activator Gpp [NH]p nor the inhibitor GDP-P-S affected metamorphosis. Therefore, neither G protein-coupled receptors nor their associated signal-transduction pathways regulate induction of metamorphosis by bacterial cues (Holm et al. 1998).

In conclusion, Wilson's remark that "All the explanations so far advanced, effect of light, texture of surface, grade of bottom soil, metamorphosis-inducing substances, etc..., are at best partial answers to that problem" still summarises the complexity of settlement (Wilson 1952 in Thorson 1957).

Juvenile growth and maturation

Growth

The rate of post-settlement growth of juvenile serpulids has been well studied for fouling species (e.g. *Ficopomatus enigmaticus*: Rullier 1946, Soldatova & Turpaeva 1960, Vuillemin 1965; *F. uschakovi*: Hill 1967, Straughan 1972 a,b; *Hvdroides dianthus*: Grave 1933;

H. elegans: Grave 1933, Paul 1937, 1942, Dew 1958, Behrens 1968, Sentz-Braconnot 1968; *H. ezoensis*: Miura & Kajihara 1981; *Pomatoceros triqueter*: Føyn & Gjøen 1954, Sentz-Braconnot 1968; *Pseudochitinopoma occidentalis*: Smith & Haderlie 1969) and the growth rate of spirorbids is known for *Spirorbis spirorbis*, *S. corallinae*, *S. tridentatus* and *Janua pagenstecheri* (de Silva 1967), *Spirorbis rupestris* (Gee 1967), *Neodexiospira* sp. (Bagaveeva 1975) and *N. brasiliensis* (Rzhavsky & Britayev 1984).

Ontogenetic changes of growth rates

Tubes of juvenile worms grow rapidly but the growth slows down in later life (ten Hove & van der Hurk 1993). Settled *Spirobranchus* juveniles put down at least a body length of tube (0.5–1 mm) per day when first settled (Smith 1985). Paul (1937) reports a growth rate of 14 mm in 9 days for *Hydroides elegans*. In *H. dianthus* the first three months increases in length by 54 mm but in the next 9 months only 12 mm are added (Grave 1933). *Pomatoleios kraussi* grows 130 μ m day⁻¹ for the first 2 months, slowing to 50 μ m day⁻¹ in the third month (Crisp 1977).

Seasonal changes in growth rates

Under natural conditions the growth of *Spirorbis spirorbis* is much slower in winter $(0.17 \text{ mm month}^{-1})$ than in summer $(0.66 \text{ mm month}^{-1})$ (de Silva 1967). The same holds true for *Pomatoceros triqueter* (20–30 mm month^{-1} in spring, 2–10 mm month^{-1} in winter) and *Hydroides elegans* (12 mm month^{-1} in spring, 4 mm month^{-1} in winter) (Sentz-Braconnot 1968). Monthly increments in coil diameter of tubes of *Spirorbis rupestris* were about 0.5 mm to 0.7 mm between September and January, but only about 0.2 mm between January and March (Gee 1967). The median summer growth rate in coil diameter of *Neodexiospira brasiliensis* for 2 months after settlement was about 0.82–0.88 mm month^{-1} (Rzhavsky & Britayev 1984). Calculated summer growth of juveniles under natural conditions is in the same range in *Neodexiospira* sp. (Bagaveeva 1975) and is about 0.66 mm month^{-1} in *Spirorbis spirorbis* (de Silva 1967). The growth of the latter species is slightly faster than calculated growth of *S. spirorbis*, *S. corallinae* and *Janua pagenstecheri* in the laboratory (0.55–0.58 mm month⁻¹, de Silva 1967) and is markedly faster than that of *Spirorbis tridentatus* (0.36 mm month⁻¹) reported by de Silva (1967).

Estimates of juvenile growth for *Pomatoceros triqueter* and *Hydroides elegans* range from 7 (Norway)–12 mm (Mediterranean) in the first month to 0.2–12 mm in winter, depending on the natural conditions (Sentz-Braconnot 1968). Klöckner (1976) found the growth rate ranging from 0.6 mm month⁻¹ in winter to 11.4 mm month⁻¹ in summer for tubes of *Pomatoceros triqueter* at Helgoland (North Sea). Klöckner (1976) found the tube regeneration by tubeless worms to be a function of body weight (the larger the worm, the slower growth) and temperature (the growth increasing between 6°C and 22°C and decreasing above 25°C).

Factors affecting juvenile growth

In addition to the above-mentioned ontogenetic and/or seasonal changes, the growth rate in serpulimorphs varies according to temperature and/or population density (e.g. *Ficopomatus uschakovi*: Straughan 1972b; *Hydroides dianthus*: Leone 1970; *Pomatoleios kraussi*: Crisp 1977), flow speed (*Pseudochitinopoma occidentalis*: Eckman & Duggins 1993), salinity (*Ficopomatus enigmaticus*: Soldatova & Turpaeva 1960, Turpaeva 1961; *Hydroides dianthus*: Leone 1970; *H. elegans*: Qiu & Qian 1998), the pollution (*H. elegans*: Moran & Grant

1984) and availability of food (*Pomatoceros triqueter*: Føyn & Gjøen 1954; *Hydroides. dianthus*: Leone 1970). Castric-Fey (1983) also mentions high density as a factor affecting growth; in closely spaced *Pomatoceros* the touch of neighbouring branchial crowns apparently decreases growth. Bianchi & Morri (1996) noted an inverse relation between settlement and growth in *Ficopomatus enigmaticus*, arguing that the alternating phases of heavy gregarious settlement and rapid vertical growth are an expression of the species' ability to shift from an r to a K strategy during the annual cycle.

Juvenile growth after the metamorphosis may be determined not only by the factors acting during the post-settlement period but also to a larger degree by factors experienced during the larval stage. In particular, juvenile growth rates have been shown to be affected in *Hydroides elegans* (Qian & Pechenik 1998) as a result of food limitation during development or delayed metamorphosis. Treatment of larvae with excess K⁺ also has adverse effects on juvenile growth (Qian & Pechenik 1998).

Maturation (size and age at first reproduction)

Serpulids and spirorbids reach sexual maturity after they achieve a certain body size. That is, maturation correlates with growth rate and depends on the factors controlling it. Animals living under conditions suboptimal for growth reach maturity slowly and some never reach it. For instance, *Ficopomatus uschakovi* juveniles growing in optimum salinity become mature in 4 wk, those that grew slowly at salinities either below 5 or above 30 never matured (Hill 1967). At salinity ≥ 25 and temperature $\geq 20^{\circ}$ C, the first spawning of *Hydroides elegans* occurred on day 16 after settlement. Both low temperature and low salinity led to slower growth and subsequently to a longer time to maturation (Qiu & Qian 1998). Spawning of *H. elegans* reared in the laboratory was observed on average 40 days after fertilisation at 23°C (Matsuo & Ko 1981). However, according to Paul (1937, 1942) *H. elegans* reaches maturity within 9 days after settlement in Madras, India at 25.5–29.5°C. Vuillemin (1965) mentions maturation in 6 wk for *Ficopomatus enigmaticus*, within 4 wk for *Hydroides elegans* (Lake of Tunis). *H. dianthus* matured within 7–8 wk at Woods Hole (Grave 1933), and within 6 wk after settlement in *Lagos*, Nigeria (Hill 1967). The first macroscopic signs of sexuality appear 1.5–3 months after settlement in *Pomatoceros triqueter* and *P. lamarckii* (Castric-Fey 1984).

Size at maturation of *Ficopomatus uschakovi* at Lagos, Nigeria started from 6 mm but not all worms of this size were mature (Hill 1967). In Japan, mature eggs or sperm in *F. enig-maticus* were first observed in individuals 6–8 mm long, 3–4 wk after settlement (Okamoto & Watanabe 1997), whereas in France *F. enigmaticus* becomes mature at 9–10 mm (Fischer-Piette 1937). The smallest mature worm of *Hydroides dianthus* was 13 mm long (Hill 1967). Tubes of reproductive individuals of *H. elegans* were usually longer than 1.2 cm (Qui & Qian 1998).

