

Inken Kruse · Karsten Reise

Reproductive isolation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae) indicates sibling species in the North Sea

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Abstract Two distinct modes of development in the common polychaete *Scoloplos armiger* (O. F. Müller, 1776) occur in the North Sea region: holobenthic development in egg cocoons and pelagic larvae hatching from suspended eggs. In the northern Wadden Sea near the island of Sylt, we observed that egg cocoons are produced intertidally while pelagic larvae originate from the adjacent subtidal zone. A previous genetic comparison between these subtidal and intertidal populations revealed distinct gene pools, suggesting that reproductive differences are not phenotypic but heritable. In this study, crossbreeding experiments show that intertidal and subtidal populations are reproductively isolated. Couples with males and females from different habitats had no offspring. Production of egg cocoons is determined by female origin from the intertidal zone. Pelagic larvae occurred only in couples with subtidal females and subtidal males. Intertidal males have spermatozoa with heads twice as long as those from subtidal males and a significantly shorter flagellum. We suspect that deviating sperm morphology may cause the reproductive breakdown at the fertilization stage. Juveniles hatching from cocoons have shorter anal cirri compared to juveniles that metamorphosed from pelagic larvae. We conclude there to be two sympatric sibling species in *S. armiger*: 'type I' in intertidal areas, which have egg cocoons, no pelagic larvae, elongated sperm heads, shortened sperm flagella and anal cirri; and a subtidal 'type S', lacking egg cocoons but with pelagic larvae, short sperm heads, long sperm flagella and anal cirri.

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I. Kruse (✉) · K. Reise
Alfred-Wegener-Institut für Polar- und Meeresforschung,
Wattenmeerstation Sylt, 25992 List, Germany
E-mail: kruse@sb-roscoff.fr
Tel.: +33-2-98292323
Fax: +33-2-98292324

Present address: I. Kruse
EGPM, UMR-CNRS 7127, Station Biologique de Roscoff,
BP 74, 29682 Roscoff cedex, France

Introduction

In marine invertebrates, species are usually diagnosed by externally visible recognition marks using pictorial keys for identification. Problems with this arise when: (1) individuals within a species vary considerably in phenotype due to environmental factors during development; (2) speciation is incomplete with some gene exchange occurring along a cline between semispecies; or (3) there are sibling species which are identical or very similar in their morphological traits yet have no viable hybrids in nature (Mayr 1963; Dobzhansky et al. 1977; Ridley 1996).

How common sibling species are in the marine environment is unknown. Knowlton (1993), however, states that widely distributed species are frequently found to consist of distinguishable subspecies or siblings when examined in sufficient detail. Morphological comparisons have therefore been extended from the outer appearance to inner anatomy and ultrastructure and to include characteristics of juveniles or sperm. In some cases, a combination of several characters achieves a good separation of different taxa (McDonald et al. 1991). Particularly powerful has been the direct measurement of genetic distance and divergence. Crucial for the biospecies concept (Mayr 1942; Dobzhansky et al. 1977), however, are field and experimental data on reproductive isolation. Isolation mechanisms may be prezygotic, such as separation by habitat, season, mating behavior, and by gametes failing to attract each other or being unable to fuse. After zygote formation, hybrid sterility or nonviability may cause a reproductive breakdown (postzygotic isolation).

The polychaete *Scoloplos armiger* (O. F. Müller, 1776) is purported to be a cosmopolitan species known from all zoogeographic regions (Hartmann-Schröder 1996). It ranges from low salinities in the Baltic Sea to fully marine conditions, from the intertidal zone down to depths of 200 m in Norwegian fjords (Holte and Gulliksen 1998) and 2,000 m off Greenland (Wesenberg-Lund

