Oceanography and Marine Biology

AN ANNUAL REVIEW

Volume 39

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Also available as a printed book
see title verso for ISBN details

OCEANOGRAPHY
and
MARINE BIOLOGY

AN ANNUAL REVIEW

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First published 2001
by Taylor & Francis
11 New Fetter Lane, London EC4P 4EE

Simultaneously published in the USA and Canada
by Taylor & Francis Inc,
29 West 35th Street, New York, NY 10001

Taylor & Francis is an imprint of the Taylor & Francis Group

This edition published in the Taylor & Francis e-Library, 2004.

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloging in Publication Data
A catalog record for this book has been requested

ISBN 0-203-24719-1 Master e-book ISBN

ISBN 0-203-22896-0 (Adobe eReader Format)
ISBN 0-415-23874-9 (Print Edition)

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PREFACE

The thirty-ninth volume of this series contains eight reviews written by an international array of authors. As usual, the reviews range widely in subject and taxonomic and geographic coverage. The majority of articles were solicited but the editors always welcome suggestions from potential authors for topics they consider could form the basis of appropriate contributions. Because an annual publication schedule necessarily places constraints on the timetable for submission, evaluation and acceptance of manuscripts, potential contributors are advised to make contact at an early stage of preparation so that the delay between submission and publication is minimised.

The editors again gratefully acknowledge the willingness and speed with which authors complied with the editors' suggestions, requests and questions and the efficiency of the copy editor and publishers in ensuring the regular annual appearance of each volume. This year has seen a further change in the editorial team and it is a pleasure to welcome Dr R.J.A. Atkinson as a co-editor for the series.

Oceanography and Marine Biology: an Annual Review 2001, **39**, 1–101

Taylor & Francis

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

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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 μm 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 hermaphroditism 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*.

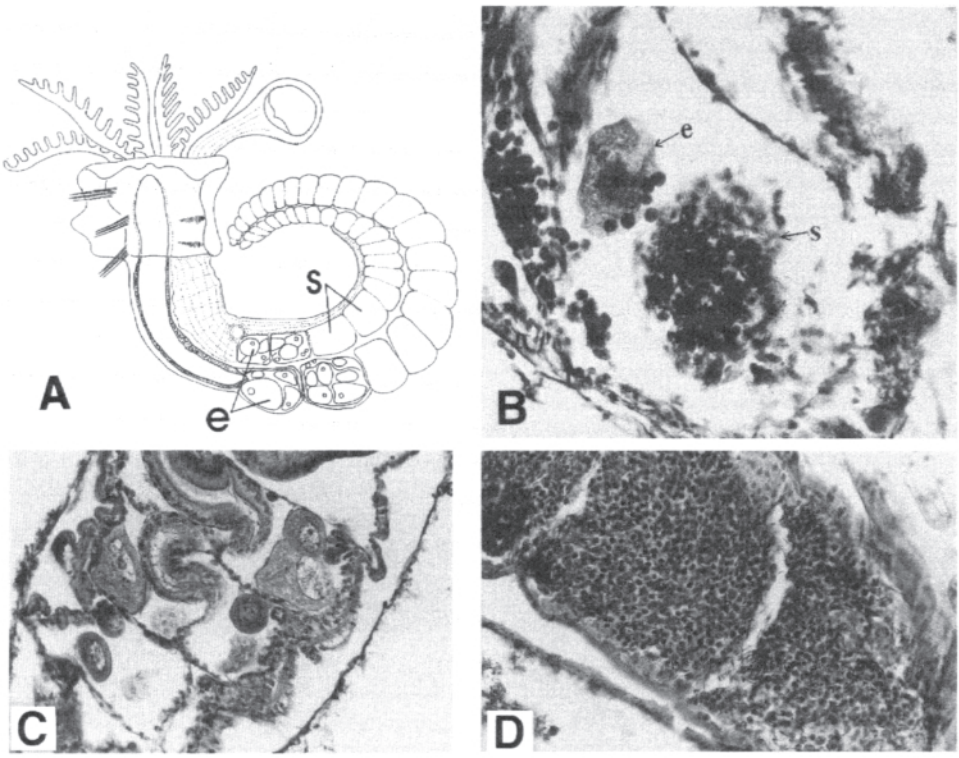

Figure 1 Simultaneous hermaphroditism in serpulids and spirorbids. A: *Spirorbis spirorbis,* schematic representation of female and male segments (after King et al. 1969 with permission of Cambridge University Press), e—eggs in female segments, s—sperm in male segments; B: *Salmacina dysteri,* histological 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

