

**Rissoa membranacea (J. Adams, 1800) (Gastropoda, Prosobranchia)  
from the Dutch Wadden Sea**

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*Rissoa membranacea* disappeared from the Dutch Wadden Sea together with the large subtidal stands of eelgrass *Zostera marina* L. in the early 1930s, due to a still not completely understood 'wasting disease' in *Zostera*. A small population of *R. membranacea* survived together with *Zostera marina* in an inland brackish water 'de Bol' on Texel until 1981. Empty shells of *R. membranacea* can still be found at these localities. The relatively large size of the top-whorl of Wadden Sea *R. membranacea* indicates that the larvae were lecithotrophic. In this respect they are comparable to *R. membranacea* type B from the Roskilde Fjord of Rehfeldt (1968) and Warén (1996) and to *R. membranacea* s.s. as described by Verduin (1982b). It is, however, questionable whether *R. membranacea* Type A of Rehfeldt and *R. labiosa* sensu Verduin can be separated from *R. membranacea* s.s. They differ only in the smaller size of the embryonic whorl indicating planktotrophic pelagic larvae. This might as well indicate two different types of larval development, lecithotrophic and planktotrophic in one and the same species *R. membranacea* s.l. Apical dimensions in samples from the Ria de Arosa (Spain) and from Dutch Eemian deposits show a gradual change from small '*R. labiosa*' to larger '*R. membranacea*' values, which supports the merging of both nominal species and corroborates Warén's suggestion of a continuum in larval development in *R. membranacea* between lecithotrophy and planktotrophy as well as newer ideas of a gradually and easily crossed transition between lecithotrophy and planktotrophy of McEdward (1997).

Key words: Gastropoda, Prosobranchia, Rissoidae, *Rissoa membranacea*, larval development, lecithotrophy, planktotrophy, Wadden Sea, Netherlands.

## INTRODUCTION

*Rissoa membranacea* (J. Adams, 1800) is a small prosobranch gastropod, occurring from Norway and the Baltic near Rügen to the Canary Islands, and probably also in the Mediterranean. It lives normally associated with eelgrass *Zostera marina* L.. It is an annual species which breeds in summer in the northern part of its distribution (Fretter & Graham, 1978). Egg capsules are deposited preferably on *Zostera* leaves (Van Goor, 1919; Lebour, 1934; Smidt, 1938). After hatching they grow rapidly. Van Goor (1919) observed 1 mm shells in July and in September they had reached already their maximum size of 5.5 - 9 mm. Smidt (1938) found an equally rapid growth in the Sound from 1 mm early August to 3.5 - 4 mm, their maximum size for this locality, in early September. During winter *Zostera* leaves fall off and the greater part of the *R. membranacea* population perishes, only a small part attains the breeding stage in the following summer (Van Goor, 1919; Smidt, 1938). In the former Zuiderzee *R. membranacea* was very common (Van Goor, 1919; Van Benthem Jutting, 1933). The species was badly affected by the *Zostera* disease in NW. Europe in the 1930s. Warén (1996) presents an up-to-date account of its taxonomy and ecology.

The highly variable shell morphology of *R. membranacea* has long ago already induced authors to a division in different species and varieties (e.g. Schwartz von Mohrenstern, 1864). Verduin (1982a,b) meticulously measured numerous Recent shells of *R. membranacea* s.l. from European seas ranging from the Black Sea and the Mediterranean to northern Europe and the Baltic. He was able to distinguish two variable 'species', which only differed in the size of the apical whorl. The forms with the smaller apex he identified as *R. labiosa* (Montagu, 1803), those with a larger apex as *R. membranacea* s.s. Verduin (1982b) mentioned Rehfeldt (1968), who also had found two types in *R. membranacea*. She was able to relate these types to a difference in larval development: pelagic larvae in type A with the slender apex, and non-pelagic larvae in type B with the larger apex. Rehfeldt's results nicely illustrated the 'apex theory' of Thorson (1950), which states that in general a clumsy large apex in gastropods points to non-pelagic development and lecithotrophic larvae (feeding on yolk and not requiring planktonic food), while a narrowly twisted apex points to a pelagic development and planktotrophic larvae. Since Thorson's seminal papers (Thorson, 1946, 1950) facultative planktonic feeding has been observed in lecithotrophic larvae e.g. in the nudibranch *Phestilla sibogae* Bergh, 1905 by Kempf & Hadfield (1985) and Miller (1993) indicating a gradual transition between lecithotrophy and planktotrophy. McEdward (1997) suggests a gradual and easily reversible transition between both feeding types. Also so-called adelphophagy (Bouchet, 1989), the ingestion by developing larvae of nurse eggs or embryo's in the same egg-capsule, has been observed and complicates the picture.