Neodexiospira brasiliensis (Rzhavsky & Britayev 1984) may start brooding when 5 wk old. Large broods were found in the tubes of 2-3 month old *Circeis armoricana* with coil diameters of at least 1.9 mm (Ivin 1997). In *Simplaria potswaldi* gametes start to differentiate when 10–12 abdominal segments are formed (Potswald 1981). Breeding begins at a coil diameter of 1.5 mm in *Spirorbis spirorbis*, 2.0 mm in *S. rupestris*, 1 mm in *S. rothlisbergi*, 1.2 mm in *Neodexiospira brasiliensis* (Gee 1967, Rothlisberg 1974, Daly 1978a, Rzhavsky & Britayev 1984). These coil diameters constitute about a half of the maximum coil diameter known for each species.

Longevity

The longevity of all organisms, including serpulimorph polychaetes, correlates with body size. The life span of small Serpulidae and Spirorbidae rarely exceeds 1 yr. For example, *N. brasiliensis* live only several months (Rzhavsky & Britayev 1984). Maximum length of tubes (1.4 mm) of *N. pseudocorrugata* was attained 25 days after settlement (Ghobashy & Selim 1979b). The maximum life span of fouling polychaetes that mainly aggregate on crustacean carapaces apparently does not exceed the intermoult period (6–7 months) of their crustacean hosts (Gili et al. 1993). Large specimens of *Janua pagenstecheri* are often found on the common lobster (*Astacus gammarus*) that moults its carapace once a year, which suggests that *Janua pagenstecheri* attain their full size in one year. Similarly, *Circeis* cf. *armoricana* of maximum size are found on the thallus of *Laminaria* that is renewed every year (Bergan 1953). *Spirorbis spirorbis* and *S. corallinae* do not reach sexual maturity until the spring of the following year (Thorson 1946, de Silva 1967, Daly 1978a), which implies a life span of at least a year. *Filograna implexa*, a small form (up to 5 mm), can possibly live two seasons (Plymouth, UK, Faulkner 1929), although asexual reproduction probably makes estimates of longevity in this species difficult.

The life span of the aquarium-reared specimens of *Hydroides elegans* and *Pseudo-chitinopoma occidentalis* was 1 yr (Grave 1933, Smith & Haderlie 1969). The free-living *Ditrupa arietina* shows a strictly linear growth-curve during its first year but growth is asymptotic in the second and final year (Medernach & Grémare1999). *Pomatoceros triqueter* has a life span of 4 yr according to Dons (1927), but estimates of the longevity for this species in northern Europe vary from 1.5 (Føyn & Gjøen 1954) to 2.5 yr (Castric-Fey 1983). Larger species, such as *Spirobranchus polycerus* and *Ficopomatus enigmaticus*, can live for 10–12 yr (Fox 1963, Marsden 1994b). The even larger forms of the *Spirobranchus giganteus* complex can live for 18–35 yr (Smith 1985, Nishi & Nishihira 1996, 1999, Nishi 1997).

Mortality

Age-specific mortality

Mortality rates may vary for different stages of the life cycle but quantitative estimates of embryonic, larval, juvenile and adult mortality are too rare for serpulimorph polychaetes to make reliable comparisons. Generally, at least two peaks of increased vulnerability and probably associated mortality have been reported for serpulids with planktonic larvae; in the early embryonic and early juvenile stages. Gray (1976) showed that 4-day-old larvae of *Serpula columbiana* were more resistant to reduced salinity at low temperatures than were gastrula and 1-day-old larvae. Qiu & Qian (1997) studied tolerances to various experimental salinities among various developmental stages of *Hydroides elegans*. Among four stages (newly-released oocyte to 2–cell stage, 2–cell to blastula, blastula to trochophore, trochophore to newly-settled juvenile) development failed at salinities of <20, 20, 25 and 15, respectively. That is, the trochophore stage seems to be slightly more tolerant to salinity stress than the embryonic and early juvenile stages. Juveniles of *H. elegans* were more vulnerable to low salinity (20) within 1 day of settlement than when older. Apparently, the early

developmental stages are more sensitive to environmental stress than late juveniles and adults and the juveniles are most vulnerable at the onset of benthic life (Qiu & Qian 1998). High natural mortality is also reported for juveniles of *Pomatoceros triqueter* (Klöckner 1976). Extreme vulnerability at the onset of juvenile life and very high juvenile mortality (>90%) are widespread among benthic marine invertebrates (see Gosselin & Qian 1997b for review).

Mortality of brooded embryos due to failure of fertilisation or any other causes acting before the time of larval release is reported to be very low (e.g. Daly 1978a,b for *Spirorbis spirorbis*) but increases in the post-settlement period. Rzhavsky & Britayev (1984) report that mortality of *Neodexiospira brasiliensis* is highest during the first week after the settlement and may reach 79.5% of the newly settled juveniles. Hamamoto et al. (1996) found two peaks of mortality in spirorbids; early post-settlement mortality and mortality of individuals with tube diameters over 1.5 mm. The second peak probably corresponds to the natural mortality of adults.

Mortality factors

Natural variation in mortality rate at any given stage is apparently due to variation in the intensity of mortality factors. Documented sources of serpulid and spirorbid mortality include the above-mentioned factors affecting development, settlement and growth, such as inadequate food conditions, physical environmental factors, pollution, lack of adequate larval settlement sites and delaying of metamorphosis.

For example, survival of *Hydroides elegans* trochophores increased with increasing algal concentrations from 0 to 10^6 cells ml⁻¹. No settlement occurred at concentrations $< 10^3$ cells ml⁻¹. Larvae that were allowed to resume feeding after 10 days starvation did not settle. Such a period of food limitation exceeds the point at which *H. elegans* retain the ability to develop to competence (Qiu & Qian 1997). Brooding success (survival of embryos) of *Pileolaria berkeleyana* sensu lato appears to be dependent on temperature (Harris 1972, Thorp 1991). Natural mortality of juveniles of *Pomatoceros triqueter* reached a maximum in late autumn, when the phytoplankton supply was approaching a minimum and water temperatures were decreasing (Klöckner 1976). Low salinity increased mortality during both the larval and early juvenile periods of *Hydroides elegans* (Qui & Qian 1997, 1998). High sedimentation contributes to juvenile and adult mortality in some spirorbids settling on rocks (Rzhavsky unpubl.) and in *Pseudochitinopoma occidentalis* (Duggins et al. 1990). Two-day-old larvae of *Serpula columbiana* died after 3 h in 0.5% of diesel oil (Chia 1973). Delaying of metamorphosis had significant adverse effects on juvenile survival of *Hydroides elegans* (Qiu & Qian 1998).

Biotic factors: predation, competition and parasitism

Natural predators Predation is an important source of mortality at all stages of the life history. However, predation on serpulid larvae is difficult to document probably because small transparent larvae are digested very fast and cannot be detected in predators' stomachs. Cowden et al. (1984) mention that suction-feeding bivalves are capable of catching serpulid larvae. Gastropod molluscs are the most commonly reported predators on juvenile and adult serpulids and spirorbids (Moran et al. 1984, O'Donnell 1984, Tan & Morton 1998,

Hoisaeter 1989, Ward 1989, ten Hove 1994a, Rzhavsky unpubl.). *Okadaia elegans*, a dorid nudibranch of the family Vayssiereidae (Opistobranchia, Gastropoda) feeds on spirorbids and serpulids (Baba 1937, Young 1969). In penetrating the tubes, specimens of *O. elegans* bore smooth round holes presumably by chemical activity and mechanical rasping (Young 1967, 1969).

Other reported predators of serpulids include crabs (*Pomatoleios kraussi*: Straughan 1969; *Ficopomatus uschakovi*: Straughan 1972a), fishes (e.g. Vinogradov 1948, Wesenberg-Lund 1951, Hiatt & Strasburg 1960, Randall 1967, Bosence 1973, Knight-Jones et al. 1973, Bailey-Brock 1976: Families Chaetodontidae, Acanthuridae, Balistidae, Labridae), Asteroidea (Christensen 1970, Bosence 1973) and Echinoidea (Chadwick 1900, Hunt 1925, Vine & Bailey-Brock 1984). However, according to ten Hove (1979a) predation by fishes generally only affects the (extended) branchial crowns, which may regenerate after removal within a couple of days. Spirorbids are occasionally found in stomachs of the sea urchin *Strongy-locentrotus polyacanthus* that indiscriminately scrapes hard substrata. Small or juvenile sea stars also sometimes consume spirorbids (Feder 1970, Rzhavsky unpubl.). There is a single record of a nereid polychaete eating *Ficopomatus* (Margalef 1962). The high frequency of occurrence of rhabdocoels and mites in tubes of spirorbids led Knight-Jones et al. (1975) to the conclusion that those animals were important predators of spirorbids.

