

# 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. Spawns 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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## 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, reviv-

ing 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.

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*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, infaunal subsurface deposit feeder (Fauchald 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 Völkl, 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

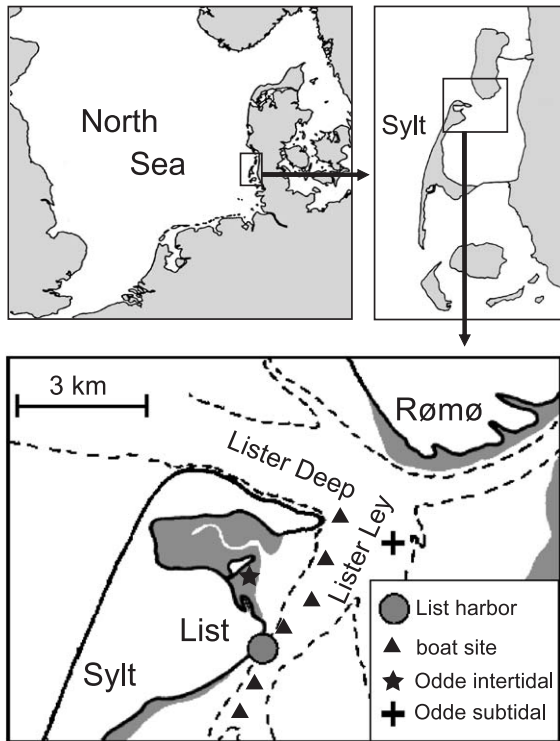


Fig. 1. Plankton sampling sites with List harbour used for the long-term survey and six boat sites (denoted by triangles: northernmost site at 55° 02,64 N; 08° 28,00 E, southernmost site at 54° 00,31 N; 08° 25,81 E) and location 'Odde' in the northern part of the island of Sylt.

Bight covers about 400 km<sup>2</sup>, of which 33% belong to the intertidal zone, 57% to the shallow subtidal (< 5 m depth) and 10% to deeper tidal channels (max. depth ~ 40 m). Water exchange between the Sylt-Rømø Bight and the open North Sea takes place through a 2.8-km-wide tidal channel. More information on the area is given in Gätje and Reise (1998).

## 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<sup>3</sup> 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.

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<sup>3</sup> 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<sup>3</sup> 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.

The spawning of egg cocoons by Type I was surveyed regularly on the Odde and Königshafen intertidal flats every 2 to 4 days during February to April and October in 1996–2001. The date of the first notable increase in overall egg cocoon abundance was recorded.

Six or seven days before the sulphide tolerance experiment, adult *S. armiger* were sieved with a 1 mm mesh from intertidal and subtidal sediments of the Odde location. Until the start of the experiment, the worms were kept at 5 °C. The Odde location is also used in earlier genetic studies on *S. armiger* (Kruse et al., 2003).

For the determination of sulphide concentrations and pH of sediment, porewater samples were taken after Howes et al. (1985). The Odde location was sampled at six sites in April and at eight or six sites (5 and 10 and 15 cm sediment depth) in June, in the intertidal as well as in the subtidal habitat. Subtidal samples were taken from box core samples that contained sediment from 10 m water depth. Total sulphide concentration was determined colorimetrically following Howarth et al. (1983). The term sulphide here refers to total dissolved sulphide, i.e. undissoci-

ated  $\text{H}_2\text{S}$ , dissociated  $\text{HS}^-$  and  $\text{S}^{2-}$ . 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  $250\text{ cm}^3$ ) 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 ( $<1\text{ }\mu\text{mol O}_2\text{ dm}^{-3}$ , Gamenick et al., 1998a). The initial sulphide concentration of  $220\text{ }\mu\text{M}$  in the sulphide treatment was achieved by addition of a 10 mM stock solution (made from  $\text{Na}_2\text{S} \cdot 9\text{H}_2\text{O}$  crystals). Sulphide