Warén (1996) studied > 1,000,000 *R. membranacea* specimens from all parts of the distributional area in western Europe and confirms the existence of Rehfeldt's type A and B, giving excellent SEM pictures of the difference in the top-whorl. Warén found Rehfeldt's type A = Verduin's *R. labiosa* (with planktotrophic larvae) from northern Europe to southern Portugal (and presumably in the Mediterranean), whereas Rehfeldt's type B = Verduin's *R. membranacea* s.s. (with development in the egg capsule, veligers feeding on nurse eggs) is known only from Roskilde fjord, south-west France and the United Kingdom. But he also reports that the situation may be more complicated: planktotrophic larvae have been found to consume undeveloped eggs before hatching, which enables them to grow to a larger size in the egg-capsule and probably abbreviate their pelagic period. Warén suggests a continuum between lecithotrophy and planktotrophy as an adaptation to local conditions.

Thorson (1950) observed a clear N-S trend in larval development throughout the North Atlantic, later named 'Thorson's rule'. He observed only prosobranchs with non-pelagic larvae in East Greenland, to the majority (68%) with pelagic and less (32%) with non-pelagic larvae at the Canary Islands. Numerous studies since 1950 support a general increase in non-pelagic, brooded development with increasing latitude, although exceptions have been found in the Antarctic and deep-sea invertebrates (see Levin & Bridge, 1995, for a review). Verduin (1982b), did not integrate Rehfeldt's results in his paper, nor did he mention how nicely his data fit in with the apex theory of Thorson: Verduin observed *R. labiosa* with the slender apex and therefore most probably with pelagic planktotrophic larvae, from the Mediterranean to Denmark. His *R. membranacea* with the large apex and probably lecithotrophic larvae did occur more to the north, in the Baltic, the North Sea, the Irish Sea and the Channel, but not south of Bretagne. There is an area of overlap of the two 'species' in which among others The Netherlands are situated, but unfortunately Verduin did not study material from there. This leaves the possibility that both his *R. membranacea* and *R. labiosa* once lived

in The Netherlands, as suggested e.g. by De Boer & De Bruyne (1991) and De Bruyne (1994).

*R. membranacea* s.l. no longer lives in the Dutch Wadden Sea (De Boer & De Bruyne, 1991) and is also extinct in the German and Danish Wadden Sea (Von Nordheim et al., 1996). With the disappearance of large sublittoral stands of *Zostera marina* in the early 1930s (Polderman & Den Hartog, 1975), *R. membranacea* and another small gastropod living on eelgrass, *Lacuna vincta* (Montagu, 1803) (synonym *L. divaricata* (Fabricius, 1780)) disappeared as well. Van Benthem Jutting (1933) still mentioned both species as very abundant in eelgrass fields, which fauna was well studied by van Goor (1919), but the species had probably already disappeared at the time of publication in 1933. On the other hand, its occurrence in the Wadden Sea was not discovered before the beginning of this century. The first specimens found of *R. membranacea* date from 1909, collected by W.C. Van Heurn on Texel (Vernhout, 1912) and from 1912 on Griend, collected by Van der Sleen (1913). In the Wadden Sea now only empty shells of both species can be found and only in small numbers (personal observations and pers. comm. R. Dekker, NIOZ). Also, the small population of *R. membranacea*, which survived among *Zostera marina* in a brackish inland water 'de Bol' on Texel, has disappeared. 'De Bol' had a connection with the Wadden Sea via an ebb-sluice which opened automatically during low tide because then the pressure of the water on the landside became higher than that from the Wadden Sea water. *R. membranacea* was discovered here in the 1950s (Swennen, 1955) and repeatedly mentioned and studied since (Reydon & Visser, 1967; Visser, 1968ab; Verhoeven & Van Vierssen, 1977, 1978). After removal of the ebb-sluice during dike reconstructions in 1979, the last Dutch population of *Rissoa membranacea* became extinct (De Jong & De Kroon, 1982; Van der Goes et al. 1996; personal observations).

