Rearing experiments on the amphibian slug *Alderia modesta*

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KURZFASSUNG: **Züchtungsversuche mit der Amphibienschnecke *Alderia modesta*.** Der saccoglosse Opisthobranchier *Alderia modesta* (LOVÉN) kommt an den europäischen Küsten und an einigen Stellen Nordamerikas häufig vor. Er lebt an der Grenze des Supralitorals bei Salzgehalten von 5 bis 40 ‰. *Alderia* zeichnet sich durch eine hohe Eiproduktion aus: Während der warmen Monate legt eine Schnecke täglich durchschnittlich 1000 Eier. Die Zahl der planktotrophen Larven wird allerdings durch hohe Verluste reduziert, die zum Teil auf eine mangelnde Brutpflege der Schnecke zurückzuführen sind. Die verschiedenen Entwicklungsstadien der Larven werden beschrieben; ferner wird ein Vergleich mit der nahe verwandten *Limapontia depressa* gegeben. Nach etwa 4 Wochen durchlaufen die Veliger die Metamorphose, die innerhalb von 24 Stunden vollzogen ist. Die gerade aus dem Haus geschlüpfte Schnecke hat noch keine Rückenanhänge. Nach 10 Tagen ist sie 3 mm lang und beginnt bereits mit der Eiproduktion. Die Dauer der Entwicklung ist von den herrschenden Temperaturen abhängig. Die Salinitätstoleranz differiert bei verschiedenen Populationen.

INTRODUCTION

Alderia modesta (LOVÉN), a saccoglossan opisthobranch, lives in many places along the European coasts. It has been recorded from the Mediterranean (THIELE 1931, RIEDL 1963), from Normandy and north up to the Drontjemfjord, from the Baltic up to the neighbourhood of Helsinki, and from the Atlantic and Pacific coast of North America (for more detailed information see DEN HARTOG 1959).

Alderia lives near the supralittoral fringe in areas which are either reached daily by high tides (tidal coasts) or only occasionally (Baltic). The green alga *Vaucheria* serves both as food and substratum. At times the slugs occur in astonishingly high numbers. DEN HARTOG found on a square decimeter 31 specimens; the author counted an average number of 14 per square decimeter in a larger area. Throughout the warm season one animal produces about 1000 eggs a day. On the German coasts they seem to retreat into the muddy substratum of their habitat during the winter.

Since *Alderia* exists in such enormous numbers and has such an immense production of eggs, the veligers must be of some importance in the plankton, the more so since the larvae are planktotrophic and need at least 4 weeks until they are ready for metamorphosis. A description of the larval development of *Alderia modesta* and the

closely related *Limapontia depressa* seemed necessary, since up to now only chance observations have been published. Only *Limapontia capitata* is dealt with in detail in THORSON's monography (1946).

METHODS

Adult *Alderias* were collected in the field and taken to the laboratory where they were put into glass dishes on cottonwool moistened with diluted sea water. Some nutrient fluid and a thin layer of natural substratum on which *Vaucheria* grew sufficiently well to serve as food were added. The egg-strings were picked out twice a day and put into petri dishes on a layer of cottonwool moistened with water of the requested salinity. The larvae were fed on *Dunaliella* sp.; after some time quite a number of them become attached to the water surface and die. Since light does not prevent them from swimming upwards and chemicals releasing the water-tension proved to be fatal even in very low concentrations, these losses could not be prevented. A sufficient number of larvae survived, however, and metamorphosed. To avoid pollution and the spreading of fungi, the snails were transferred into clean dishes at regular intervals. Unless otherwise stated the time intervals required for the diverse phases of development refer to a water temperature of 20° C.

RESULTS

One copulation is sufficient for the fertilization of several egg strings. The slugs attach their egg masses to the surface of the substratum. They prefer the steep side of little slopes and do not care whether or not they are in or out of the water. At first a hyaline substance appears with which the spawn is fixed to the ground. Later it contains the spirally coiled egg string. Cleavage starts very soon. It takes only 20 minutes until the two-cell stage is completed. After about two days the embryo begins to move and after another 24 hours the veliger is discernible. The larvae will hatch regardless of the water level. Thus a considerable number die because they do not reach the water. If an egg sausage is partly damaged so that only few embryos develop normally, they succeed in hatching but are trapped in the surrounding jelly, which has a relatively strong outer layer. It takes a good number of young ones to tear it with the help of the vela.