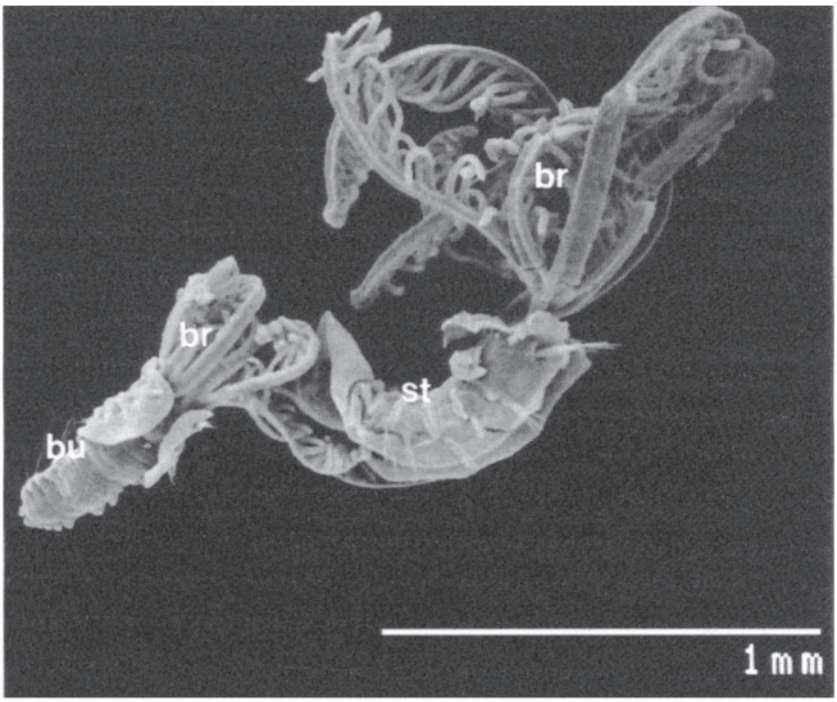

Figure 2 Asexual reproduction of *Salmacina dysteri* (scanning electron microphotograph). The asexual bud (bu) and parental worm (st) both have extended branchial crowns (br) (Nishi unpubl.). Scale: 1 mm.

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 vermicularis* 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 in

Table 1 Chromosome numbers of serpulids and spirorbids.

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 *Filograna* and *Salmacina*)	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; Palermo, Italy	Dasgupta & Austin 1960, 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 *P. lamarckii*	Dasgupta & Austin 1960
P. triqueter	12	24	Oslofjord, Norway	Jyssum 1957, Olsen 1970
Serpula vermicularis	7			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

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 μm 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 30000 (Leone 1970),

Table 2 Descriptive 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.

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
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		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 2 *continued*

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
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 1983
Marifugia cavatica	12						FS					Matjasic & Sket 1966
Microprotula ovicellata	5				80		BR	NF				Uchida 1978
Metavermilia cf. *ovata*							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

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

Table 2 *continued*

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
S. tetraceros		GH			60		FS	F		360	28	Gaikwad 1988
Vermiliopsis infundibulum–glandigera complex	10						FS					Nishi 1993
FAMILY SPIRORBIDAE												
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

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, Picard 1980
Neodexiospira alveolata	2.8	SM			140 × 160	40	BR			370		Okuda 1946
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

Table 2 *continued*

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
N. formosa	1‡	(SM)				8–12	BR	(NF)				Knight-Jones 1972, Knight-Jones et al. 1974
N. kayi	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
P. parallela	2	(SM)				About 10	BR	(NF)				Vine 1977
Romanchellinae												
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

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		Yes	About 30‡	BR	NF	300	Picard 1980, Quievreux 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	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

Table 2 *continued*

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)				2–4	BR	(NF)				Knight-Jones 1978

*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 600–180000. 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 1000–10000 (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 34000 at a salinity of 35 to 28000 at 25 and to 13000 at 15. Average fecundity of *H. dianthus* and *H. elegans* was similar at salinities $\geqslant$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 μm in *Ficopomatus miamiensis* (Lacalli 1976) and *Hydroides ezoensis* (Miura & Kajihara 1981, 1984) to 180–200 μm in *Chitinopoma serrula* (Dons 1933). Egg size in spirorbids ranges from 80 μm in *Neodexiospira foraminosa* (Nishi & Yamasu 1992d) to 230 μm 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