In this note I report on *R. membranacea* from the Wadden Sea. Some hundred specimens were collected as empty shells from drift along the Wadden Sea coast south of the tidal marshes 'De Schorren', Texel, in June 1997. Also a sample of empty shells from the inland brackish water 'de Bol', Texel, sieved from a bottom sample taken in July 1997, was studied. In addition, samples of *R. membranacea* collected alive in the Wadden Sea between 1909 and 1929 (collection Zoological Museum Amsterdam, ZMA) and from 'de Bol' collected in 1966 and 1968 (kindly provided by G.J.M. Visser, Terschelling, now donated to ZMA) were studied. For comparison Recent specimens from the province of Zeeland and from the Ria de Arosa (Spain) and fossil material from Eemian deposits near Amsterdam were used (see table 1 for data on all samples used).

## METHODS

Measurements of the top-whorl were made following Verduin (1982b) (d and Do, see fig. 1a). The shells were vertically positioned in sand and drawings were made of the first whorl using a drawing tube on a Wild M5 stereo microscope and 50x magnification, resulting in a magnification of 56.8x of the drawing. Do and d were measured on these drawings. They have the advantage over direct micrometer measurements of giving a visual record of the data. Verduin (1982b) estimated the accuracy of measurements of Do at 0.003 mm and d at 0.005 mm, when apices were in excellent condition. He did not mention that measurements also depend on the accurate vertical position of the shell and the somewhat arbitrary location of the line along which d and Do are measured. I measured d and Do ten times in one specimen, every time

positioning the shell anew in a vertical position. This gave averages and standard deviation of  $0.139 \pm 0.009$  mm for  $d$  and  $0.248 \pm 0.010$  mm for  $D_o$ . In general at least ten specimens were measured per sample (if available, see table 1).