Competition Competition for space is an important determinant of mortality in many sessile organisms. The outcome of such competition depends on the serpulid species and the composition of the fouling community (e.g. Straughan 1972a). For example, *Pomatoceros triqueter* successfully competed for space with bryozoans (Rubin 1985), whereas *Pseudo-chitinopoma occidentalis* was completely smothered by encrusting bryozoans after several months following settlement (Haderlie 1974). Overgrowth by bryozoans and tunicates (Castric 1977) and by the soft coral *Xenia* (Vine & Bailey-Brock 1984) has been reported as a source of serpulid mortality.

Mortality and competitive abilities of juveniles of *Pomatoleios kraussi* varies according to tidal height and the intensity of settlement. At low level exposure sites, encrusting ectoprocts, sponges and filamentous algae cause heavy mortality among low density populations of *P. kraussi*. At the mid-tidal level, where the most abundant larval settlement occurs, *P. kraussi* almost completely smothers *Balanus amphitrite*, whereas at the highest level the competition for space is almost completely eliminated because the intensity of larval settlement is low (Mohammad 1975).

Spirorbids are often overgrown by encrusting species (Stebbing 1973, O'Connor & Lamont 1978) and whereas some redirection of growth in an attempt to elevate the tube orifice above the competing species is possible, most individuals are ultimately smothered. Such observations thus confirm Jackson's (1977) assertion that colonial species can generally outcompete solitary species.

Parasites Parasitism may also control populations to some extent but there is no overview of parasites and/or commensals occurring in or on serpulids. Host specificity of parasites can be used as a tool in resolving evolutionary pathways in different host groups although a complete evaluation requires a profound knowledge of the various parasitic or commensal groups, and even then the precise nature of the symbiosis will not always be clear. This difficulty may be illustrated by a remark by Gotto (1993) regarding the copepod *Acaenomolgus protulae* (Stock 1979), reported from *Protula intestinum* and *P. tubularia*:

"Unlike *Sabelliphilus*, it is probably a commensal rather than a parasite." Host specificity is difficult to prove:

Despite the fact that previous authors have reported many different, most probably only occasional hosts of *Pseudanthessius gracilis*, the true natural host (Gotto 1993), still remains unknown. Our study has identified the polychaete *Hydroides elegans* as at least one of the true hosts of this species, since we have managed to rear all copepodids up to the adult stage in its presence. (Costanzo et al. 1996)

However, this copepod is not a true parasite but is a kleptoparasite stealing slime and particles from ciliary ducts (Stock pers. comm.). It is thus not relevant to the present discussion.

A number of older references mention infestations of serpulids by protists like the Gregarinidae (known as endoparasites in various invertebrates). The nature of these infestations is not always clear, nor is their effect on the well-being of the hosts. Species mentioned include *Pomatoceros triqueter*, *Protula tubularia*, *Salmacina dysteri*, *Serpula vermicularis*, *Spirobranchus latiscapus* and *Janua pagenstecheri* and the nominal infesting taxa are *Anoplophyra spirorbis*, *Haplosporidium marchouxi*, *Monocystis serpulae*, *Polyrhabdina serpulae*, *Selenidium caulleryi*, *Selenidium* sp. (Lankester 1863, McIntosh 1885, Mingazzini 1893, Caullery & Mesnil 1899, 1905, Brasil 1907, Lee 1912, Hempelmann 1930). There is just one remark about the frequency of occurrence: "there is no individual of *Protula tubularia* from the coast of Calvados [France] of which the alimentary canal does not contain a great number [of *Selenidium*]" (Brasil 1907).

Margolis (1971) reviews the role of polychaetes as intermediate hosts of helminth parasites of vertebrates, of which only trematodes are known from serpulids. The sporocysts of one species, *Cercaria loossi*, develop in the coelom of *Hydroides dianthus* as first intermediate host, in the Woods Hole area, USA (see also Stunkard 1970). It is apparently a specific parasite for *H. dianthus*. Whether or not it castrates its host, like in the comparable situation of *Aporocotyle simplex* in the terebellid polychaete *Arctacama proboscidea* (Køie 1982) is unknown. The sporocysts (with cercariae) leave the polychaete through its genital pores on the way to their definitive fish host (Martin 1944) but this may be an artefact (Køie 1982). Another digenetic trematode, *Proctoeces maculatus* uses *Hydroides elegans* as a secondary host in the Mediterranean (Prévot 1965). It is not an obligatory parasite of the serpulid because it is known from the errant polychaete *Nereis* and even also from molluscs.

It is a matter of semantics whether the Pyramidellidae (Gastropoda), which suck fluids from various invertebrates with their long proboscis, should be regarded as ectoparasites or as micro-predators. Their occurrence in serpulids has been reviewed by ten Hove (1994a). On the one hand, species of the genus *Fargoa* seem to be genus-specific ectoparasites of the genus *Hydroides*, while on the other hand, members of the genus *Boonea* are generalists that also occur on various molluscan hosts (Robertson & Mau-Lastovicka 1979). In the genus *Odostomia* one species is reported to be specific to *Pomatoceros triqueter*, another to the mussel *Mytilus edulis* and a third is associated with many bivalve molluscs (Baer 1971). The small size of the gastropod, however, makes field observations difficult. The question of host-specificity is further obscured by the fact that their most frequently mentioned serpulid hosts (*Pomatoceros triqueter*, *Galeolaria caespitosa* and *Hydroides dianthus*) occur in dense masses with a diverse accompanying fauna. The statement "found on *H. dianthus*" is thus no guarantee that the host was indeed the serpulid (ten Hove 1994a).

Several other gastropods are known as kleptoparasites. *Trichotropis cancellata*, (Family Capulidae) inserts its proboscis into the mouth of *Serpula columbiana* (as well as sabellids and sabellariids) and removes food from the worm (Pernet & Kohn 1998). Unpublished results of experiments (Pernet & Iyengar pers. comm) show that parasitic snails substantially reduce growth rates (measured as tube extension) of *S. columbiana* in the field.

There is a single record of a polychaete endoparasite in a serpulid, that of *Drilonereis* sp. in *Serpula vermicularis* (Pérès 1949, Paris 1955). The parasitic worm penetrates its host in the 6th abdominal chaetiger, makes a loop almost throughout the entire abdomen in such a way that its prostomium is situated in the first abdominal chaetiger; the posterior 4 cm of the parasite remain outside its host.

The literature on parasitic copepods is vast. One of the first records of copepods on serpulids may be that on *Hyalopomatus claparedii* by von Marenzeller (1878), without further taxonomic details of the copepods involved. Other old records include those by McIntosh (1885, 1919, 1923) and Gravier (1912, 1913). In her review of the association of copepods with marine invertebrates, Gotto (1979) concludes: "few hard and fast rules can be applied to the incidence of host specificity." She also states: "If older records could be relied on, the genus occurs in quite an array of ascidian hosts; but this is almost certainly erroneous and stems from the confusing synonymies which have accreted over the years for ascidians and copepods alike."

This statement also holds true for the situation in serpulids. For instance, Faulkner (1929) ascribes differences in size between colonies of *Filograna implexa* (Plymouth, UK) to the presence of the endoparasitic monstrillid *Haemocera* in some colonies but it is not clear if the author distinguished between the operculate *Filograna implexa* and the non-operculate *Salmacina dysteri*. Nelson-Smith & Gee (1966) explicitly state: "At Plymouth, *Cymbasoma filogranarum* [senior synonym of *Haemocera*] is said to infect *Filograna implexa* but not *Salmacina dysteri*..., which reinforces the proposal of Gee (1963b) that these two species should remain distinct." However, this is in contradiction to the drawing by Malaquin (1901; copied by e.g. Baer 1952, 1971, Davies 1984), clearly showing the non-operculate *Salmacina* as host of the monstrillid. Isaac (1974) attributes the monstrillid to yet another taxon, *Thoumaleus rigidus*.

