The role of ecological divergence in speciation between intertidal and subtidal *Scoloplos armiger* (Polychaeta, Orbiniidae)

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**Abstract**

The concept of ecological speciation implies that habitat differences may split a species by strong selection and rapid adaptation even under sympatric conditions. Studies on the polychaete *Scoloplos armiger* in the Wadden Sea (North Sea) indicate sibling species existing in sympatry: the intertidal ‘Type I’ with holobenthic development out of egg cocoons and the subtidal ‘Type S’ producing pelagic larvae. In the current study, Types I and S are compared in habitat-related traits of reproductive timing and physiological response to hypoxia and sulphide. Spawnings of Type I and Type S recorded over six years overlap in spring and both appear to be triggered by a rise in seawater temperature above 5 °C. Type S exhibits an additional autumn spawning (at seawater temperatures around 10 °C) which was previously unknown and is absent in Type I. The overall abundance of pelagic larvae in the Wadden Sea is higher in spring than in autumn. Tolerance of both sulphide and hypoxia was lower in Type S than in Type I. This correlates with a 5 to 10-fold lower sulphide concentration in the subtidal compared to the intertidal habitat. Physiological tolerance and divergence in developmental mode appear as traits which may have led to reproductive isolation between Type I and Type S. Their role in allopatric and sympatric speciation scenarios in *S. armiger* is discussed. Since the pelagic dispersal mode has been neglected so far, a reassessment of population dynamics models for *S. armiger* is suggested.

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**Keywords:** Sibling species; Speciation; Sulphide; Hypoxia; Pelagic larvae; Reproductive timing; Germany; North Sea; Wadden Sea

**1. Introduction**

In cases of suspected speciation, elucidation of the ecological background of diverging populations may reveal pathways fundamental to the speciation process. Currently, this approach is making a comeback, reviving the ecological speciation model (Morell, 1999; Schluter, 2001). According to this model, the barriers that cause new species to originate can be ecological rather than geographic and selection may be paramount. A particular selective factor is assumed to push two populations down separate evolutionary paths.

The polychaete *Scoloplos armiger* (O. F. Müller, 1776) is one of the most common macrofauna species of the eastern North Atlantic with purported cosmopolitan occurrence in all zoogeographic regions (Hartmann-Schröder, 1996). With its global distribution *S.*
armiger populates environments as different as the tropics and the Arctic, low and high salinities, intertidal and deep-sea habitats. However, on a small scale within the Wadden Sea, significant divergence between intertidal and subtidal S. armiger has been discovered leading to the suggestion that here, two sympatric sibling species exist: the intertidal species named ‘Type I’ and the subtidal species named ‘Type S’ (Kruse, 2003; Kruse and Reise, 2003; Kruse et al., 2003). Accordingly, traits distinguishing the two types are (1) mode of development which is holobenthic in egg cocoons in the intertidal zone and pelagic for subtidal specimens, (2) genetic markers, (3) morphology of spermatozoa and anal cirri and (4) an unknown divergence leading to reproductive isolation in a crossbreeding experiment. The present paper investigates whether ecological barriers can be responsible for speciation in this area. It examines the existence of reproductive barriers in the field, and laboratory experiments were carried out to study a possible difference in physiological response.

Analysis of ecological divergence indicated the existence of several other polychaete sibling species. Reproductive timing (Healy and Wells, 1959; Gibbs, 1971; Christie, 1982, 1985; Westheide and Rieger, 1987) and physiological responses (Mangum, 1963; Curtis, 1978; Rice and Simon, 1980; Gamenick et al., 1998b) have emerged as important diverging characteristics.

The pelagic mode of development was attributed to S. armiger only a decade ago by Plate and Husemann (1991), while an exclusively holobenthic development had been assumed before. As yet, only Plate and Husemann (1991) have provided information on seasonal larval occurrence in the plankton, solely referring to the island of Helgoland, North Sea. They found pelagic S. armiger larvae occurring for eight weeks between February and April in the course of three spring seasons. These larvae were of different developmental stages. They stayed in the water column for about 11 days and were lecithotrophic like their intertidal congeners. The existence of pelagic larvae implies a much higher dispersal potential for this species than proposed so far in assessments of population dynamics of S. armiger.