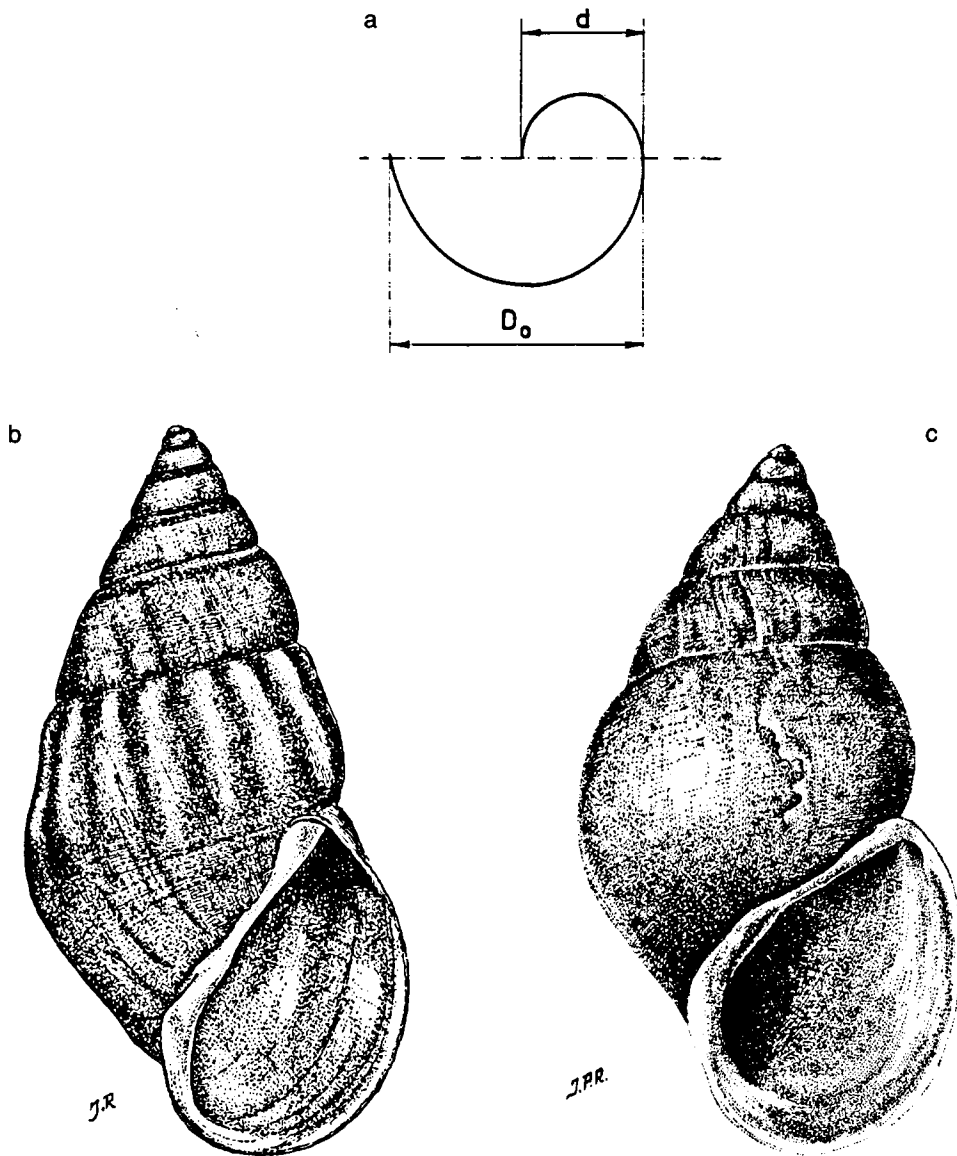


Fig. 1. *Rissoa membranacea* (J. Adams), (a) the apex seen from above and definition of  $d$  and  $D_o$  following Verduin (1982a,b); (b) the ribbed form (drawing by J.P. Reydon, 1997, length 6.4 mm); (c) the ribless form that occurred in the brackish inland water 'de Bol' on Texel (drawing by J.P. Reydon, from Reydon & Visser, 1967, length 5.2 mm).

## RESULTS

The empty shells from the Wadden Sea collected among *Hydrobia*-rich shell drift along the high water line of the wadden coast of Texel S of 'de Schorren' in June 1997, ranged in size from 3.3 to 7.1 mm (average 4.9 mm), which indicates that juvenile shells were not present. The sculpture varied from smooth ribless shells to a clear presence of ribs (fig. 1b), some 16 per whorl. Most specimens still had marks of the original colour. Only 9 specimens had a well preserved top-whorl for measurements of *d* and *Do* (see table 1). The average of *d* was 0.145 mm, and for *Do* 0.252 mm. Verduin (1982b) observed two clusters in his measurements, shells with the larger top-whorl with values of  $Do + 0.55d > 0.237$  (see oblique line in fig. 2) he assigned to *R. membranacea* s.s., those with the smaller top-whorl to *R. labiosa*.  $Do + 0.55d$  for the 9 shells from Texel ranges from 0.319 to 0.428, indicating that all these shells belong to Verduin's *R. membranacea* s.s.