The eggs of just deposited spawn are dark yellow. When the development is nearly finished, the egg strings appear greyish. A close inspection reveals that this is caused by the pigmentation of the veligers (Fig. 1a). Usually the fringe of the velum, the mouth and the oesophagus are dark. In addition there are dark patches on the wall of the stomach and, sometimes, along the gut and on the foot. The rest of the larva is of a light yellow colour. Eyes are not yet developed. Two large statocysts are distinctly visible. The shell is transparent and without any sculpture. When it has reached a length of 90 to 110 μ, the veliger hatches. The young of *Limapontia depressa* have a conspicuous black anal gland next to the anus. Except for this gland they are very similar to *Alderia*.

After being in the plankton for about 14 days, the larvae have grown considerably (Fig. 1b). The digestive gland has moved into the first whorl. Head and foot become dark except for the typical yellowish area around the eyes. A very mobile propodium is formed. The vela are transparent. Usually they have a dark stripe at the upper fringe, but fairly often this is not the case. Stomach and liver are

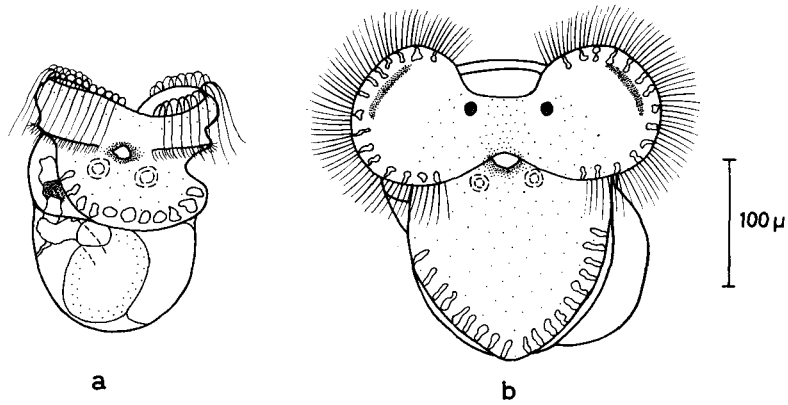

Fig. 1: Veliger of *Alderia modesta*. (a) 5 days old; (b) 14 days old

coloured by the food-contents. If the larva always has enough food available, the delicate shell – which is now about 200 µ long – grows regularly. If the amount of food differs greatly, the outline of the shell becomes rather uneven. *Limapontia depressa* differs from *Alderia* in that the foot remains yellow, the anal gland is darker and the dark stripe on the vela is seldom absent; in addition, there is usually a darkish patch in the center.

After about another three weeks the shell is 300 to 340 µ long and the veliger is ready for metamorphosis. The slug is only attached to the shell with its hindermost part. Except for this region containing the distinctly visible anal gland, the stomach, and the digestive gland, the whole veliger has become fairly dark, showing the pigmentation typical of the adult animal. The vela are still transparent with or without the dark stripe. Most of the time the larva is still swimming about, sometimes it is crawling on its foot, both ends of which are by now very movable and change their form every second. It takes about 12 hours to reduce the vela completely (Fig. 2a). At the same time the digestive gland is withdrawn from the whorl. Most of the time the larva crawls about; sometimes it stays immobile half withdrawn in its shell. It examines every filament it comes across. If it is cottonwool, the larva quickly leaves it alone; if it proves to be *Vaucheria*, it tries to eat it. Now the change of feeding habit occurs. It takes about another 12 hours until the digestive gland is completely withdrawn from the whorl of the shell. If *Vaucheria* is available, the larvae move very skilfully about on the thalli.

Without any interruption they suddenly move out of the shell, shedding it together with the operculum (Fig. 2b). The visceral hump slightly protrudes at the

left side where the digestive gland was situated. The anal aperture lies asymmetrically on the right side. It is slightly elevated. The visceral hump is longer than the foot; there is a split between the two, which disappears the next day. The whole body is covered with cilia.

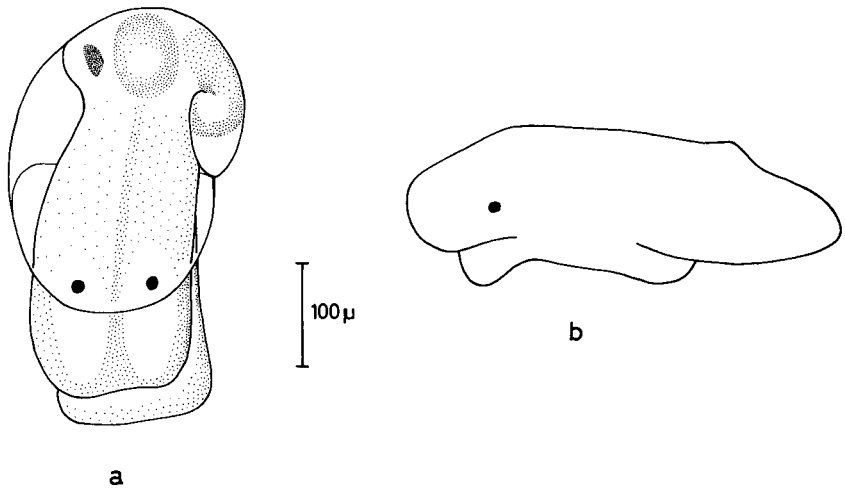

Fig. 2: (a) Larva of *Alderia modesta* ready to shed the shell; (b) *Alderia modesta* just after metamorphosis