1950) or off Japan (Annenkova 1938), and from tropical sites (Frith et al. 1976) to polar regions (Sveshnikov 1960). Beesley et al. (2000), however, doubted that *S. armiger* found around Australia and elsewhere in the world all belong to the same species. In the eastern North Atlantic, two developmental types have been reported: (1) holobenthic development in egg cocoons in the intertidal zone (Gibbs 1968 and references therein); and (2) pelagic larvae in open water (Banse 1955; Sveshnikov 1960; Giere 1968; Bosselmann 1991; Plate and Husemann 1991). After comparing descriptions of both *S. armiger* larval types from the Atlantic (Anderson 1959) and the White Sea (Sveshnikov 1960) with those of Orbiniidae from California, Blake (1980) suspected sibling species or misidentification in *S. armiger*. He noted that holobenthic larvae of *S. armiger* more closely resemble those of *Leitoscoloplos pugettensis* than pelagic *S. armiger* larvae and that the latter are more similar to the larvae of *S. acmeceps* than to holobenthic *S. armiger* larvae.

Our own observations near the island of Sylt in the eastern North Sea revealed that holobenthic development in egg cocoons is confined to intertidal habitats, while pelagic larvae originate from adjacent subtidal areas. Adjacent intertidal and subtidal gene pools have a greater genetic distance than do gene pools from within these habitats over a wider area (Kruse et al. 2003). This suggests that there may be two species of *Scoloplos* in the North Sea, separated by habitat and by their mode of development.

The aim of this study is to test for reproductive isolation using crossbreeding experiments, coupling mates from adjacent intertidal and subtidal sediments and comparing results of couples from within or between the two habitats. Evidence of sufficient reproductive isolation to prevent all or most gene exchange would provide further evidence for the existence of two sibling species within *S. armiger*. A clarification of the species status is of some interest because not only is *S. armiger* widespread and one of the most dominant members of the macrofauna in soft-sediments of the eastern North Atlantic (e.g. Stripp 1969; Beukema 1976; Ziegelmeier 1978; Olenin and Schiedek 1996) but also this case could show that the lower tide line suffices as a divide for speciation.

Materials and methods

Study area

Scoloplos armiger was collected in the Sylt-Rømø Bight, a tidal basin in the North Sea (Fig. 1). The bight is part of a continuous tidal area extending over 500 km of coastline, called the Wadden Sea. Tides are semidiurnal with a range of about 2 m. The Sylt-Rømø Bight covers about 400 km², of which 33% belong to the intertidal zone, 57% is shallow subtidal habitat (< 5 m depth) and 10% consists of deeper tidal channels (max. depth ~ 40 m). Exchange of water between the Sylt-Rømø Bight and the open North Sea takes place through a 2.8-km-wide tidal channel. More information about the area was given in Gätje and Reise (1998).

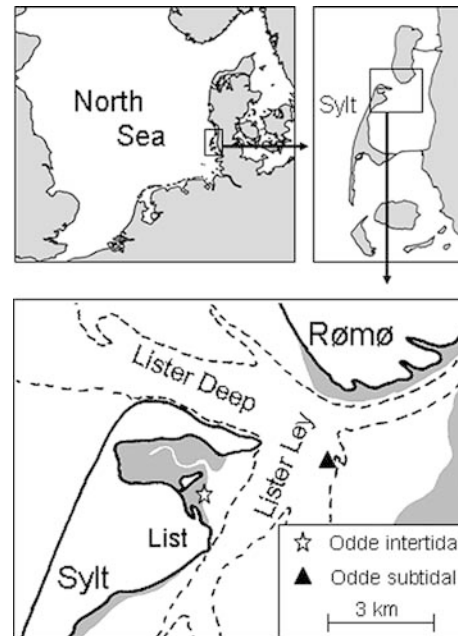


Fig. 1 Intertidal and subtidal sampling sites at location “Odde” in the North of the island of Sylt, North Sea

S. armiger was collected at intertidal or subtidal sites at location “Odde” (Fig. 1) for crossbreeding experiments and for comparison of spermatozoa. The subtidal position was at 55° 1.47' N, 8° 27.98' E; the intertidal position was at 55° 1.09' N, 8° 26.00' E. The location “Odde” refers to earlier genetic studies on *S. armiger* (Kruse et al. 2003).