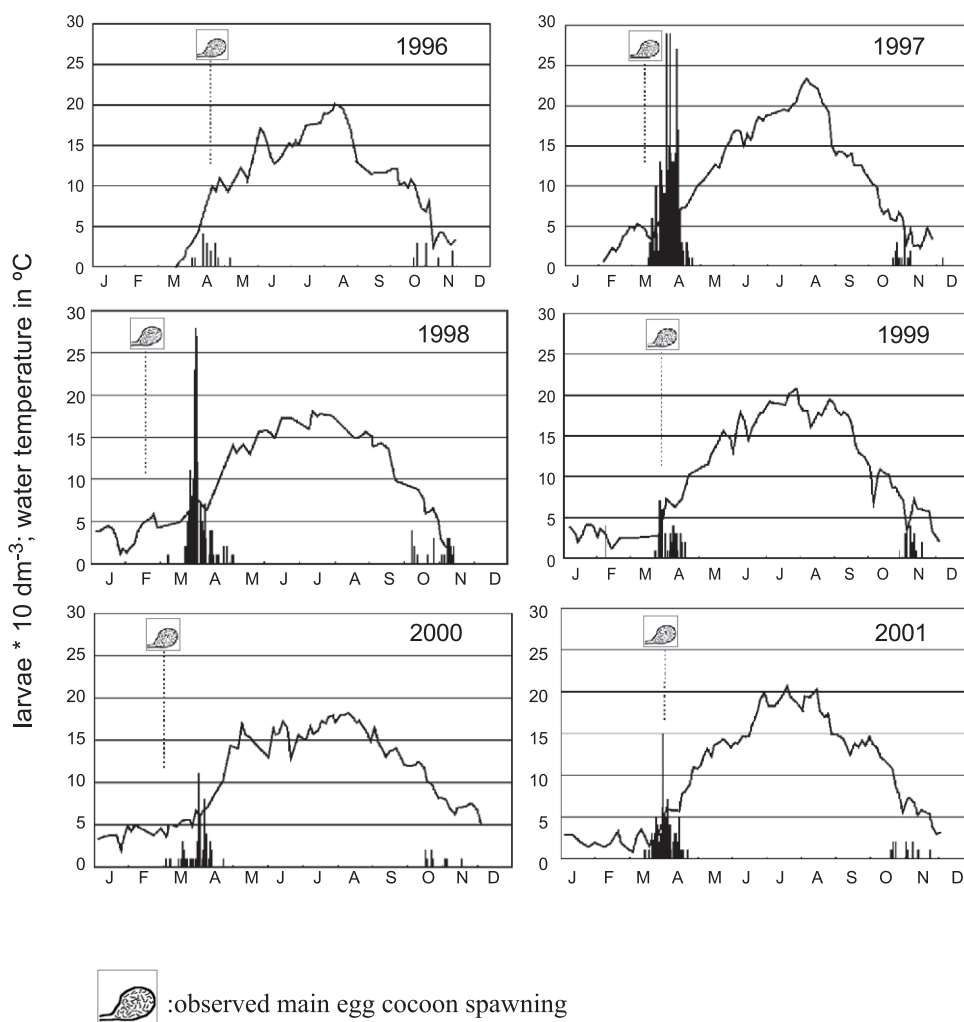


Fig. 2. Abundances of pelagic *Scoloplos armiger* larvae at List harbour (columns) and water temperatures (lines) in 1996–2001; larval numbers and °C at the same scale.

Table 1

Large-scale distribution of pelagic *Scoloplos armiger* larvae in mean abundances  $\pm$  standard deviation

Water depth	1 m	5 m	10 m				
Mean per 10 dm <sup>3</sup> ( $\pm$ SD)	1.4 $\pm$ 1.4	1.3 $\pm$ 1.3	1.3 $\pm$ 1.3				
Sites in Lister Ley	1	2	3	4	5	6	List harbour
Mean per 10 dm <sup>3</sup> ( $\pm$ SD)	1.2 $\pm$ 1.3	1.1 $\pm$ 0.5	0.4 $\pm$ 0.3	1.4 $\pm$ 1.1	1.1 $\pm$ 0.6	1.1 $\pm$ 1.1	2.2 $\pm$ 2.3

Vertical distribution defined by three water depths; horizontal distribution defined by six sites in Lister Ley, and one in List harbour.

concentrations were measured at the beginning and the end of experiments, as described above (start: 223  $\mu$ M, end: 168  $\mu$ M, mean: 195  $\mu$ M).

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 ( $\pm$  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 (= LT<sub>50</sub>, 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 dm<sup>3</sup> in spring. Autumn spawnings occurred

in October when the water temperature dropped to about 10 °C, with a maximum of 5 larvae per 10 dm<sup>3</sup>.

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  $\pm$  0.73 larvae per 10 dm<sup>3</sup>) were not significantly different from the List harbour site (2.25  $\pm$  2.3 larvae per 10 dm<sup>3</sup>) ( $t$ -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  $\pm$  4.6 larvae per 10 dm<sup>3</sup> at night compared to 5.2  $\pm$  4.4 larvae per 10 dm<sup>3</sup> during the day). There was no significant difference between

Table 2

Abiotic sediment characteristics from subtidal and intertidal sites where *Scoloplos armiger* were sampled for hypoxia and sulphide tolerance experiments