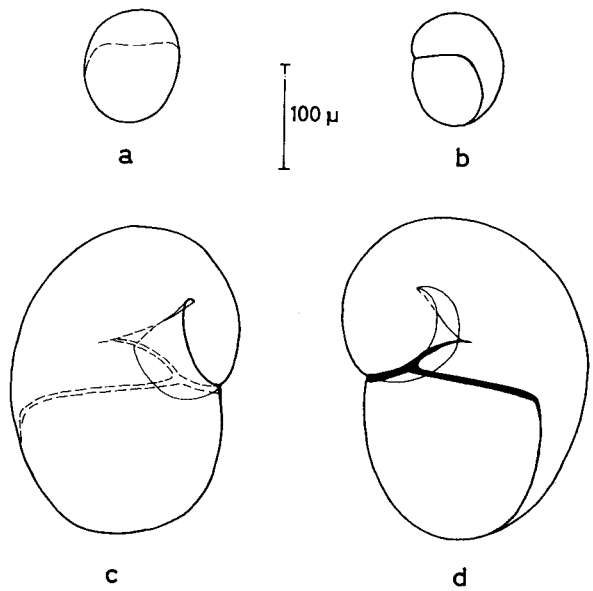

Fig. 3: Shells of *Alderia modesta*. (a) and (b) shell of a one day old larva; (c) and (d) shell shed at the metamorphosis

The young slug immediately feeds on the *Vaucheria* thalli. It embraces a filament with its propodium and bites a hole into it to suck out some juice.

If the veliger does not come across *Vaucheria*, metamorphosis is delayed for some time. Finally it takes place on the glass wall of the vessel, or sometimes the larva crawls out of the water.

Metamorphosis of *Limapontia depressa* takes place in the same way. Since the pigmentation of the head and the size of the young are the same as in *Alderia*, the

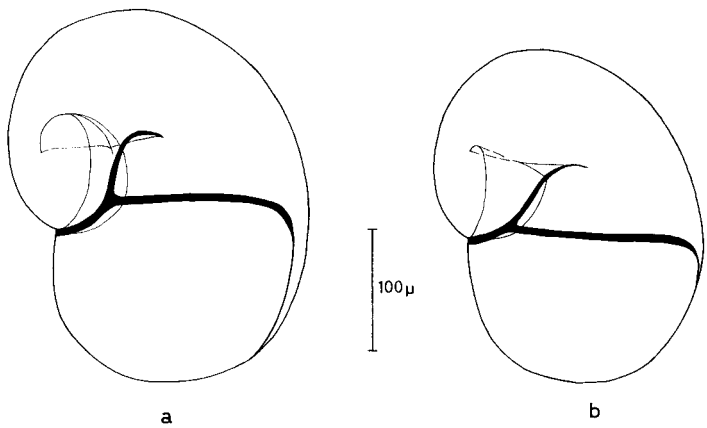

Fig. 4: Shells of *Limapontia depressa* (a), and *Alderia modesta* (b), both being shed at metamorphosis

species cannot easily be distinguished. Even the smell is the same. The only reliable difference seems to be the lightly coloured foot of *Limapontia*. The shells are slightly different as illustrated in Figure 4.

After two days the first pair of cerates grows next to the anus, which by now has moved towards the middle. The number of cerates increases with the growth of the animal from the first pair towards the front (Fig. 5).

After ten days *Alderia* has reached a size of about 3 mm and starts producing eggs. The animals are still growing. The average size of fully grown individuals from the coasts of the North Sea is 5 mm, from the Baltic, 8 mm (the largest being 12 mm). The duration of development depends mainly on the prevailing temperature. A prolongation of the planktonic phase of several weeks, perhaps months, seems possible when water temperatures fall. The same is true for the period between uncleaved egg and hatching of the veliger. If the salinity is suitable, the larvae hatch after $3^1/_2$ days at 20^0 C; this takes 5 days at 14^0 C and 4 weeks at an average temperature of 2^0 C. It seems justified to extend these results on the duration of the veliger phase.