S. armiger is classified as a mobile, vagile, infraunal subsurface deposit feeder (Fauchauld and Jumars, 1979; Hongguang et al., 1995). The worms live in many types of sediment down to 15 cm depth and normally do not appear at the sediment surface. In the intertidal, S. armiger is exposed to diminished oxygen supply at low tide (Schöttler, 1980). Intertidal S. armiger are adapted to these conditions by producing energy via an anaerobic metabolism (Schöttler and Grieshaber, 1988); however, subtidal S. armiger have not been tested. Oxygen depletion and sulphide accumulation are correlated in that sulphide develops under hypoxic conditions in the sediment and is oxidised to non-toxic compounds in the presence of oxygen. The effect of sulphide, known to intensify the effect of hypoxia in invertebrates (Vismann, 1991; Grieshaber and Völk, 1998), has as yet not been tested in subtidal or intertidal S. armiger. Sulphide concentrations are higher in depositional systems like the intertidal where the finer organic material usually accumulates, and lower in the subtidal with stronger currents and less organic material (De Wilde and Beukema, 1984). These differences between habitats make hypoxia and sulphide tolerance one possible factor for divergent or disruptive selection during sympatric speciation in S. armiger. Oxygen depletion but also sulphide accumulation are regarded as key factors in the benthic environment (Giere, 1992).

The first part of this study is a plankton survey on S. armiger over six years (1996 to 2001) conducted in the Wadden Sea near the island of Sylt. Temporal occurrence of pelagic larvae will be compared with egg cocoon spawning in the intertidal. The second part of this study comprises an experimental comparison of tolerance to hypoxic and sulphidic environments in subtidal and intertidal S. armiger. The sediment of both habitats is characterised by its sulphide concentration, pH and grain size. In a final synthesis, we discuss possible scenarios for the speciation process of S. armiger Type I and Type S.

2. Materials and methods

2.1. 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
More details about the sampling method are given in Strasser and Günther (2001). Water temperatures are measured biweekly in an ongoing monitoring programme (Martens, 1995).

Plankton samples on a larger temporal and spatial scale were taken in 2000. The vertical stratification of larvae was assessed by sampling at three water depths (1, 5, 10 m) using a 9 dm$^3$ Niskin bottle at six sites along the Lister Ley gully (Fig. 1) during the spring spawning period; on 22 March at high and low tide, and on 24 March at low tide. Horizontal larval distribution was surveyed by comparing 35 dm$^3$ of surface water from each site on the same cruises as the vertical sampling. An additional sample was also taken for this purpose at high tide on 20 March. A survey of larval abundances on a larger temporal scale was performed on 30 successive tides (15 high tides and 15 low tides, night and day) between 20 and 28 March. For night-day comparisons only equivalent tides (high and low water) were compared and, accordingly, comparisons of high and low tide abundances were done only between night and between day samples. All plankton samples were sieved through a 80 μm mesh and the residue preserved in 2% formalin-seawater solution buffered with 10% hexamethylenetetramine.

Fig. 1. Plankton sampling sites with List harbour used for the long-term survey and six boat sites (denoted by triangles: northernmost site at 55° 02.64 N; 08° 28.00 E, southernmost site at 54° 00.31 N; 08° 25.81 E) and location ‘Odde’ in the northern part of the island of Sylt.

2.2. Sampling and field survey

Samples to record planktonic S. armiger larvae of Type S over the 6 years of study (1996–2001) were taken from the seaward end of the ferry landing pier close to List harbour. Larvae were obtained by sampling 10 dm$^3$ of surface water generally daily from March to October and weekly from November to February. Such a high temporal sampling resolution enabled us to detect even short spawning periods.
ated H$_2$S, dissociated HS$^-$ and S$^{2-}$, Sediment grain size in the intertidal and subtidal habitat was determined following Giere et al. (1988).