Ectoparasitic (or commensal) copepods have been recorded from abdomens, inside the tube (e.g. Southward 1964: Salmacina setosa, Filogranula stellata and Placostegus tridentatus) and from branchial crowns in serpulids. Our knowledge is far from complete, as is shown by the high proportion of new genera and species described by Stock (1979, 1988, 1989, 1995a,b) based on accidental collections by one of us (tH). In one case, a single serpulid (*Spirobranchus corniculatus*) even yielded two different genera of ectoparasitic copepods (Stock 1995a), suggestive either of different microniches or of different food sources utilised by the copepods (cf. Gotto 1979). Humes & Stock (1973) revised the Lichomolgidae, of which a number of taxa are associated with various serpulids (*Filograna, Pomatoceros triqueter, Pomatostegus stellatus, Protula tubularia, P. intestinum, Serpula vermicularis* and *Spirobranchus giganteus*). Later records include those by Humes & Grassle (1979, *Josephella* sp.), Bailey-Brock (1985, *Spirobranchus corniculatus, S. gardineri*). Although the overall pattern suggests that copepod taxa are specific to certain genera of serpulids rather than to species, a complete evaluation should be done in a joint effort by serpulid and copepod taxonomists.

Haswell (1884, 1885 cited by Augener 1914, McIntosh 1923) reported a new genus *Eisothistos* (= "invader") of parasitic isopod inhabiting tubes of *Serpula vasifera*. These

isopods prey on serpulids and rear broods in their tubes (Haswell 1884). Wägele (1979, 1981) found two more *Eisothistos* species in serpulid tubes and studied their growth, maturation, brooding, and adaptation to the occupied niche. Finally, Knight-Jones & Knight-Jones (in prep., pers. comm.) described five new species of the genus *Eisothistos* inhabiting tubes of various spirorbid species.

From all these scattered records, the general impression is that parasitism does not play a major role in the population dynamics of serpulids.

Discussion

While many polychaetes show extremely high overall diversity and flexibility of life histories, such diversity varies significantly among families (Wilson 1991, Giangrande 1997). For example, the families Capitellidae and Spionidae show the highest variability and flexibility in their life cycles, whereas the Sabellariidae, Spirorbidae and Nepthyidae show the least variability. The question is whether ecology and morphology of various polychaete groups impose constraints on the evolutionary diversity of their life-history and reproductive traits. Such constraints may be related to the morphological design, ecology, and habitats used by a group (McHugh 1993, Giangrande 1997). Phylogenetic constraints (defined as a result of the phylogenetic history of a lineage that prevents anticipated course of evolution) might be tested only within a phylogenetic framework. Variability of life histories may also be limited because life-history traits are known to covary and co-evolve.

Some constraints on the reproductive biology of serpulimorph polychaetes are apparently imposed by their obligatory sessile life style. The features typical for mobile and some sedentary polychaetes (e.g. spionids, cirratulids) such as swarming, epitoky, hypodermic insemination, mating by direct copulation and some active forms of parental care are not found in serpulimorph polychaetes. Other constraints and life-history patterns are not so obvious. For example, sessile life style has been proposed to explain the evolution of hermaphroditism in some groups. Ghiselin (1969, 1974) suggests that simultaneous hermaphroditism is advantageous in sessile species or in low-density populations because each contact of adults can lead to reproduction. However, his hypothesis fails to account for the observed gonochorism and/or protandric hermaphroditism in serpulimorphs. Moreover, some simultaneous hermaphrodites (e.g. species of the *Filograna/Salmacina* complex) are found in high-density colonies.

Below we consider the patterns in serpulid egg size, larval feeding modes, parental care, planktonic and benthic developmental habitats and investigate if the hypotheses proposed to explain evolution of these life-history traits can be applied to serpulimorphs.

Trends in egg size and larval feeding modes

The egg size, an indicator of energy investment per offspring, is one of the most important life-history traits. The evolution of egg size has been of considerable interest to evolutionary biologists. The original fecundity-time Vance model and its modifications (Vance 1973a,b, Christiansen & Fenchel 1979, Perron & Carrier 1981, Grant 1983) predict that reproductive success for planktonic larvae is maximised in species with the smallest eggs that require

larval feeding or in the largest eggs associated with non-feeding development. Therefore, bimodal egg size distribution with modes corresponding to feeding and non-feeding development is expected.

The pattern of egg size distribution in serpulimorph polychaetes shows some expected and unexpected trends. Egg sizes in serpulimorphs vary from 45 μ m to 230 μ m. As expected, smaller eggs (<80 μ m) correlate with feeding larval development and larger eggs (>80 μ m) correlate with non-feeding development.

The egg size distribution is visually bimodal if data for serpulids and spirorbids are pooled (Fig. 12A) but the observed modes do not correspond to feeding and non-feeding development, as predicted by the Vance model. Rather, they reflect taxonomic differences. If distributions of serpulid and spirorbid eggs are considered separately, the egg size distributions are clearly unimodal (Fig. 12B, C). Moreover, the egg sizes of feeding and non-feeding larvae partially overlap; intermediate egg sizes ($80-90 \mu m$) are found both in species with feeding larvae and non-feeding larvae.

One explanation of this pattern is that egg diameters are not reliable indicators of parental investment in scrpulimorph polychaetes, especially because the overall differences in egg size are relatively small. Both total organic content and organic content per volume may vary significantly among species. Another explanation of this pattern is that larvae of some planktotrophic species with larger eggs are facultative feeders, that is, they are capable of completing metamorphosis without feeding. Incorporation of facultative feeding into the fecundity-time model showed that reproductive success can be maximised at intermediate egg sizes depending on larval food availability and the intensity of planktonic mortality (McEdward 1997). The facultative feeding model predicts that a continuum of nutritional strategies exist between planktotrophy and lecitotrophy and that planktotrophic species should differ in parental investment, susceptibility to food limitation, development rate, growth and size at metamorphosis. At present there is insufficient information and additional studies are needed to determine whether facultative feeding is common in serpulids and in other polychaetes and whether it can account for egg size variability and distribution.

An alternative hypothesis that explains continuous variation in egg size between species from the perspective of fertilisation kinetics was proposed by Levitan (1993). He suggested that larger eggs present a larger target for sperm and will be fertilised at higher rates. Therefore, for broadcast-spawning species there is a trade-off between the production of many small eggs with low probability of fertilisation and fewer large eggs with higher probability of fertilisation. Although there is some variation in egg size of free-spawning serpulids, it is unknown whether such a difference is translated into differences in fertilisation rates. More important, the model does not explain the predominance of relatively small eggs corresponding to planktotrophy and almost total lack of larger eggs corresponding to planktonic lecithotrophy in serpulids. Two related questions here are how broadcasting serpulids overcome the potential problem of sperm limitation and why planktonic lecithotrophy is so rare.

Why not planktonic lecithotrophy?

The dominance of larval feeding in serpulids is intriguing because the closely related Sabellidae have exclusively non-feeding larval development. The question arises whether serpulids are constrained in their mode of larval nutrition or whether larval feeding is selectively advantageous for this group.



Figure 12 Egg size distribution in serpulimorph polychaetes. Above, serpulids and spirorbids combined. Centre, serpulids only. Below, spirorbids only.

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Figure 13 Relationship between maximum adult size and maximum egg size in planktotrophic serpulids.

Since larval feeding usually corresponds to smaller eggs, it offers the advantage of higher fecundity than lecithotrophy. However, serpulids with planktotrophic larvae show a significant positive correlation between the maximum adult size and maximum egg size (Fig. 13), suggesting that fecundity is not necessarily maximised with increased body size.

The duration of non-feeding larval development depends primarily on temperature, whereas the duration of feeding development is also affected by food availability. Low food levels may lead to longer development and increased mortality due to predation and other factors. Apparently, any adaptation to decrease development time should increase overall fitness. Havenhand (1993) developed a model that considers the effect of the development time on the evolution of egg size and larval type. According to the model, there are selective pressures that reduce the egg-to-juvenile period. Since species with non-feeding larvae tend to have a shorter development time, this means selective pressure towards non-feeding development. Interestingly, because this effect is more pronounced at shorter life cycle durations (Havenhand 1993), the model probably better explains the selective pressures towards lecitotrophy connected with small body size and brooding (see below) than towards planktonic lecitotrophy of larger species with longer life cycles.