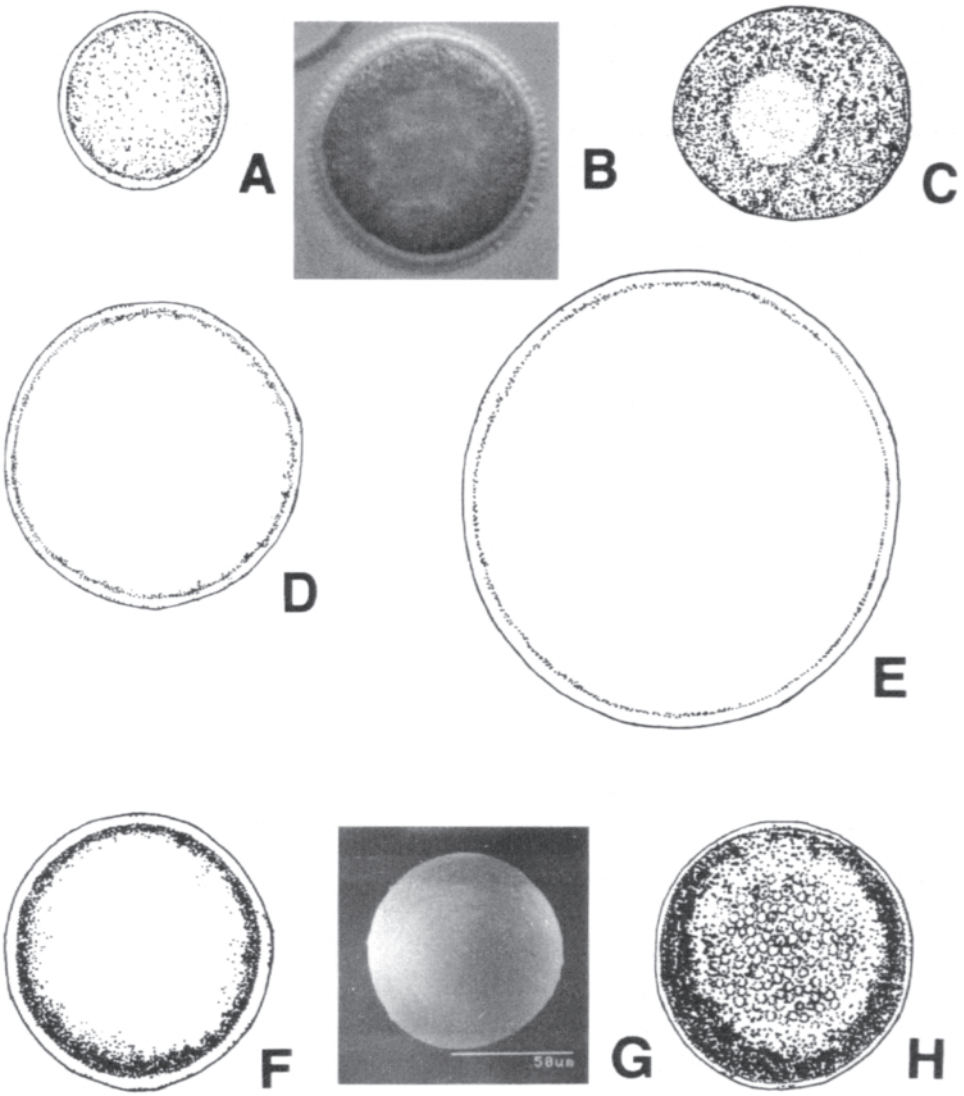

Figure 3 Eggs of serpulids and spirorbids. A: *Hydroides elegans* 50 µm (after Wisely 1958 by permission of CSIRO Australia); B: *Galeolaria hystrix,* 60 µm (Kupriyanova unpubl.); C: *Pomatoceros triqueter, 75* µm (after Segrove 1941); D: *Rhodopsis pusilla,* 90 µm (after Nishi & Yamasu 1992a); E: *Salmacina 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).