The data for the shells collected alive in the Wadden Sea between 1909 and 1926 (table 1 and fig. 2a) indicate that all had the large type of top-whorl with average values for *d* of between 0.153 and 0.171 mm and for *Do* of between 0.259 and 0.282 mm, thus pointing to *R. membranacea* s.s. of Verduin (1982b).

The specimens from the inland brackish water 'de Bol' were all ribless (see fig. 1c). The empty shells were well preserved, the top-whorl intact; apparently the black mud rich in calcareous material such as shells and bryozoans is a good preserving medium. Measurements of these empty shells as well as from those collected alive here in 1966 all indicate the same large type of top-whorl as the Wadden Sea specimens (table 1 and fig. 2b).

Locality	collector and year	av. <i>d</i> (s.d.) µm	av. <i>Do</i> (s.d.) µm	number measured	coll.
Texel	W.C. v. Heurn 1909	153 (20)	261 (32)	9	ZMA
Den Helder	H. Boschma 1915	161 (23)	264 (24)	12	ZMA
Den Helder	H. Boschma 1915	163 (21)	276 (22)	4	ZMA
Den Helder Vangdam	T. v. Benthem Jutting 1919	144 (20)	259 (31)	10	ZMA
Den Helder oesterput	T. v. Benthem Jutting 1919	171 (33)	282 (26)	10	ZMA
Waddenzee, Doove Balg	T. v. Benthem Jutting 1926	164 (14)	282 (27)	10	ZMA
Texel, Schorren (empty)	G.C. Cadée 1997	155 (22)	270 (25)	9	GCC
De Bol Texel	C.J.M. Visser 1966	170 (18)	280 (18)	10	ZMA
De Bol Texel (empty)	C.J.M. Visser 1968	158 (17)	273 (21)	10	GCC
De Bol Texel (empty)	H & G.C. Cadée 1997	145 (17)	252 (18)	21	GCC
Zeeland Nw Stjoostrand	C. Brakman 1922	161 (20)	274 (20)	10	ZMA
Zeeland Wemeldinge	B. Hubert 1925	138 (8)	251 (7)	2	ZMA
Zeeland Kattendijke	C. Brakman 1942	161 (2)	275 (36)	2	ZMA
Eemian Amsterdam (fossil)	K. Jonges 1964-7	110 (17)	186 (28)	21	ZMA
Eemian Amsterdam (fossil)	G.C. Cadée c. 1960	122 (23)	226 (24)	11	GCC
Ria de Arosa	G.C. Cadée 1964	104 (10)	180 (15)	15	GCC

Table 1. Samples of *Rissoa membranacea* measured, shells collected alive except when indicated otherwise. Columns from left to right: sampling locality, collector and year of collection, average and standard deviation for *d* and *Do*, number of specimens measured, and collection (ZMA = Zoological Museum Amsterdam, GCC = G.C. Cadée).