Crossbreeding experiments

To investigate interbreeding of intertidal and subtidal *S. armiger*, one male and one female from the same habitat or different habitat (subtidal or intertidal) were placed together in aquaria (21.5 cm×10.5 cm×23 cm). Reciprocal crosses between habitats and crosses within habitats were replicated seven times. Additionally, seven intertidal females were cultured in isolation. Worms were collected in the field prior to the spawning season in February, when gonads are ripe and males and females are easily distinguishable. Subtidal specimens were sampled from a research vessel at 5 m water depth and 3 km from where intertidal specimens were collected. These sampling sites at location “Odde” refer to earlier genetic studies on *S. armiger* (Kruse et al. 2003). The experiment was set up on 3 March 2000. All 35 aquaria contained 4.5 cm sediment from the subtidal habitat, which was sieved through 1-mm meshes and covered with 14 cm seawater, filtered through a 40-µm mesh. Aquaria were aerated and subject to artificial light in day-night rhythm (14 h light and 10 h darkness). Temperature was first adjusted to the current water temperature in the field (5°C) and then gradually raised to 14°C over a period of 7 days. Each day, deposition of egg cocoons was controlled. Occurrence of pelagic larvae and eggs was recorded by sampling the water column every 3rd day, using a tube to take a 3-l water sample from each aquarium and filtering it through an 80-µm mesh. Water was replaced by new 40-µm-filtered seawater. Three weeks after no more spawning could be observed, the occurrence of benthic larvae was examined. The sediment surface of the aquaria was sampled by sucking up the upper few millimeters using a tube of 6 mm width. Juvenile worms were extracted by shaking this sediment with added seawater within a beaker and decanting the supernatant water, with suspended sediment, through an 80-µm mesh. The residue in the sieve was examined for larvae using a dissecting microscope.

Sperm morphology

After the crossing experiment ended on 22 March 2002, male *S. armiger* were used for comparison of spermatozoa from intertidal and subtidal specimens. Three males with ripe gametes of each habitat were harvested from the experiments. Additional males with ripe spermatozoa were collected in the field at the sites already sampled for the crossbreeding experiment. The intertidal site was sampled on 24 March 2002, harvesting 10 unspawned worms; the subtidal site was sampled on 28 March 2002, when 6 unspawned males were collected.

Spermatozoa of all males were gained by tapping their body walls. Morphology of spermatozoa was examined by immersion light microscope and by scanning electron microscope (SEM). For the latter, spermatozoa were fixed with 2.5% glutaraldehyde in sea water and dehydrated with 30%, 50% and 70% ethanol in sea water. Using a vacuum pump they were put on membrane filters (Nucleopore), laid in an acidified dimethoxypropane (DMP) bath for 30 min (0.1 ml concentrated HCl per 100 ml DMP) and then transferred to neutral DMP for 2 days until the DMP had evaporated. Filters were then glued onto aluminium stubs and sputtered with gold-palladium using a BAL-TEC SCD 50. Spermatozoa were examined and pictures taken using a Zeiss DSM 940 SEM. Heads and flagella were measured from SEM photos of five sperm from each male from the intertidal and subtidal habitats.

Length of anal cirri

Juvenile *S. armiger* of early benthic stages raised in laboratory cultures were noted to differ in length of anal cirri depending on mode of development (i.e. holobenthic or pelagic). Samples of worms were collected on 16 May 1998 when strong easterly winds caused an extraordinary exposure of the subtidal habitat, allowing access. The subtidal sample site (55° 1.09' N, 8° 26.06' E) was 700 m northeast of the intertidal site (55° 1.85' N, 8° 25.82' E) and 0.8 m below spring low tide level. Anal cirri of the worms from the two habitats were systematically compared under a microscope (magnification 200–400).