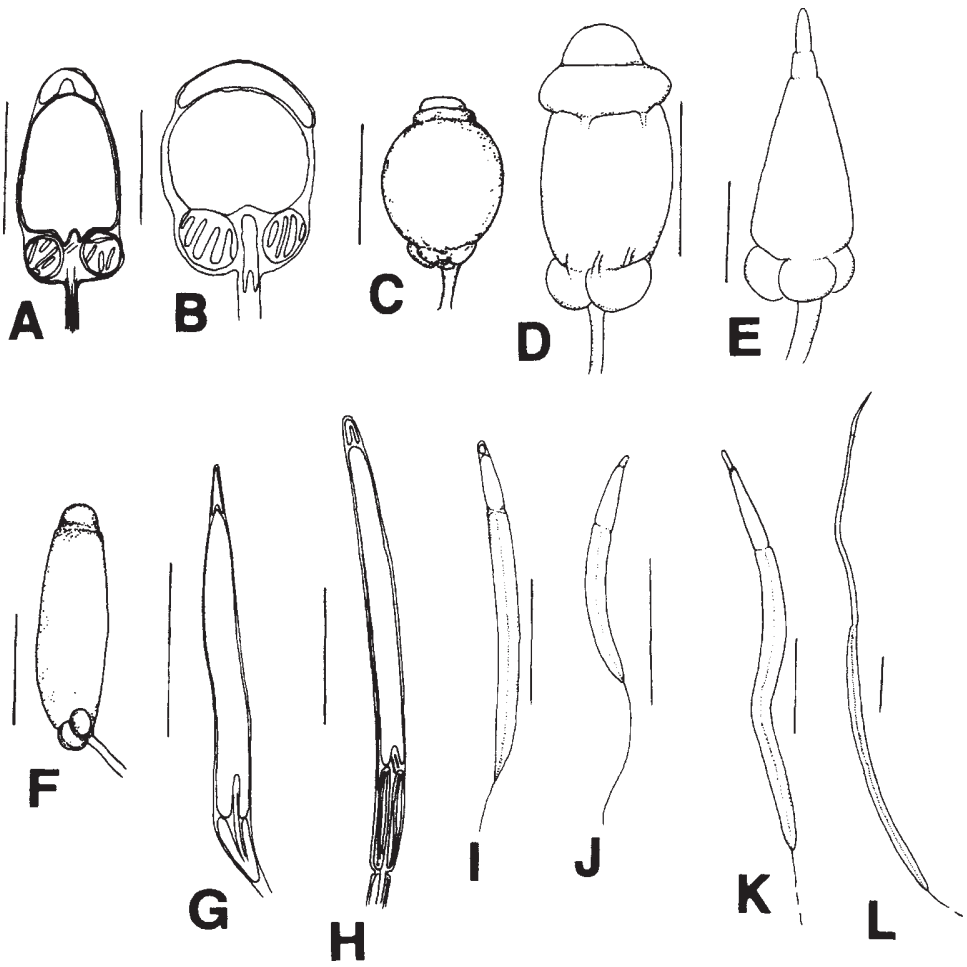

Figure 4 Sperm morphology of serpulimorph polychaetes. Broadcasting species, A: *Serpula* sp. (after Jamieson & Rouse 1989 with permission of Cambridge University Press); B: *Pomatoleios kraussi* (after Jamieson & Rouse 1989); C: *Spirobranchus giganteus corniculatus* (after Nishi 1992b); D: *Galeolaria 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.

are 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 (AlOgily & 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°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 co-ordinate 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. inornatus, 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 three-chaetiger 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,