2.3. Tolerance to sulphidic and hypoxic conditions

The survival of subtidal and intertidal *S. armiger* under hypoxic, sulphidic and normoxic (control) conditions was studied in June 2000. For each experimental condition, eight specimens were incubated at room temperature in glass jars (Schott standard wide neck bottles of 250 cm$^3$) containing 3 cm of subtidal sediment and seawater. Each treatment was replicated three times. At the beginning of the experiments pH values were adjusted to 8.0 (using HCl, NaOH, HEPES buffer) and at the end they were determined again (start: 7.9, end: 7.5, mean: 7.7). Severe hypoxia was obtained by percolation with nitrogen for 1 h, which reduced the oxygen tension below the detection limits of polarographic oxygen electrodes (<1 μmol O$_2$ dm$^{-3}$, Gamenick et al., 1998a). The initial sulphide concentration of 220 μM in the sulphide treatment was achieved by addition of a 10 mM stock solution (made from Na$_2$S * 9H$_2$O crystals). Sulphide

![Graph showing abundances of pelagic *Scoloplos armiger* larvae at List harbour (columns) and water temperatures (lines) in 1996-2001; larval numbers and °C at the same scale.](image)

Fig. 2. Abundances of pelagic *Scoloplos armiger* larvae at List harbour (columns) and water temperatures (lines) in 1996–2001; larval numbers and °C at the same scale.
concentrations were measured at the beginning and the end of experiments, as described above (start: 223 μM, end: 168 μM, mean: 195 μM).

After insertion of the polychaetes, the jars were closed and submerged in a seawater bath which was permanently percolated with nitrogen to prevent influx of oxygen. Normoxic control replicates were kept in open jars in a water bath that was aerated with atmospheric air. Survival of the worms was recorded without removing the worms from the jars. Survival rates were assessed every two hours, after 33 h every hour, and after 49 h again every two hours until the end of the experiment. Worms were considered dead when no tactile response was observed after stirring. Hence, ‘mortality’ in the present paper refers to both anaesthetised and really dead worms. Mean sizes of the experimental worms were 1.52 mm (± 0.33) thorax width, ranging between 0.76 and 2.24 mm. There was no significant difference in worm sizes between treatments (t-test, p>0.05). Mean lethal time (LT50, i.e. the point in time or time span when four worms were dead) was determined for all treatments of the two types.

3. Results

3.1. Spawning

Pelagic S. armiger larvae were found both in spring and autumn of all years, with higher abundances in spring (Fig. 2). In contrast, intertidal S. armiger produced egg cocoons only in spring. The date of first high increase of egg cocoons usually fell within the period when pelagic larvae were present. In spring, pelagic larvae usually appeared in March, except for 1996 - after an exceptionally cold winter - when they appeared in April. In all years, peak larval abundances coincided with water temperatures around 5 °C. The maximum abundance recorded was 29 S. armiger larvae per 10 dm³ in spring. Autumn spawnsings occurred in October when the water temperature dropped to about 10 °C, with a maximum of 5 larvae per 10 dm³.

Plankton samples collected at a larger spatial scale support our belief that our long-term sampling from List harbour are representative of at least the water body in the Lister Ley gully. There was no significant difference in the number of pelagic larvae at three water depths (10, 5 and 1 m) (ANOVA, p>0.05; n = 18 for each water depth; means see Table 1). Mean larval abundances at the six Lister Ley sites of 4 sampling days (1.06 ± 0.73 larvae per 10 dm³) were not significantly different from the List harbour site (2.25 ± 2.3 larvae per 10 dm³) (t-test p>0.05, n = 4; means see Table 1). At a higher temporal resolution (15 successive high and low tides each), higher larval abundances were detected at night (Wilcoxon-test, p<0.05, n = 13 pairs; 9.1 ± 4.6 larvae per 10 dm³ at night compared to 5.2 ± 4.4 larvae per 10 dm³ during the day). There was no significant difference between

<table>
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<th>Table 1</th>
<th>Large-scale distribution of pelagic Scoloplos armiger larvae in mean abundances ± standard deviation</th>
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<tr>
<td>Water depth</td>
<td>Mean per 10 dm³ (± SD)</td>
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<td>m</td>
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<tr>
<td>1</td>
<td>1.4 ± 1.4</td>
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<tr>
<td>5</td>
<td>1.3 ± 1.3</td>
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<tr>
<td>10</td>
<td>1.3 ± 1.3</td>
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Vertical distribution defined by three water depths; horizontal distribution defined by six sites in Lister Ley, and one in List harbour.