Anal cirri of 50 intertidal and 45 subtidal juvenile *S. armiger* were measured after worms were anesthetized with magnesium chloride (8% in sea water) and placed on microscope slides. *S. armiger* has two anal cirri of equal length. Only specimens with both anal cirri of equal length were included in the analysis. Developmental stage of individuals was determined by counting setigers of the juveniles to ensure that equal size groups of intertidal and subtidal habitat were compared.

Results

Crossing experiments

Only couples where male and female came from the same habitat produced viable offspring (Fig. 2, where symbols are as follows:



egg cocoon;



pelagic larvae;



benthic juveniles). Egg cocoons were produced by intertidal parents in five out of seven replicates, giving

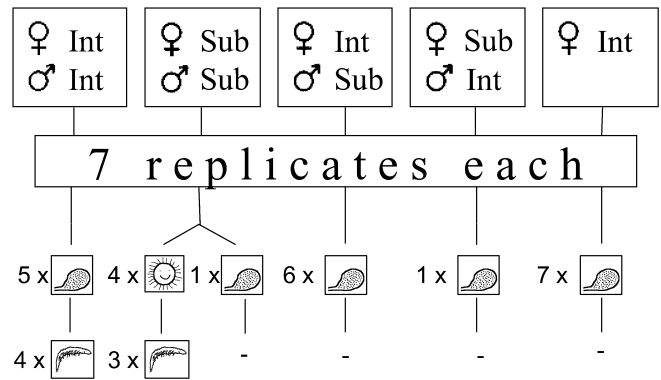


Fig. 2 Crossbreeding experiment with couples consisting of one male and one female of *Scoloplos armiger* from different habitats and the same habitat. Each combination was replicated seven times. In the third and fourth rows, results are indicated by symbols with numbers showing replicates with reproductive output. *Int* intertidal specimen, *Sub* subtidal specimen

rise to benthic juveniles in four replicates. The eggs in the cocoons turned from orange to the brown color of hatching juveniles. Pelagic larvae were recorded in four of seven replicates from subtidal parents, developing to benthic juveniles in three replicates. In mixed couples, with specimens from different habitats, no viable pelagic larvae could be raised. In crosses with intertidal females and subtidal males, egg cocoons were produced in six replicates, but several days after being spawned, the eggs decayed. Under a dissecting microscope the eggs appeared paler and inflated compared to those from intertidal couples. The eggs turned from orange to pale pink, presumably indicating bacterial infection. The eggs produced by the seven intertidal females kept on their own suffered the same fate.

The females from the intertidal habitat produced egg cocoons only. Two females from the subtidal site also spawned egg cocoons, where eggs decayed. In the experiment, egg cocoons were spawned from 11 March to 29 March; eggs were shed into the water from 27 March to 4 April.

The experimental set-up was maintained. In March of the following year a second spawning was observed. All spawning females maintained their egg spawning behavior. Seventeen females of the intertidal, which had spawned egg cocoons did so again and one female that had spawned pelagic larvae did so again.

Spermatozoa

Intertidal and subtidal *Scoloplos armiger* show remarkable differences in spermatozoa morphology. Sperms of subtidal worms have significantly shorter heads (sperm head length $3.6 \pm 0.1 \mu\text{m}$) than sperms of intertidal specimens ($8.2 \pm 0.3 \mu\text{m}$), where sperm heads have elongated nuclei (Fig. 3) ($n=5$, t -test, $P < 0.01$). Additionally, sperm flagella of subtidal *S. armiger* were longer ($61.5 \pm 1.2 \mu\text{m}$) than those of intertidal origin ($52.9 \pm 4.7 \mu\text{m}$) ($n=5$, t -test, $P < 0.01$). Sperm of all the