Increased dispersal distance is a consequence of the longer planktonic life of feeding larvae. However, an increased scale of dispersal offers little if any advantage for feeding larvae (Palmer & Strathmann 1981). The evolutionary importance of a planktonic stage in serpulids is likely to be in small-scale habitat selection rather than in long-distance dispersal because serpulid larvae require specific cues for settlement and suitable habitats are commonly patchy in their distribution. The question is whether larval feeding improves habitat selection relative to non-feeding larvae.

Consequences of larval feeding for habitat selection and postmetamorphic growth and survival have not been well studied. It is obvious from the literature that successful settlement in serpulids is dependent both on how well larvae are preconditioned to respond to metamorphic cues and whether the required cues are available (see pp. 44–56). Larval feeding allows extension of the period when larvae remain competent to metamorphose thus increasing the possibility of locating a suitable substratum, although such an extension is not without a cost (see pp. 44–56). It appears that there is a trade-off between mortality due to the lack of suitable substrata and mortality due to postponed settlement. Further studies could show whether better habitat selection by planktotrophic larvae does make serpulid larval feeding selectively advantageous.

Fertilisation success

It has been suggested that low fertilisation rates resulting from gamete dilution may constrain reproductive success in free-spawning organisms (Levitan 1995). The nature of the adaptations to decrease the effects of sperm dilution is not clear. It is likely, for example, that high fecundity of large serpulids and high population density of species that settle gregariously offset these factors to some extent, yet some relatively small-bodied freespawning serpulids are common in low-density populations. Therefore, further studies of fertilisation success in serpulids should address gamete longevity, concentration, and postspawning behaviour, as well as the size of adults and their distribution in the field.

Planktonic and non-planktonic development

Egg size and corresponding larval feeding modes (planktotrophy and lecitotrophy) are so closely connected to the habitat where the larval development takes place (benthos or plankton) that they are not always distinguished. Thorson's classification of reproductive modes into planktotrophy, lecithotrophy and brooding (Thorson 1950) stressed that invertebrate larvae developing in the plankton can be either feeding or non-feeding but during brooding (or any encapsulated benthic development) larvae are usually lecithotrophic. However, an initial benthic stage in the form of encapsulation or brooding is followed by later release of feeding larvae in "mixed" development in some molluscs and crustaceans (Pechenik 1979).

In serpulimorph polychaetes, planktonic development correlates with larval feeding (see above) and benthic development in the form of brooding is associated with lecithotrophy. This association is especially true for spirorbids that have only brooded lecithotrophic larvae with a short habitat-selecting stage. Whether the association of brooding with non-feeding development in serpulids is universal or some brooding species can release feeding larvae is not known because the frequency and variability of brooding methods has been significantly under-reported. Observations by one of us (ten Hove, see p. 41) suggest that a short period of initial brooding may be present in *Pseudochitinopoma occidentalis*, a species with typical planktotrophic larvae but confirmatory studies are needed.

Factors influencing the evolutionary maintenance or loss of planktonic dispersive stages may be closely interconnected with those affecting evolution of feeding and non-feeding development (see above). Some factors include the nature of habitats used and effects of the body size.

Obrebski (1979) developed a model of colonising strategy in planktonic larvae that links the availability of adult habitats with energy allocation to habitat search and larval

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metamorphosis. The model predicts that benthic organisms that colonise abundant habitats, such as coastal sandy and muddy sediments, will lose dispersive larval stages more often than species inhabiting rocky shores or highly specific habitats. From this perspective, planktonic larvae of serpulimorph polychaetes, even short-swimming spirorbid larvae, should be retained. Bhaud & Duchene (1996), on the contrary, suggested that for species inhabiting highly specialised and restricted habitats (such as bays, lagoons, and fissured hard bottoms) the reduction of larval dispersal is a prerequisite for the maintenance of populations. However, reduction of a planktonic stage does not always reduce dispersal. Drifting and rafting may serve as efficient means of long-distance dispersal (Highsmith 1985, Johannesson 1988, Martel & Chia 1991), especially if adults are small, as in spirorbids inhabiting algae.

Covariates of body size

Body size is an important determinant of life history in many marine invertebrates but it seems to be of paramount importance in the life history of polychaetes (Giangrande 1997). Large body size is almost universally correlated with higher longevity and fecundity (see Fig. 14 and p. 18 for spirorbids). Increased longevity allows an adult to produce offspring over a longer period of time and the onset of sexual maturation is delayed. In such cases generation time and number of reproductive events are increased. In contrast, small adult size is associated with lower longevity and fecundity, earlier sexual maturation, and shorter generation time. Other very important life-history covariates of body size include sexuality patterns and developmental habitats (planktonic or benthic).



Figure 14 Relationship between tube coil diameter and maximum fecundity in spirorbids.

Body size and sexuality patterns

Evolution of protandric hermaphroditism as observed in serpulids is well explained by the size-advantage hypothesis (Ghiselin 1969, 1974, Warner 1988). According to the hypothesis, sequential hermaphroditism is favoured when an individual can reproduce most efficiently as a member of one sex when small but as a member of the other sex when it gets older and larger. Since larger body size usually increases female fecundity more than male fecundity, small individuals are expected to be males and larger individuals to become female, providing that cost of sex reversal is not too high. The observed pattern of serpulid protandric hermaphroditism (e.g. *Pomatoceros triqueter*: Føyn & Gjøen 1954) fits well into the size-advantage hypothesis.

Simultaneous hermaphroditism correlates not only with small body size but also with brooding (see below), the trend exemplified by all spirorbids as well as by small serpulids. According to Heath's (1979) hypothesis, given that brooding is internal, hermaphroditism may evolve if the resources a female can allocate to ova production are limited by lack of brooding space. In this case, spare resources then could be allocated to produce male gametes in a hermaphrodite.

Correlation of small body size and brooding

The correlation of small size with brooding has been observed in many marine invertebrates (e.g. Chia 1974, Menge 1975, Knight-Jones & Bowden 1979). In serpulimorph polychaetes brooding is typical for all spirorbids and small serpulids (usually <10 mm in length), whereas large serpulids with a body size of >20 mm tend to be broadcasters (see Table 2, pp. 9–16). Several hypotheses have been proposed to explain such a correlation.

The most intuitive hypothesis, that of Chia (1974), states that brooding should be advantageous in small organisms with low energy reserves for gamete production because planktonic mortality is high. Low fecundity (of small species) means there is a high probability that no embryos will survive because they are exposed to the hazards of planktonic life.

According to the recruitment hypothesis (Strathmann & Strathmann 1982), predictable recruitment typical for brooding species is more important for small than for large species. If recruitment is unpredictable, and larval or juvenile survival is more variable than survival of adults (which is apparently the case for serpulids), selection may favour greater adult longevity with ensuring higher fecundity. Thus, varying survival may link absence of brooding to higher longevity and therefore, larger body size.

The dispersal hypothesis (Strathmann & Strathmann 1982) states that the advantages of brooding for smaller species exceed potential advantages provided by greater dispersal. Given that small spirorbids can disperse considerable distances using rafting, drifting and floating, any disadvantages of limited larval dispersal in brooders may be compensated. Long-term dispersal may be disadvantageous and Bhaud & Duchene (1996) even suggested that brooding evolved as an adaptation for reduced dispersal to ensure fertilisation in a dispersive environment. However, their hypothesis.does not suggest that brooding is more beneficial for small species than for large.

The allometry hypothesis (Strathmann & Strathmann 1982) states that with increased body size, the capacity for egg production may increase faster than space for brooding. Hess (1993) found no evidence that scaling limits brood size in spirorbids. However, her test may not be decisive because she compared four spirorbid species with *Pseudochitinopoma* *occidentalis*, the small-bodied serpulid species that probably provides early embryos with short-term parental care (see pp. 41-4). Because the validity of the allometry hypothesis depends on the type and geometry of the brood space provided, it may be only applicable to certain methods of internal brooding. For example, it probably is not applicable to brooding in gelatinous masses outside the tube as found in *Protula* and inside the branchial crown as in *Paraprotis*. While the allometry hypothesis explains why brooding is not a beneficial strategy for larger organisms, it does not necessarily imply that brooding should be a preferred mode for small species.