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<th>Table 2</th>
<th>Abiotic sediment characteristics from subtidal and intertidal sites where Scoloplos armiger were sampled for hypoxia and sulphide tolerance experiments</th>
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<tr>
<td></td>
<td>Intertidal</td>
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<tr>
<td>Sulphide (μmol per dm⁻³)</td>
<td>mean</td>
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<td>April sediment depth:</td>
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<tr>
<td>5 cm</td>
<td>106.22</td>
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<tr>
<td>10 cm</td>
<td>98.73</td>
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<tr>
<td>15 cm</td>
<td>87.27</td>
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<td>June sediment depth:</td>
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<td>5 cm</td>
<td>70.10</td>
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<td>10 cm</td>
<td>78.69</td>
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<tr>
<td>pH</td>
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<td>QDI</td>
<td>0.81</td>
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<td>classification</td>
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<td>moderately sorted</td>
<td>medium sand</td>
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abundances at high tide (6.1 ± 4.8 larvae per 10 dm$^3$) and low tide (7.3 ± 4.9 larvae per 10 dm$^3$) (Wilcoxon-test, p>0.05, n = 13 pairs).

3.2. Abiotic sediment factors

In the field, sulphide concentrations in the intertidal were significantly higher, viz. between 5 and 10-fold, than at the subtidal sampling site. Higher sulphide concentrations were accompanied by lower pH (Table 2). Sediment grain size in the intertidal (moderately sorted medium sand) was similar to that in the subtidal, only a little coarser (moderately sorted fine sand) (Table 2).

3.3. Tolerance to sulphide and hypoxia

Experiments testing their tolerance to hypoxia showed that subtidal *S. armiger* were more sensitive.

![Graph](image-url)

Fig. 3. Experimental mean survival of subtidal and intertidal adult *Scoloplos armiger* subject to hypoxia (top graph) and hypoxia plus sulphide (bottom graph), ± SE; LT$^{50}$ indicated by dotted line (n = 3 jars with 8 individuals each for each experimental run).
than intertidal specimens. The $LT_{50}$ value for intertidal
$S. \text{armiger}$ exposed to hypoxic conditions was 46
h against 36 to 37 h for subtidal specimens (Fig. 3).
The first subtidal individual died after 21 h and the
first intertidal individual after 36 h. The last subtidal
individual died after 51 h and the last intertidal
individual after 61 h. Hypoxic and sulphidic condi­
tions in combination led to a $LT_{50}$ of 39 h for intertidal
$S. \text{armiger}$ and of 31–33 h for subtidal specimens
(Fig. 3). Under this treatment, the first subtidal indi­
vidual died after 19 h and the first intertidal individual
after 33 h. The last subtidal individual died after 39
h and the last intertidal individual after 47 h. Control
animals showed no mortality. Survival analysis using
significant differences between intertidal and subtidal
$S. \text{armiger}$ in both treatments (Wilcoxon-test of Chi­
squares, $p<0.05$).

4. Discussion

Populations inhabiting different environments may
exhibit differential adaptation either as a plastic re­
response or as genetic differences resulting from distinct
selection in the particular habitats. The latter seems to
be the case in intertidal and subtidal $Scoloplos \text{armiger}$,
where a species split-up has been suggested (Kruse et
al., 2003). Decision for a speciation scenario requires
elucidation of selective pressures in the two habitats. In
sympatric populations reproductive isolation may be
driven by selection when gene flow is not too high and
selective pressure is strong enough (Via, 2001). Dis­
ruptive selective pressures may be revealed from
population divergence in characteristics that are direct­
ly linked to habitat differences. Whether these charac­
teristics played the role of proximate or ultimate causes
in a speciation process needs to be decided in the
assessment of the overall species characteristics and
environment divergences.