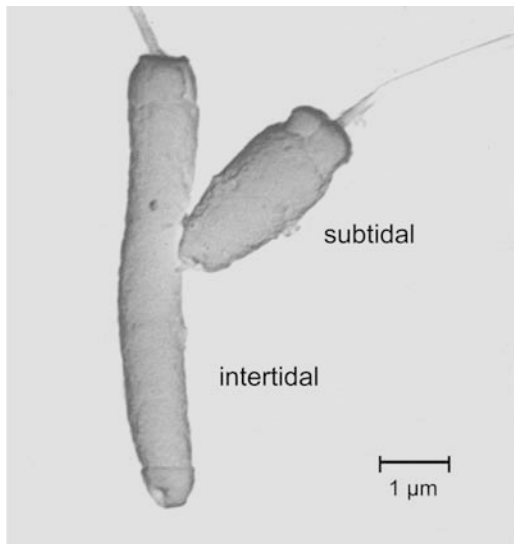


Fig. 3 Sperm heads of intertidal (*left*) and subtidal (*right*) males of *S. armiger*. Intertidal male sperm has an elongated nucleus more than twice as long as the subtidal sperm

examined males, 13 from the intertidal and 9 from the subtidal site, looked the same within each habitat.

Anal cirri length of subtidal and intertidal benthic juveniles

Subtidal benthic juveniles of *S. armiger* had longer anal cirri ($25.2 \pm 10.8 \mu\text{m}$) than juveniles from the intertidal habitat ($9.8 \pm 3.1 \mu\text{m}$) (Figs. 4 and 5a, b). At 95% confidence limits, regression lines showed no overlap (the equation for intertidal specimens was $y = 1.759 + 0.34x + \text{eps}$; for subtidal specimens, $y = 8.025 + 0.69x + \text{eps}$). Compared juveniles had the same setiger

Fig. 4 Length of anal cirri plotted against the number of setigers of benthic juveniles from intertidal ($n = 50$) and subtidal ($n = 45$) habitat

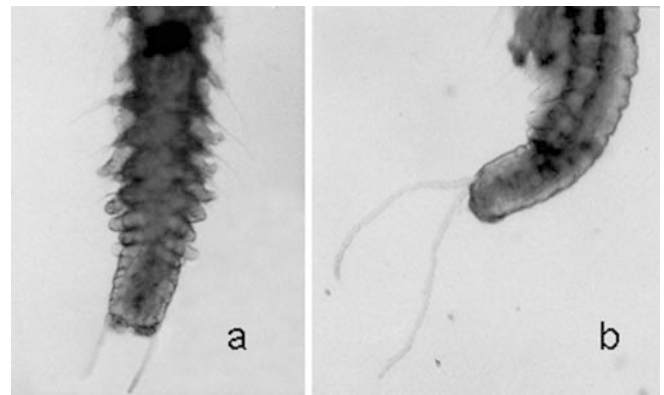
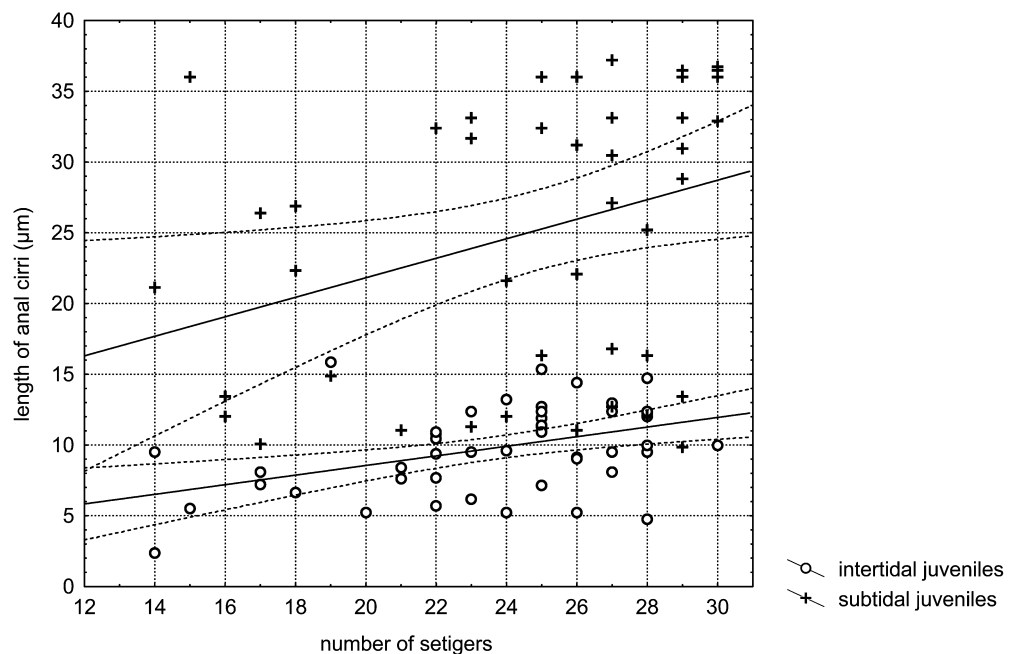