	Intertidal mean	SD	n	Subtidal mean	SD	n
Sulphide ( $\mu$ mol per dm <sup>-3</sup> )						
April						
sediment depth:						
5 cm	106.22	32.70	6	12.93	6.72	6
10 cm	98.73	35.60	6	11.90	5.52	6
15 cm	87.27	20.88	6	17.00	8.94	6
June						
sediment depth:						
5 cm	70.10	16.49	8	15.3	3.4	6
10 cm	78.69	25.06	8	9.5	5.6	6
pH	7.80	0.19	5	8.06	0.24	35
grain size						
MD	423.94	18.24	16	291.87	54.32	23
QDI	0.81	0.03	16	0.78	0.13	23
classification	moderately sorted medium sand			moderately sorted fine sand		

abundances at high tide ( $6.1 \pm 4.8$  larvae per  $10 \text{ dm}^3$ ) and low tide ( $7.3 \pm 4.9$  larvae per  $10 \text{ dm}^3$ ) (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 con-

centrations 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

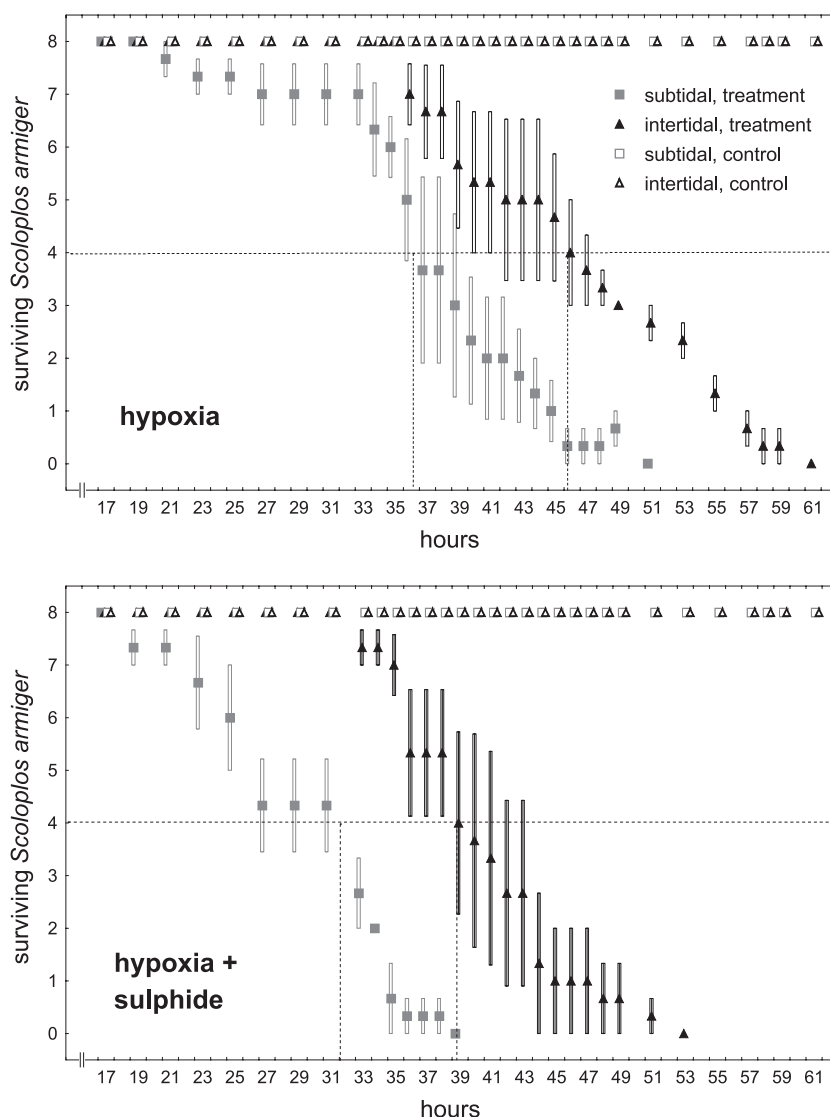


Fig. 3. Experimental mean survival of subtidal and intertidal adult *Scoloplos armiger* subject to hypoxia (top graph) and hypoxia plus sulphide (bottom graph),  $\pm$  SE;  $LT_{50}$  indicated by dotted line ( $n = 3$  jars with 8 individuals each for each experimental run).



than intertidal specimens. The  $LT_{50}$  value for intertidal *S. 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 conditions in combination led to a  $LT_{50}$  of 39 h for intertidal *S. armiger* and of 31–33 h for subtidal specimens (Fig. 3). Under this treatment, the first subtidal individual 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 JMP 5.0.1.2 (SAS Institute Inc., 1989–2003) revealed significant differences between intertidal and subtidal *S. 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 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 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). Disruptive selective pressures may be revealed from population divergence in characteristics that are directly linked to habitat differences. Whether these characteristics 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 environments. However, our results show that spawning asynchrony of intertidal and subtidal *S. armiger* as the cause of reproductive isolation is to be rejected. Spring spawning of *S. 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. 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. 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. 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 second spawning for intertidal *S. armiger* Type I may be avoidance of frost. Juveniles inhabit the upper sediment layer and would risk death by freezing when the flats are exposed at low tide in winter. Only those species of intertidal polychaetes that spawn in autumn broadcast their juveniles into the subtidal or low intertidal, undertaking re-immigration to the upper intertidal the next spring. *Arenicola marina* is one prominent example of such juvenile migration (Reise, 1985).

##### 4.2. Tolerance to hypoxia and sulphide

Intertidal *S. 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-

ciated 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 Orbiniidae 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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