4.1. Reproductive timing in Scoloplos armiger
colonising intertidal and subtidal habitats

Spawning asynchrony is a conspicuous difference
between many marine sibling species living in sympatry
(Knowlton, 1993) and between closely related
polychaetes (Giangrande, 1997). It may establish re­
productive isolation in a simple way while spawning is
most often triggered differently by different environ­
ments. However, our results show that spawning
asynchrony of intertidal and subtidal $S. \text{armiger}$ as
the cause of reproductive isolation is to be rejected.
Spring spawning of $S. \text{armiger}$ Type I and Type S
overlap temporally, which is the first report of both
Types occurring within one area. Earlier reports of
spawning periods of egg cocoons given by Gibbs
(1968) for Whitstable, east coast of Scotland, and for
pelagic larvae given by Plate and Husemann (1991) for
Helgoland are all consistent with our results, reporting
the period late February to April. Our results further
indicate that a rise in sea temperature above 5 °C is the
main trigger for spawning of pelagic larvae and seems
to be of significance also for the intertidal $S. \text{armiger}$
Type I (Wolff, 1973). Gibbs (1968) found egg cocoons
at Whitstable when the seawater temperature was
above 5 °C, but like Chapman (1965) also observed
increased spawning after spring tides.

In autumn, we registered a second spawning of
pelagic larvae. Giere (1968) found pelagic $S. \text{armiger}$
larvae in autumn in the North Sea and attributes these
to eroded stages from an autumn benthic spawning.
Smidt (1951) also suspects an autumn spawning after
finding 1–2 mm long juveniles in December. Since
egg cocoons of $S. \text{armiger}$ have not been reported in
autumn, the larvae seem to originate only from the
subtidal population. Thus, the absence of an autumn
spawning of egg cocoons by the intertidal population
represents a reproductive divergence from the subtidal
population. The adaptive value of the absence of a se­
cond spawning for intertidal $S. \text{armiger}$ Type I may be
avoidance of frost. Juveniles inhabit the upper sedi­
mens layer and would risk death by freezing when the
flats are exposed at low tide in winter. Only those spe­
cies of intertidal polychaetes that spawn in autumn
broadcast their juveniles into the subtidal or low interti­
dal, undertaking re-immigration to the upper intertidal
the next spring. $Arenicola \text{marina}$ is one prominent
example of such juvenile migration (Reise, 1985).

4.2. Tolerance to hypoxia and sulphide

Intertidal $S. \text{armiger}$ are, in contrast to subtidal
specimens, subject to hypoxia when tidal flats are
without oxygenated seawater during low tide. As
confirmed by our field data, hypoxia is mostly asso­
associated with free sulphide. Accordingly, intertidal *S. armiger* turned out to be better adapted to hypoxic and hypoxic plus sulphidic conditions in the experiment.

Tolerance of hypoxic conditions in intertidal *S. armiger* is based on their ability to produce anaerobic energy as shown by Schöttler and Grieshaber (1988). These authors observed anaerobic metabolism maintained for 24 h before greater mortality occurred and a 40 h threshold for survival determined by total exploitation of glycogen reserves. This 40 h threshold is 5 h below the LT$_{50}$ in our experiment. Presumably, our worms survive longer because of more natural experimental conditions with sediment in the experimental jars. However, in spite of these diverging results, *S. armiger* may still be classified as a species with moderate resistance to anoxia in comparison with other infaunal marine invertebrates (Schöttler et al., 1984; Schöttler and Grieshaber, 1988; Gamenick et al., 1998b; Thiermann et al., 2000). Tolerance to sulphide depends on a sulphide detoxification system. As with the tolerance of hypoxia this has been shown to be species-specific in marine invertebrates (Vismann, 1990; Völkel and Grieshaber, 1994; Gamenick et al., 1998a; Hauschild et al., 1999). In conclusion, physiological adaptations to both hypoxia and sulphide appear as traits under selection during speciation in *S. armiger*.

4.3. Role of adaptation to subtidal and intertidal habitats in a speciation process

Distinct gene pools between subtidal and intertidal *S. armiger* characterised by neutral, random markers (Kruse et al., 2003) suggest that the potential of *S. armiger* Type I and Type S to adapt to hypoxia and sulphide may be genetically fixed. Poor performance in anaerobiosis and sulphide detoxification in *S. armiger* Type S may exclude them from invasion of the intertidal and thus isolate them from Type I. If speciation has occurred under the distributional situation present in the Wadden Sea, a sympatric speciation scenario is probable. Under this scenario, moderate gene flow may be present during population divergence, selection must be strong enough and the traits under divergent selection must provide intrinsic barriers to gene flow (Via, 2001). If allopatric speciation is assumed, reproductive isolation evolved as a by-product of population divergence in the absence of gene flow.