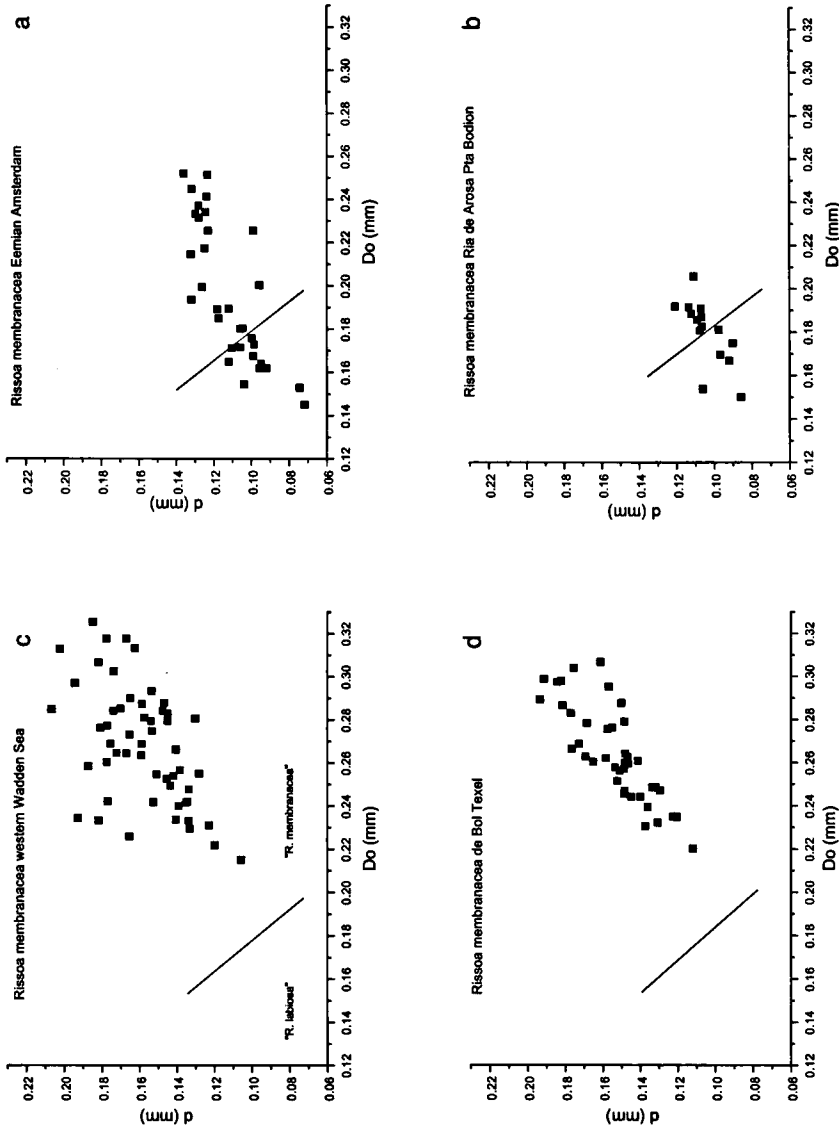


Fig. 2. Measurements of apical dimensions of d and Do for *Rissoa membranacea*, following Verduin (1982 a,b), the oblique line in the graph indicates Verduin's line separating his *R. membranacea* and *R. labiosa*, see also table 1: (a) Wadden Sea population, both specimens collected alive between 1909 and 1926 and empty shells collected in 1997; (b) population from 'de Bol' based on specimens collected alive 1966 and as empty shells in 1968 and 1997; (c) shells from Eemian deposits near Amsterdam collected from dredged sand; (d) specimens from de Ria de Arosa collected alive in 1964.

For comparison measurements were taken of three samples from the province of Zeeland of which only the sample of Nieuw en St. Joosland was large enough for reliable average values (table 1). The measurements of *d* and *Do* also fall in the range of the Wadden Sea and 'de Bol' specimens. We can conclude that all this material belongs to *R. membranacea* s.s. Verduin (1982b).

The only Dutch samples of *R. membranacea* in which I did find also the smaller type of apex were from the Eemian, the averages for *d* and *Do* are clearly lower than for the Recent Dutch specimens (table 1, fig. 2d). Unfortunately in most specimens the apex was not sufficiently preserved for measurements. There is, however, no clear-cut difference between specimens with the different types of apex as suggested by Verduin (1982b), the transition is gradual, indicating the impossibility in the Eemian material to distinguish his *R. labiosa* and *R. membranacea* on the base of apical dimensions.

For comparison I included a sample from the Ria de Arosa (table 1, fig. 2d). Apical dimension appeared comparable to those of the Dutch Eemian sample and also showed a gradual transition of lower values for *d* and *Do* to higher values, not separated in a '*R. labiosa*' and a '*R. membranacea*' cluster as suggested by Verduin (1982b, fig. 1). Even in Verduin's fig. 1, based on material from Bretagne, one can see in my opinion a gradual transition in apical dimensions. Based on measurements presented here, I doubt whether both nominal species can be distinguished in the Ria de Vigo as Rolan (1983) did. For the nearby Ria de Arosa Cadée (1968) mentioned only *R. membranacea*, this is confirmed by the measurements given here.