The model of Havenhand (1993, see p. 67), which stresses the selective pressures toward reduction of development time to metamorphosis, indirectly emphasises the importance of brooding in small organisms, because brooders are commonly lecithotrophic and tend to have shorter development time than planktotrophs.

All the hypotheses outlined here are not mutually exclusive and some of them emphasise the association of large body size with absence of brooding more than the association of small size with brooding. While in serpulimorph polychaetes the association of brooding and broadcasting with extreme body sizes is well expressed, there is a range of intermediate body sizes (approximately 10-20 mm) where both brooding and broadcasting species can be found.

Direction of evolution of life history traits

In marine invertebrates in general, planktotrophic larvae are often assumed to be primitive, while lecithotrophic development with or without brood care is thought to be advanced (e.g. Jägersten 1972, Strathmann 1985). One of the arguments in favour of the evolution of non-feeding from feeding planktonic development involves loss of complex ciliary feeding bands. According to Strathmann (1985), if such structures are lost, their "re-evolution" seems so improbable that a biased unidirectional transition has been hypothesised. The transitional bias argument is well supported by comparative morphology data for echinoderms. However, the two major ciliary bands used for both swimming and feeding in polychaete trochophores can hardly be classified as complex structures. In serpulids there is no significant difference in morphology of feeding and non-feeding larvae: both the metatroch and the prototroch are present in lecithotrophic larvae which have guts filled with yolk.

The assumptions about the direction of evolutionary transitions from feeding to nonfeeding development in life-history traits were developed in the absence of rigorous phylogenetic methods (McHugh & Rouse 1998). Recent phylogenetic evidence suggests multiple origins of planktonic larvae and plesiomorphy of benthic development for some spiralian taxa (Reid 1989, for molluscs; Rouse & Fitzhugh 1994, for sabellid polychaetes). Further integration of phylogenetic analyses into life-history evolution studies is essential to infer accurately the original condition of reproductive traits for serpulimorph polychaetes and other groups.

Conclusions

The reviewed literature data indicate that, like many other groups of marine invertebrates, serpulimorph polychaetes show correlation of smaller eggs with feeding and larger eggs
with non-feeding larval development, as well as correlation of small body size with simultaneous hermaphroditism, lecithotrophy and brooding. Less common features include overlap in egg sizes of species with feeding and non-feeding development and rarity of planktonic lecithotrophy. Many aspects of serpulimorph life histories are still poorly known and because of this lack of knowledge, any generalisations about the observed patterns may be biased. Nothing is known about the energetic content of serpulid and spirorbid eggs, the ecology of external fertilisation or any adaptations that increase fertilisation success. Knowledge of reproduction and development of many more species is required to determine the real distribution of brooding and non-feeding planktonic development in the group. Broader generalisations also require better information on egg sizes, larval and juvenile mortality and growth, development rates, size at metamorphosis, larval feeding and susceptibility to food limitation. Finally, robust hypotheses of phylogenetic relationships in serpulimorph polychaetes are necessary to determine whether phylogenetic constraints may explain some life-history features of this group.

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Taxonomic addendum

Serpulidae

Apomatolos simplex Uchida, 1978 see Rhodopsis pusilla: Uchida 1978

Apomatus globifer Willey, 1905 see Protula globifera

Chitinopoma occidentalis Bush, 1905 see Pseudochitinopoma occidentalis: Smith & Haderlie 1969 Chitinopoma arndti Zibrowius, 1983

Chitinopoma rzhavskii (Kupriyanova, 1993), new combination, originally described as *Filogranula rzhavskii*. However, thoracic uncini with single row of teeth all over (in *Filogranula* with multiple rows above fang) and presence of brood-chambers as in *Chitinopoma serrula* (Rzhavsky unpubl.) rather place the taxon in *Chitinopoma*.

Chitinopoma serrula (Stimpson, 1853)

Crucigera irregularis Bush, 1905

Crucigera zygophora (Johnson, 1901)

Ditrupa arietina (Müller, 1776)

Ficopomatus enigmaticus (Fauvel, 1923)

Ficopomatus miamiensis (Treadwell, 1934)

Ficopomatus uschakovi (Pillai, 1960)

Filograna implexa M. Berkeley, 1835: the Filograna/Salmacina complex needs revision; some authors regard the genera as synonymous, even synonymise operculate and non-operculate forms (e.g.

Faulkner 1929), others maintain a generic distinction. We quoted various names at face value, but

added localities (if known to us).

Filograna tribranchiata Moore, 1923

Filogranella elatensis Ben-Eliahu & Dafni, 1979

Filogranula gracilis Langerhans, 1884

Filogranula rzhavskii Kupriyanova, 1993 see Chitinopoma rzhavskii

Filogranula stellata (Southward, 1963)

Floriprotis sabiuraensis Uchida, 1978

Galeolaria caespitosa Lamarck, 1818

- Galeolaria hystrix Mörch, 1863
- Hyalopomatus claparedii von Marenzeller, 1878
- Hydroides dianthus (Verrill, 1873)
- Hydroides diramphus Mörch, 1863
- Hydroides elegans (Haswell, 1883)
- Hydroides ezoensis Okuda, 1934

Hydroides fusicola Mörch, 1863

Hydroides hexagonis/us (Bosc, 1802) see H. dianthus: Colwin & Colwin 1961a,b,c

Hydroides norvegica/us see H. elegans: Monroy 1954, Wisely 1958, Reish 1961, Ranzoli 1962, Sentz-Braconnot 1964, Prévot 1965, Srinivasagam 1966, Margolis 1971, Ghobashy & Selim 1979a

Hydroides norvegicus Gunnerus, 1768; (sub)tropical records most probably belong to H. elegans

Hydroides pectinatus (Philippi, 1844) see H. elegans: Zeleny 1905

Hydroides tuberculatus Imajima, 1976

Hydroides uncinatus (Philippi, 1844) see *H. dianthus*: Shearer 1911, Ivanoff 1928, Hill 1967 (probably)

Josephella marenzelleri Caullery & Mesnil, 1896

Josephella spec. Humes & Grassle, 1979; the genus Josephella is known only from shelf depths, this bathyal (2500 m) record should be checked

Marifugia cavatica Absolon & Hrabě, 1930

Mercierella enigmatica Fauvel, 1923, see Ficopomatus enigmaticus: Fischer-Piette 1937, Vuillemin 1954, 1962a,b, 1965, 1968, Dixon 1977

Mercierella enigmatica: see Ficopomatus uschakovi: Hill 1967, Straughan 1968 (in part, Victorian material is enigmaticus), Straughan 1972 a,b

Metavermilia cf. ovata Imajima, 1978

Microprotula ovicellata Uchida, 1978

- Mi(c)roserpula inflata Dons, 1930 see Chitinopoma serrula
- Neosabellaria cementarium (Moore, 1906) N. B. Sabellariidae, not serpulid

Omphalopoma stellata Southward, 1963 see Filogranula stellata

Paraprotis dendrova Uchida, 1978

Paraprotula apomatoides Uchida, 1978

- Placostegus tridentatus (Fabricius, 1779)
- *Pomatoceros lamarckii* (Quatrefages, 1865), in shallow Mediterranean/Atlantic waters often confused with *P. triqueter*
- Pomatoceros strigiceps Mörch, 1863 see Spirobranchus latiscapus: McIntosh 1885

Pomatoceros terranovae Benham, 1927

- Pomatoceros triqueter (Linnaeus, 1758)
- Pomatoleios kraussi (Baird, 1865)
- Pomatostegus actinoceras Mörch, 1863
- Pomatostegus stellatus (Abildgaard, 1789): a Caribbean taxon; Indo-Pacific records belong to P. actinoceras: Nishi 1993
- *Protula globifera* (Théel, 1878); although the species is classified in the genus *Protula* here, it should be noted that ten Hove & Pantus (1985) are of the opinion that *Apomatus* is a valid genus.