Fig. 5a, b Anal cirri at posterior ends of benthic juveniles, visible as filamentous appendices below. **a** Intertidal specimen. **b** Subtidal specimen. Both juveniles are at the 17 setiger stage

number and there was no significant difference between intertidal (24 ± 4 setigers) and subtidal *S. armiger* (25 ± 7 setigers) (t -test, $P > 0.1$). Worm size differences and length of anal cirri between intertidal and subtidal habitats were analysed using STATISTICA 5.1. Heterogeneous variances were log-transformed.

Discussion

Proof of reproductive isolation

The crossbreeding experiment between intertidal and subtidal *Scoloplos armiger* suggests complete reproductive isolation because between-habitat couples lacked offspring while within-habitat couples produced benthic juveniles and pelagic larvae, respectively. The experiment simulated subtidal conditions. Nevertheless,

intertidal females produced egg cocoons. This rejects the possibility of a phenotypic switch in reproductive mode induced by tidal exposure.

On the other hand, two females of subtidal origin produced egg cocoons, one in the presence of an intertidal male. If this female were of intertidal origin, the eggs should have been fertilized and should have developed into viable larvae. No explanation can be provided for the observed failure. Similarly, there was a failure of larval development in one of the egg cocoons in an intertidal-intertidal crossing. Possibly laboratory conditions were unfavorable for further development or we misclassified some individuals. We assume that our operational categories of intertidal and subtidal worms defined by their occurrence at two respective sites has its limits. Although egg cocoons are anchored in the sediment and juveniles hatch through the vertical stalks directly into subsurface sediment, which may help to keep worms within the narrow tidal zone (Gibbs 1968; Reise 1979), resuspension and subsequent drift of benthic juveniles with tidal currents has been recorded during phases of strong wave action (Armonies 1994, 1998). With respect to the propagules of the subtidal *S. armiger*, no mechanism is known by which pelagic larvae could avoid settlement in the intertidal zone. Thus we expect the lower tide line to be a permeable borderline allowing for some overlap in occurrence between intertidal and subtidal *S. armiger*. Consequently, there was no guarantee that all experimental worms belonged to the designated categories. However, the complete lack of offspring out of the six egg cocoons in the cross between intertidal female and subtidal male compared with the emergence of viable larvae in four replicates in the intertidal-intertidal cross allows us to conclude that reproductive isolation between intertidal and subtidal *S. armiger* exists. Infertility in couples of mates from different habitats was shown in spite of a potential mix-up of intertidal and subtidal population, which is conservative in respect to the hypothesis being tested.

Intertidal females also produced egg cocoons when kept alone and in the presence of subtidal males. Apparently these eggs remained unfertilized. Thus, there is no indication of parthenogenesis, and ripe females may simply have to get rid of the egg load in absence of males by spawning in an ordinary way. Worms surviving the spawning season spawned again in the next year and stuck to the original mode of reproduction. This corroborates respective inferences from field data (Gibbs 1968) that individuals may spawn in more than one season, and provides additional support for the view that the mode of reproduction is inherited and not triggered by environmental conditions prevalent during gonad development.