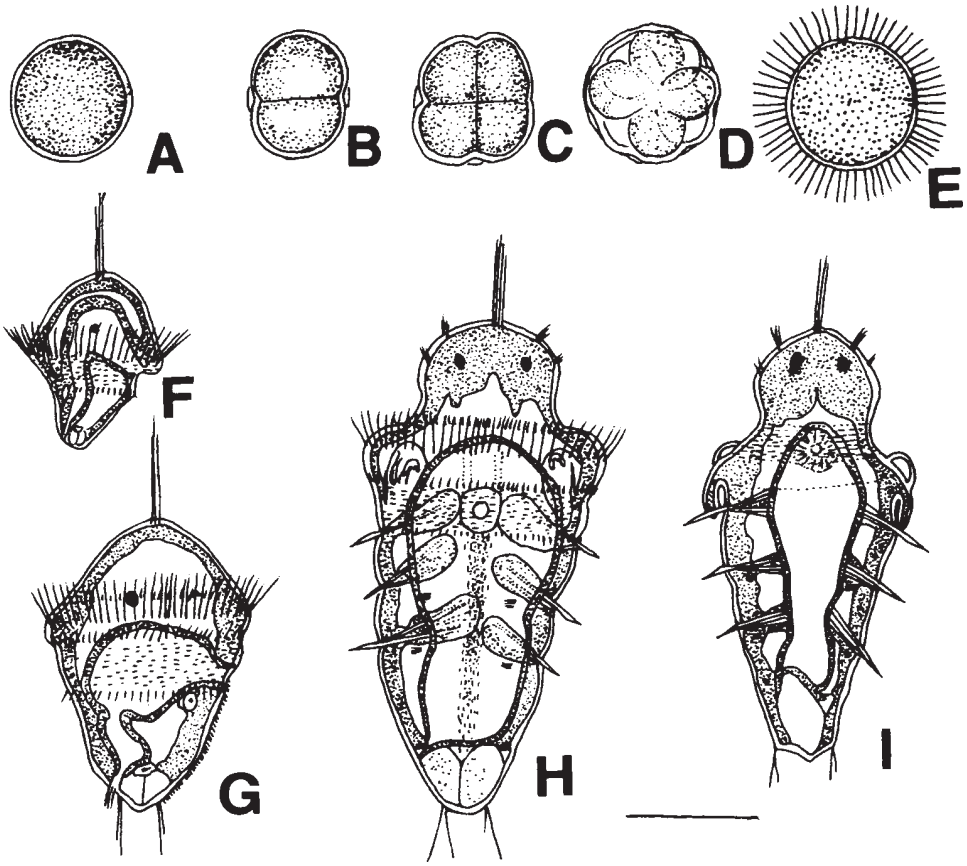

Figure 5 Development of serpulids with planktotrophic larvae. *Hydroides elegans* (after Wisely 1958 by permission of CSIRO Australia). A: egg, B: 2-cell stage; C: 4-cell stage; D: 8-cell stage; E: early trochophore, apical view; F: the same, lateral view; G: later metatrochophore, lateral view; H: 3-chaetiger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

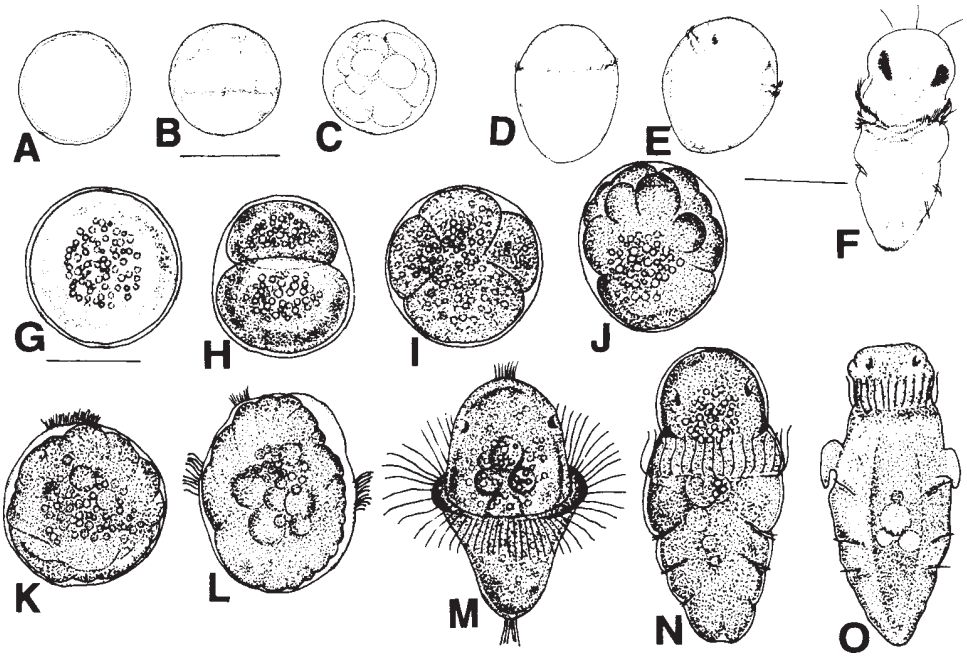

Figure 6 Development of serpulids with lecithotrophic larvae. Brooded larvae: *Salmacina dysteri,* development inside the adult tube, A: egg; B: 2-cell stage; C: late stage of cleavage; D and E: early trochophore; F: 3-chaetigerous competent larva (after Nishi & Yamasu 1992d). Planktonic larvae: *Protula* 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 dorsally.