Protula intestinum (Lamarck, 1818)

- Protula meilhaci Marion, 1875 see Protula tubularia: Soulier 1917
- Protula palliata (Willey, 1905)
- Protula tubularia (Montagu, 1803)
- Protula tubularia: Pérès' (1949) Figure 1 (also in Paris 1955) clearly shows two club-like pseudopercula, referring his specimen to Serpula vermicularis
- Pseudochitinopoma occidentalis (Bush, 1905)
- Pseudovermilia conchata ten Hove, 1975
- Pseudovermilia occidentalis (McIntosh, 1885)
- Psygmobranchus protensus Philippi, 1844 see Protula tubularia: LoBianco 1888, 1909, Meyer 1888
- Rhodopsis pusilla Bush, 1905
- Sabellaria alveolata (Linnaeus, 1767); N. B. Sabellariidae, not serpulid
- Sabellaria cementarium Moore, 1906 see Neosabellaria cementarium: Cowden et al. 1984 N. B. Sabellariidae, not serpulid
- Salmacina aedificatrix Claparède, 1870
- Salmacina amphidentata Jones, 1962
- Salmacina aedificatrix Claparède, 1870: generally synonymised with S. dysteri.
- Salmacina dysteri Huxley, 1855; see remark under Filograna implexa
- Salmacina dysteri var. tribranchiata (Moore, 1923) see Filograna tribranchiata: MacGinitie & MacGinitie 1949
- Salmacina setosa Langerhans, 1884
- Semivermilia aff. uchidai Imajima & ten Hove, 1986
- Serpula columbiana Johnson, 1901
- Serpula concharum Langerhans, 1880
- Serpula concharum see Hydroides elegans: Sentz-Braconnot 1964
- Serpula contortuplicata Linnaeus, 1767: confused, in the sense as used by Lankester (1863) probably see *S. vermicularis*
- Serpula hartmanae Reish, 1968
- Serpula sp.
- Serpula uncinata see Hydroides dianthus: Schenk 1875
- Serpula vasifera Haswell, 1885
- Serpula vermicularis Linnaeus, 1767; this name has been used for all larger representatives of the genus from all over the world. Recent work has shown that *S. vermicularis* sensu auctores is a complex of species (ten Hove & Jansen-Jacobs 1984, Kupriyanova 1999), and the species *S. vermicularis* sensu stricto most probably only occurs in the North Atlantic and Mediterranean (Pillai, pers. comm.)
- Serpula vermicularis see S. columbiana: Gray 1976, Young & Chia 1982, Paulay et al. 1985, Strathmann 1987
- Serpula uschakovi Kupriyanova, 1999
- Sphaeropomatus miamiensis Treadwell, 1934 see Ficopomatus miamiensis
- Spiraserpula snellii Pillai & ten Hove, 1984
- Spirobranchus corniculatus (Grube, 1862)
- *Spirobranchus corniculatus* complex, essentially three morphologically close species occurring in the Indo-Pacific: *S. corniculatus* sensu stricto, *S. cruciger* and *S. gaymardi* (Quatrefages, 1865)
- Spirobranchus cruciger (Grube, 1862)
- Spirobranchus gardineri Pixell, 1913
- Spirobranchus gaymardi (Quatrefages, 1865)
- Spirobranchus giganteus (Pallas, 1766); has long been regarded as a circumtropical species but was split by ten Hove (1970) into two, possibly three subspecies: *S. giganteus giganteus* from the Caribbean, *S. g. corniculatus* from the Indo-Pacific and possibly *S. g. incrassatus* (Krøyer) Mörch, 1863 from the tropical Pacific Americas. Recent work has shown that this was an over-simplification,

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and that ten Hove's subspecies are species-complexes (see Fiege & ten Hove 1999 for a full survey). Where possible we attribute the literature records to their proper species, sometimes we have to refer

to the next level, that of a geographically defined complex.

Spirobranchus giganteus: see Spirobranchus corniculatus complex White 1976

Spirobranchus giganteus corniculatus: see Spirobranchus corniculatus complex Smith 1984a,b, Nishi 1992b

Spirobranchus latiscapus (Marenzeller, 1885)

Spirobranchus polycerus sensu stricto (Schmarda, 1861)

Spirobranchus spinosus Moore, 1923, Californian representative of the S. giganteus complex

Spirobranchus tetraceros (Schmarda, 1861)

Spirobranchus tricornis Ehlers, 1887: see S. giganteus: Allen 1957

Vermiliopsis infundibulum (Philippi, 1844) see Vermiliopsis infundibulum–glandigera complex: Nishi 1993

Spirorbidae

Bushiella (B.) abnormis (Bush, 1905)

Bushiella (Jugaria) granulata (L., 1767)

Bushiella (Jugaria) kofiadii (Rzhavsky, 1988) often recorded as "Spirorbis granulatus"

Bushiella (Jugaria) quadrangularis (Stimpson, 1854) often recorded as "Spirorbis granulatus"

Bushiella (Jugaria) similis (Bush, 1905) often recorded as "Spirorbis granulatus"

Bushiella (Jugaria) atlantica (Knight-Jones, 1978)

Bushiella sp. True species identity of some "Spirorbis granulatus" records cannot be recognised. It could be Bushiella (Jugaria) quadrangularis, Bushiella (Jugaria) similis, Bushiella (Jugaria) kofiadii, Bushiella (Jugaria) granulata sensu stricto or any other Bushiella species

Circeis armoricana Saint-Joseph, 1894. Often recorded as "*Spirorbis spirillum*". This species is found on algae, stones, crustaceans, and molluscs and is distinct from *C. spirillum*, which is found on hydrozoans and bryozoans.

Circeis cf. *armoricana* most records of "Spirorbis spirillum" from algae, stones, crustaceans and molluse shells apparently belong to *Circeis armoricana*.

Circeis oshurkovi Rzhavsky, 1998

Circeis paguri Knight-Jones & Knight-Jones, 1977

Circeis spirillum (L., 1758). This species inhabits mostly branching bryozoans and hydrozoans, whereas most records from algae, stones, crustaceans and molluses refer to *Circeis armoricana*.

Dexiospira foraminosa see Neodexiospira foraminosa: Nishi & Yamasu 1992d

Eulaeospira convexis (Wisely, 1963)

Helicosiphon biscoeensis Gravier, 1907

Helicosiphon platyspira Knight-Jones, 1978

Janua (Dexiospira) alveolata see Neodexiospira alveolata: Rzhavsky & Britayev 1984

Janua (Dexiospira) brasiliensis see Neodexiospira brasiliensis: Nelson 1979, Kirchman et al. 1982a,b

Janua (Dexiospira) formosa see Neodexiospira formosa: Knight-Jones 1972, Knight-Jones et al. 1974

Janua (Dexiospira) lamellosa see Neodexiospira lamellosa: Knight-Jones et al. 1974

Janua (Dexiospira) nipponica see Neodexiospira brasiliensis: Rzhavsky & Britayev 1984

Janua (Dexiospira) steuri see Neodexiospira steueri: Knight-Jones 1972; Knight-Jones et al. 1974

Janua (Fauveledora) kayi see Neodexiospira kayi: Knight-Jones 1972

Janua (Pillaiospira) trifurcata see Pillaiospira trifurcata: Knight-Jones 1973

Janua pagenstecheri (Quatrefages, 1865)

Metalaeospira clasmani Vine, 1977

Metalaeospira pixelli (Harris, 1969)

Metalaeospira tenuis Knight-Jones, 1973

Neodexiospira alveolata (Zachs, 1933)

Neodexiospira brasiliensis (Grube, 1872)