Construction of a speciation scenario requires a decision on which mode of development is primitive and which one is derived. The phylogeny of developmental mode in polychaetes is still under discussion (Schroeder and Hermans, 1975; Wilson, 1991; Rouse and Fitzhugh, 1994; Rouse and Fauchald, 1998; Eckelbarger and Young, 2002). Also for the Orbiniiidae no such assessment exists to date. Half of the orbiniid species spawn directly into seawater (Blake, 1996). In the following scenarios we consider the holobenthic development for *Scoloplos* spp. as derived, assuming that the common ancestor produced pelagic larvae. *S. armiger* Type I with egg cocoons are restricted to a small area (North Sea region and adjacent waters), while *Scoloplos armiger* found in the rest of the world, with no reports of egg cocoons, is most likely *S. armiger* Type S.

In case physiological adaptation was the ultimate cause of divergence in *S. armiger*, only an allopatric scenario of speciation appears possible. There is no obvious propensity of these physiological traits to build up intrinsic barriers to gene flow. In this scenario a species splits up from an ancestral *S. armiger* under selection for high physiological tolerance to anoxia and sulphide in a geographically isolated area, keeping pelagic larvae. These are able to invade the intertidal as a novel habitat since they are pre-adapted to it in their physiological tolerance. Egg cocoons have then emerged as a secondary trait in the intertidal habitat. *S. armiger* from the Baltic may represent such a distant population pre-adapted to invading the intertidal. Baltic *S. armiger*, which lacks egg cocoons, may be attributable to Type S (Kruse, 2003). They have been reported to tolerate low oxygen concentration, to withstand the presence of hydrogen sulphide, and to be the only infaunal species involved in bioturbation process in large suboxic areas below the subhalocline in the Eastern Gotland and Northern Basins (Schulz, 1969; Olenin and Schiedek, 1996). However, the question of whether Baltic *S. armiger* are reproductively isolated from the North Sea Type I needs to be examined.

The formation of egg cocoons emerging prior to physiological adaptation allows both an allopatric and a sympatric scenario. In the allopatric scenario, in some coastal part of the distributional range of *S. armiger*, strong selective pressure occurs against pelagic larvae, i.e. by strong and only offshore currents or very heavy larval mortality (predation, high annual variation in
suitable water masses, etc.). Such a coastal part becomes geographically isolated and the direct mode of development in egg cocoons emerges as an adaptation to protect the larvae. After the geographic barrier is abolished, S. armiger with advanced direct development turns out to be pre-adapted to evolving specific tolerances required for survival in the intertidal zone.

According to a sympatric speciation model, larval development within egg cocoons may represent the only way for S. armiger to colonise the harsh intertidal environment with shifting sands during high tide, extreme temperatures that threaten desiccation, and anoxia during low tide. Only some specimens invading the intertidal which have the phenotypically plastic ability to develop egg cocoons may keep their genes in the intertidal or in the transition zone, all others are sent away with pelagic larvae in the next generation. Continued retention of larvae as well as assortative mating within the intertidal habitat, both provided by development in egg cocoons, reinforces adaptation to the intertidal habitat, e.g. in physiological tolerance. In turn, the environmentally induced loss of pelagic larvae reaching the intertidal, or avoidance of the intertidal, and poor adaptation of adults to anoxia and sulphide prevent mixing of the gene pool of the intertidal population. Intrinsic barriers to gene flow emerge.

However, further investigation is needed to decide which of these scenarios is the most likely. Genetic testing for phylogenetic relatedness between subtidal and intertidal populations of S. armiger relative to the other species of this genus on the one hand, and of subtidal S. armiger on a global range on the other hand, appears to be a promising approach. Combined with information on dispersal, physiology and reproductive behaviour of the populations, such data may then elucidate processes of ecological speciation in S. armiger which could be fundamental to the marine environment.

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References