How is reproductive isolation achieved?

Intertidal and adjacent subtidal *S. armiger* may often get into contact with each other, and there is no sign of a

temporal mismatch in spawning time. A behavioral mismatch may be likely. Weber (1992) observed intertidal males and females in the same burrow tube when egg cocoons are produced, and Chapman (1965) assumed that male and female *S. armiger* come together in a burrow so that the eggs are fertilized as they leave the nephridia of the female. Further, in the cocoon-spawning polychaete *Anaitides mucosa*, sperms and eggs are shed right after cocoon jelly has been secreted (Sach 1975), representing the only detailed observation on mating behavior, to our knowledge, of polychaetes that spawn egg cocoons. Subtidal males and females of *S. armiger* may not associate that closely, releasing sperms and eggs into the water column. However, this aspect needs further study.

The striking difference in sperm morphology originating from intertidal and subtidal males strongly suggests gametic isolation. Sperm morphology has been widely regarded as a valid means to separate sibling species from another (Franzén 1956; Rice and Simon 1980; Olive 1983; Pfannenstiel and Gruenig 1990). Among nine *Capitella*, *Capitomastus* and *Capitellides* species, significant differences were found in nucleus lengths (Eckelbarger and Grassle 1987). Representing a case similar to *S. armiger*, all these species differ strikingly in reproductive modes, while they are hard to distinguish morphologically. Variations in sperm dimensions were quite low within the species but overlap within the genera. According to Jamieson and Rouse (1989), elongation of the nucleus is a common evolutionary trend in polychaete sperm related to a close association of male and female during sperm transfer. Intertidal *S. armiger* support this model. Correspondingly, the short nucleus and long flagella in the sperm of subtidal *S. armiger* suggests fertilization in the water column. A similar correspondence between sperm morphology and mode of reproduction is known from the siblings *Platynereis dumerilii*, which has short-headed spermatozoa and releases gametes into the water, and *P. massiliensis*, which has long-headed spermatozoa and spawns within a brooding tube (Pfannenstiel et al. 1987).

Two sibling species in *S. armiger* in the North Sea

Based on habitat separation and distinct gene pools (Kruse et al. 2003), contrasting mode of reproduction, lack of viable hybrids in crossbreeding experiments, differences in sperm shape and in anal cirri length of juveniles, though adult morphology reveals no other differential characters, we suggest the existence of two sympatric sibling species termed *S. armiger* 'type I' dwelling in the intertidal and 'type S' in the adjacent subtidal zone of the North Sea.

The geographic ranges of these siblings still need to be investigated. Reports of egg cocoon occurrence of *S. armiger* in the literature are restricted mainly to the soft bottom intertidal of the North Sea region (e.g. Schultz 1855; De Groot 1907; Thamdrup 1935; Gibbs 1968), and

adjacent waters [for the English Channel, see Prenant in Cabioch et al. (1968); for the Irish Sea see Hornell (1891); and for the Kattegat, which is the transition zone between the North Sea and the Baltic Sea and lacks an extended intertidal zone, see Rasmussen (1973)]. From the Baltic, Mau (1882) reports short sperm heads (3.9 µm) and Banse (1955) mentions pelagic larvae. From the Skagerrak, Franzén (1956) depicts *S. armiger* sperm with a short, spherical head. Presumably all these may belong to our 'type S'. Outside the North Sea, pelagic larvae of *S. armiger* have been reported from the White Sea (Sveshnikov 1960).

Further investigation is needed to decide if *S. armiger* 'type I' and 'type S' have separated within the North Sea region and if they speciated in allopatry or in sympatry, a distributional situation which is present in the Wadden Sea. If sympatric speciation has occurred, the question is whether the lower tide line suffices as a dividing barrier for a speciation process. However, in face of the cosmopolitan distribution of *S. armiger*, the many siblings in *Capitella* (Grassle and Grassle 1976) may serve as a warning against the assumption that all *S. armiger* without egg cocoons belong to a single species.

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