- Neodexiospira foraminosa (Moore & Bush, 1904)
- Neodexiospira formosa (Bush, 1905)
- Neodexiospira kayi (Knight-Jones, 1972)
- Neodexiospira lamellosa (Lamarck, 1818)
- Neodexiospira pseudocorrugata (Bush, 1905)
- Neodexiospira sp. The material identified by Sveshnikov (1967) and Bagaveeva (1975) as "Spirorbis alveolatus" may belong to Neodexiospira alveolata or N. brasiliensis
- Neodexiospira steueri (Sterzinger, 1909)
- Nidificaria nidica (Knight-Jones, 1978)
- Paradexiospira (Spirorbides) vitrea (Fabricius, 1780)
- Paradexiospira nakamurai see Paradexiospira (Spirorbides) vitrea: Uchida 1971
- Paralaeospira levinseni Caullery & Mesnil, 1897
- Paralaeospira malardi Caullery & Mesnil, 1897
- Paralaeospira parallela Vine, 1977
- Pileaolaria spinifer Knight-Jones, 1978
- Pileolaria (Duplicaria) zibrowii see Vinearia zibrowii: Knight-Jones 1978
- Pileolaria (Jugaria) atlantica see Bushiella (Jugaria) atlantica: Knight-Jones 1978
- Pileolaria (Nidularia) nidica see Nidificaria nidica: Knight-Jones 1978
- Pileolaria (Nidularia) palliata see Nidificaria palliata: Knight-Jones 1978
- Pileolaria (P.) granulata see Bushiella (Jugaria) granulata: Thorp 1975
- *Pileolaria berkeleyana* (Rioja, 1942) sensu lato This species currently considered as cosmopolitan, is probably a complex of sibling species that includes *Pileolaria berkeleyana* sensu stricto, *Pileolaria rosepigmentata* Uchida, 1971 and some others. This problem has been studied (Rzhavsky unpubl.)
- Pileolaria cf. militaris The species of Pileolaria described by Salensky (1882) is probably Pileolaria militaris
- Pileolaria daijonesi Knight-Jones, 1972
- Pileolaria dakarensis Knight-Jones, 1978
- Pileolaria lateralis Knight-Jones, 1978
- Pileolaria marginata Knight-Jones, 1978
- Pileolaria militaris Claparède, 1868
- Pileolaria moerchi (Levinsen, 1883)
- Pileolaria pseudoclavus Vine, 1972
- Pileolaria pseudomilitaris, Pileolaria (Simplicaria) pseudomilitaris see Simplaria pseudomilitaris: Beckwitt 1982, Knight-Jones et al. 1974
- *Pileolaria rosepigmentata* Uchida, 1971 is currently synonymised with *Pileolaria berkeleyana* (Rioja, 1942) by Thorp et al. 1986. However, the validity of this species is currently being re-examined (Rzhavsky unpubl.)
- Pileolaria sp. 1 (connexa) Rzhavsky & Knight-Jones, 2000
- Pileolaria sp. 2 (invultuosa) Rzhavsky & Knight-Jones, 2000
- Pileolaria sp. see Pileolaria cf. militaris: Salensky 1882
- Pileolaria tiarata Knight-Jones, 1978
- Pillaiospira trifurcata (Knight-Jones, 1973)
- Protolaeospira (Dextralia) stalagmia Knight-Jones & Walker, 1972
- Protolaeospira (P.) canina see Protolaeospira (P.) tricostalis: Knight-Jones 1973
- Protolaeospira (P.) pedalis Knight-Jones & Knight-Jones, 1994
- Protolaeospira (P.) striata Quievreux, 1963
- Protolaeospira (P.) tricostalis (Lamarck, 1818)
- Protolaeospira (P.) triflabellis Knight-Jones, 1973
- Protolaeospira (P.) eximia (Bush, 1905)
- Protoleodora uschakovi Knight-Jones, 1984
- Romanchella quadricostalis Knight-Jones, 1973

- Romanchella scoresbyi (Harris, 1969)
- Romanchella solea Vine, 1977
- Romanchella pustulata Knight-Jones, 1978
- Simplaria potswaldi (Knight-Jones, 1978)
- Simplaria pseudomilitaris (Thiriot-Quievreux, 1965)
- Spirorbis (S.) strigatus Knight-Jones, 1978
- Spirorbis (S.) bifurcatus Knight-Jones, 1978
- Spirorbis (S.) corallinae de Silva & Knight-Jones, 1962 see S. inornatus: Ryland 1972, Stebbing 1972. Since S. corallinae settle almost exclusively on calcareous alga Corallina officinalis, the above records of this species from Laminaria probably refer to Spirorbis inornatus.
- Spirorbis (S.) cuneatus Gee, 1964
- Spirorbis (S.) infundibulum Harris & Knight-Jones, 1964
- Spirorbis (S.) inornatus L'Hardy & Quievreux, 1962. This species is usually found on Laminaria
- Spirorbis (S.) rothlisbergi Knight-Jones, 1978
- Spirorbis (S.) rupestris Gee & Knight-Jones, 1962
- Spirorbis (S.) spatulatus Knight-Jones, 1978
- *Spirorbis (S.) spirorbis* (L, 1758) is often recorded as *S. borealis*. All records of "*spirorbis*" or "*borealis*" from *Fucus* in the intertidal zone of the Atlantic and Arctic European coast certainly belong to *S. (S.) spirorbis*.
- Spirorbis (S.) tridentatus Levinsen, 1883. Some earlier workers considered "tridentatus" as an operculumincubating variety of "Spirorbis granulatus", but later the name started to refer to the tubeincubating form.
- Spirorbis (Spirorbella) marioni see Spirorbis (S.) rothlisbergi: Rothlisberg 1974
- Spirorbis (Velorbis) gesae Knight-Jones & Knight-Jones, 1995
- Spirorbis alveolatus see Neodexiospira sp.: Sveshnikov 1967, Bagaveeva 1975
- Spirorbis ambilateralis see Protolaeospira (P.) eximia: Potswald 1967b.
- Spirorbis argutus see Neodexiospira cf. brasiliensis: Abe 1943. This species name is a nomen dubium that was assigned to one of Eulaeospira species.
- Spirorbis borealis or Spirorbis (Laeospira) borealis see Spirorbis (S.) spirorbis: Babbage & King 1970, Bergan 1953, Crisp & Ryland 1960, Dasgupta & Austin 1960, Doyle 1974, Fewkes 1885, Franzén 1956, 1970, Garbarini 1933, 1936a,b, Gee 1963a, 1964, 1965, 1967, Gee & Williams 1965, Knight-Jones 1951, 1953, King et al. 1969, Mackay & Doyle 1978, Meadows & Williams 1963, Nott 1973, Potswald 1969, 1972, de Silva 1962, 1967, Thorson 1946, Williams 1964, Wisely 1960
- Spirorbis borealis var. tridentatus see Spirorbis (S.) tridentatus: Franzén 1956, 1970
- Spirorbis convexis see Eulaeospira convexis: Wisely 1964
- Spirorbis corrugatus see Neodexiospira pseudocorrugata: Casanova 1954, Vuillemin 1965, Ghobashy & Selim 1979b
- Spirorbis granulatus see Bushiella sp.: Bergan 1953, Franzén 1956, 1970
- Spirorbis lamellosa see Neodexiospira lamellosa: Wisely 1964
- Spirorbis malardi see Paralaeospira malardi: Quievreux 1962
- Spirorbis militaris see Pileolaria militaris: Franzén 1958, 1970, Kiseleva 1957
- Spirorbis moerchi, Spirorbis (Laeospira) moerchi see Simplaria potswaldi: Potswald 1964, 1966, 1967a,b, 1968, 1969, 1977, 1978, 1981. The taxonomic status of some similar species, including *Pileolaria moerchi, Pileolaria berkeleyana*, and *Pileolaria rosepigmentata* have been recently studied (Rzhavsky unpubl.)
- Spirorbis nipponicus see Neodexiospira alveolata: Okuda 1946. Neodexiospira brasiliensis or any other Neodexiospira species can be also mis-identified as "Spirorbis nipponicus"
- Spirorbis pagenstecheri, Spirorbis (Janua) pagenstecheri see Janua pagenstecheri: Bergan 1953, Dasgupta & Austin 1960, Franzén 1958, 1970, Gee & Williams 1965, de Silva 1967, Stagni 1959, 1961, Stebbing 1972
- Spirorbis pusill/a(us) see Janua pagenstecheri: Kiseleva 1957, Hempelmann 1930

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Spirorbis pusilloides see Janua pagenstecheri: Thorp & Segrove 1975

Spirorbis scoresbyi see Romanchella scoresbyi: Harris 1969

Spirorbis spirillum, Spirorbis (Dexiospira) spirillum see Circeis spirillum: Potswald 1967b, see Circeis cf. armoricana: Bergan 1953, Dasgupta & Austin 1960, Dirnberger 1990, 1993, 1994, Okuda 1946, Potswald 1978, Sveshnikov 1967

Spirorbis vitreus or Spirorbis (Paradexiospira) vitreus see Paradexiospira (Spirorbides) vitrea: Bergan 1953, Franzén 1956, 1970, Potswald 1967b, 1978.

Vinearia zibrowii (Knight-Jones, 1978)

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LIFE-HISTORY PATTERNS IN SERPULIMORPH POLYCHAETES

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