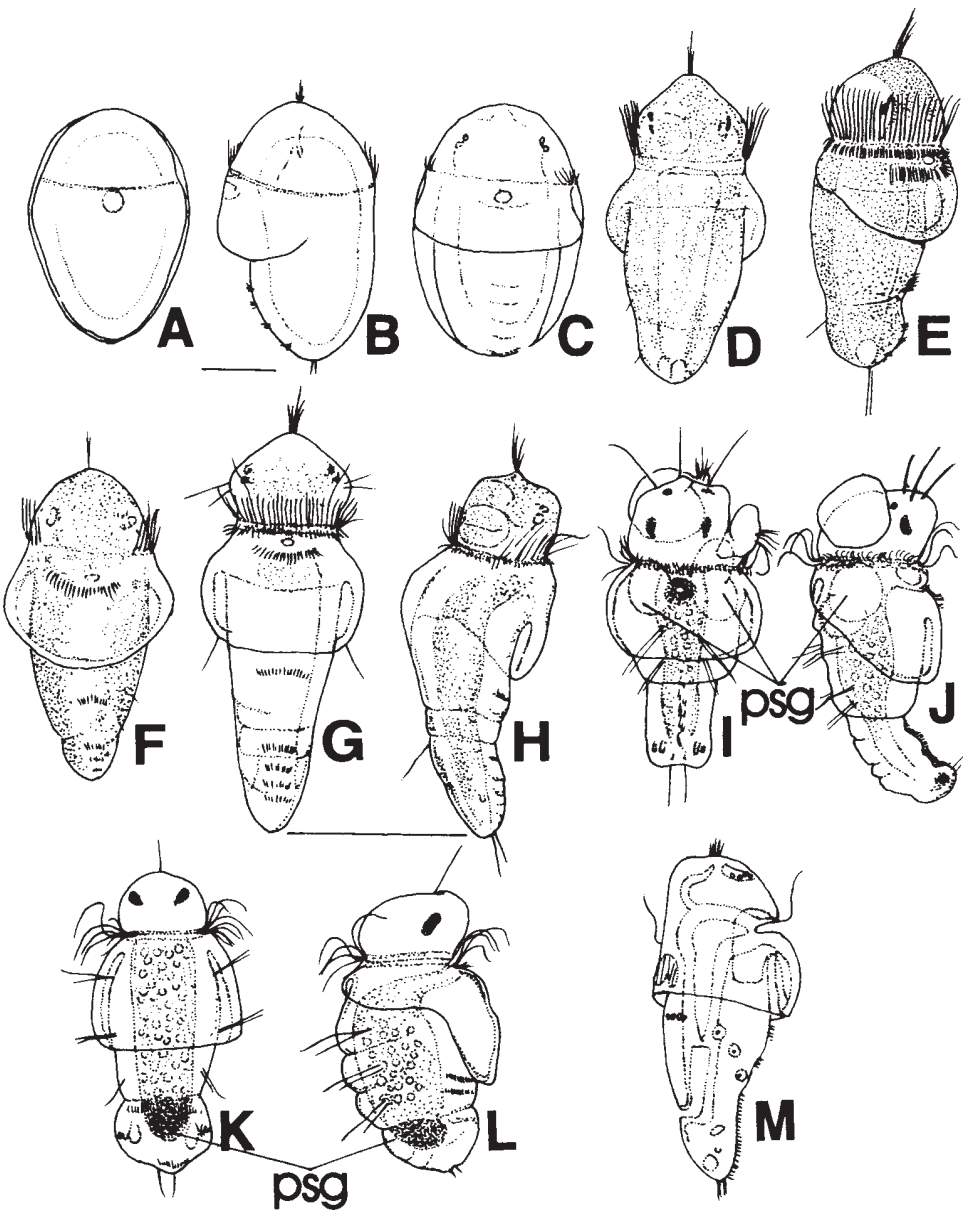

Figure 7 Development of spirorbid larvae. *Circeis* cf. *armoricana,* A: trochophores, ventral view; B and C: early metatrochophores, lateral and ventral views; D-F: late metatrochophores, dorsal, lateral, and ventral views; G: pre-release larva ventral view; H: swimming larva (no primary shell glands) 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.

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 newly-settled juvenile and reduced survival and settlement of *Hydroides elegans* (Qiu & Qian 1997). Paulay et al. (1985) demonstrated that larvae of *Serpula columbiana* grew significantly

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 pre-settlement 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 Ca^{2+}-free sea water, i.e. under conditions that interfere with the supply of external Ca^{2+}. They concluded that there is a Ca^{2+}-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 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 photorespouse

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