## DISCUSSION

The specimens collected alive as well as the empty shells from the Wadden Sea and 'de Bol' on Texel and also the two samples collected alive in Zeeland all belong to type B of Rehfeldt (1968) and Warén (1996) with the large top-whorl indicative of lecithotrophic larvae without or with only a short period of pelagic life following Thorson (1950). Therefore I conclude that all Dutch Wadden Sea *R. membranacea* belonged to one and the same type, to which Verduin (1982 a,b) gave the name *R. membranacea* s.s. (J. Adams, 1800). I propose, however, not to separate the specimens with a more slender top-whorl, of which some were found in the Ria de Arosa and Eemian samples, as a different species *R. labiosa* (Montagu, 1803) as Verduin did (supported later by Bouchet, 1989), but to follow older authors (e.g. Jeffreys, 1867; Fretter & Graham, 1978) and assemble all in one variable species *R. membranacea* s.l., because the transition from large to slender apices is gradual (see the Ria de Arosa and Eemian samples, fig. 2cd). I propose also to include in *R. membranacea* both type A and B of Rehfeldt (1968) as also Warén (1996) did. I agree with Warén that *Rissoa membranacea* has to be seen as a species with two different types of larval development, a phenomenon not common in gastropods (Thorson, 1950 gives a few examples), but more common in other groups e.g. polychaetes (Thorson, 1950). If the lecithotrophic larvae predominate in the northern part of its distribution, and the planktotrophic in the southern part, the average size of the top in fossil *R. membranacea* might be a useful indicator of palaeotemperature. Bouchet (1989) critically reviewed published data on poecilogony (variation in mode of development) in prosobranchs; most reports were not documented well enough, but Bouchet (1989) and Warén later (1996) do not exclude the possibility of poecilogony. Warén (1996) suggests adaptation to local conditions to regulate the presence of planktotrophy or lecithotrophy in *R. membranacea*.

More than one larval development type within a species (feeding - non-feeding) is relatively rare and ranges from interbreeding of populations with different larval types to hatching of larvae of different size from a single egg mass (Havenhand, 1995). It has the potential advantages of both larval types: maximal utilisation of local resources and ability to colonise distant habitats. In the Roskilde fjord Rehfeldt observed both pelagic and non-pelagic development of larvae (her type A and type B), she presents drawings of the difference in larval shell size, and did not mention intermediate specimens. Warén (personal communication, 1997) studied *R. membranacea* from the Roskilde fjord and other Danish localities and found no intermediate specimens, but either type A or B, with a wide gap in the dimensions. Measurements of Verduin (1982b) for a sample from Bretagne and those presented here from de Ria de Arosa and the Eemian sample, however, suggest a gradual transition between both types also expressed in the dimensions of the larval shell. This casts doubt on Rehfeldt's statement (l.c.: 170) that dimensions of the initial embryonic shell are "undoubtedly genetically determined".

The occurrence of only one type of larval development in the Dutch Wadden Sea viz. lecithotrophic larvae with no, or only a short, period of pelagic life, might have evolved here to minimise the loss of larvae from the eelgrass beds and thus illustrates Warén's suggestion of the influence of local adaptation (Warén, 1996). Strong tidal currents and relatively short flushing times of the western Wadden Sea (now in the order of one to two weeks, Zimmerman, 1976) will make return of open water pelagic larvae to the eelgrass beds difficult. Thus lecithotrophy and non-pelagic larvae, or only a short pelagic stage among the *Zostera* leaves as described by Smidt (1938) and Thorson (1946) will be an advantage. Moreover, in this short-lived species, where adults die after egg-laying, there will be no food competition between juveniles and adults of the same species, whereas such a possible competition in other longer-living species might favour dispersal by pelagic larvae.

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