Experiments carried out to test the salinity tolerance of *Alderia modesta* revealed that those from the North Sea react differently than those from the Baltic. The latter get on well at lower salinities, and their eggs can stand fresh water flooding far better than the North Sea animals. The tested slugs from the Baltic, which were accustomed

to a salinity of about 17 ‰, cannot withstand a permanent dilution down to 5 ‰. This means they cannot exist near Helsinki, where *Alderia* has been recorded. There seem to be genetic differences in the different populations. Whether different species, subspecies or clines are involved, cannot yet be decided. RIEDL's statement that *Alderia*

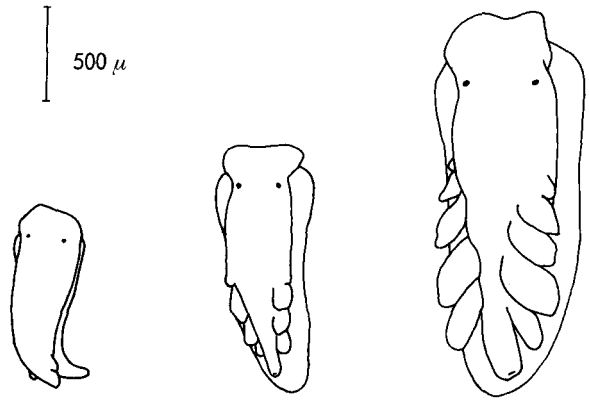

Fig. 5: Three specimens of *Alderia modesta* illustrating the development of the cerates

modesta lives on rocky shores of the Adria seems to show that perhaps a review on the systematics of *Alderia* might be desirable (RIEDL 1963). The results submitted in this paper must be considered in this light.

SUMMARY

1. *Alderia modesta* LOVÉN lives in enormous numbers on *Vaucheria*-cushions near the supralittoral fringe of the European coasts in salinities from 5 to 40 ‰.
2. Eggs are produced throughout the year whenever the temperature permits.
3. During the warm season one adult animal deposits about 1,000 eggs per day.
4. After 4 to 5 days, the larvae hatch and begin their planktonic life. They are planktotrophic and require at least 30 days until they are ready for metamorphosis. Consequently, they contribute considerably to the number of veligers in the plankton; a fact which has hitherto not been realized. Descriptions and figures of the larvae are presented.
5. Adults, larvae and eggs are very sensitive to changes in salinity. A differentiation between populations from the western Baltic and from the North Sea must be made. The latter are much more sensitive to fresh water than those from the Baltic. The species *Alderia* may by regarded as euryhaline, but the individual slugs are stenohaline.
6. Reconsideration of the taxonomy of the genus *Alderia* appears desirable.

Die Untersuchungen wurden mit Hilfe einer Sachbeihilfe der Deutschen Forschungsgemeinschaft durchgeführt, die Herrn Prof. Dr. REMMERT für seine Arbeiten an der biologischen Grenze zwischen Land und Meer zur Verfügung gestellt wurde.

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Discussion following the paper by SEELEMANN

WEBB: Is the colour difference in this animal a case of genetic polymorphism, and if so, do the different colours occur in different proportions or different substrates possibly due to predation?

SEELEMANN: Die mitgeteilten Farbdifferenzen zwischen *Alderia* und *Limapontia* sind sicher genetisch bedingt. Die Färbungsdifferenzen zwischen den verschiedenen Alderien sind sehr wahrscheinlich auf verschiedenes Nahrungsangebot zurückzuführen.

THORSON: Was passiert, wenn *Alderia* ohne *Vaucheria* gehalten wird?

SEELEMANN: Die Metamorphose von *Alderia* verzögert sich bei Fehlen von *Vaucheria* im Zuchtgefäß um etwa 10 Tage.

THORSON: Wieviel Eier vermag eine *Alderia* während ihres Gesamtlebens zu produzieren?

SEELEMANN: Das läßt sich derzeit nicht exakt sagen. Durch einen Monat hindurch hatte ich im Labor einen Tagesdurchschnitt von etwa 1000 Eiern (zwischen 80 und mehr als 2000 Eiern pro Tag).

THORSON: Haben Sie Gelegenheit gehabt, die Wirkung von Hochfluten auf *Alderia* und *Vaucheria* zu beobachten?

SEELEMANN: *Alderia*-Populationen werden ebenso wie *Vaucheria*-Rasen durch Hochfluten stark in Mitleidenschaft gezogen. Wo man vorher Tausende von Schnecken fand, sucht man sie nach einer Hochflut vergebens.