Larval Development of Benthic Invertebrates in Antarctic Seas: Early Development of Nothria notialis (Monro) and Paronuphis antarctica (Monro) in Bransfield Strait, Antarctic Peninsula

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Abstract: Larval development of Antarctic polychaetes is reviewed. The brood care of two species of Onuphidae, Nothria notialis Monro and Paronuphis antarcticus (Monro) is illustrated for populations in the Bransfield Strait, Antarctic Peninsula, in depths of about 800 to 900 m.

Larval development of invertebrate metazoan animals in polar seas is generally believed to proceed from relatively few, large ova which develop without planktonic stages. This is in contrast to the development of related animals in warm seas, where numerous small ova develop in the plankton before transforming to bottom stages (THORSON, 1956). Direct development has the advantages of guaranteeing the stability of a population; the larvae are sustained on yolk and are thus not dependent on plankton; they are protected in their early growth stages by the presence of egg-cases which afford protection from adverse conditions, and the emerging larvae find a suitable biotope on escaping from the oothecae. Polar species in shallow seas are believed to breed periodically, at a time most favorable to the emerging young. External factors triggering the release of ova may be various; they are concerned with a raising or lowering of water temperature, a change in intensities of light, and a decrease in hydrostatic pressure, such as occurs in tidal depths. The importance of the water pressure in littoral species has been shown for a serpulid, Spirorbis borealis Daudin; ova are liberated during neap tides when hydrostatic pressures are lowest (KNIGHT-JONES et al., 1965, p. 1). The effect of decreased hydrostatic pressure was earlier suggested by FRIEDLANDER (1898) for the great swarms of Palola viridis Gray, which spawn in the Fiji Islands on the day of the last quarter of the October or November moon.

The benthos of Antarctic deep seas is characterized by absence of light, uniformly low temperatures with no seasonal changes, and hydrostatic pressures which do not vary as do those in intertidal zones.

Incubation in Antarctic and Subantarctic polychaetes is only sparsely recorded. The polynoids coming from latitudes beyond 50° S are known for at

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least 52 species in 19 genera. Four pelagic species are known to incubate ova under their scales; they are Antinoella pelagica (Monro), Harmothoe benthophila intermedia Stop-Bowitz, both from South Georgia; Harmothoe lagiscoides Willey from Enderby Land, Sheila bathypelagica Monro, from off South Africa, and Lagisca hubrechti (McIntosh) ranging through Atlantic and Antarctic oceans. A benthic polynoid, Polynoe antarctica Kinberg, in the Magellan and Palmer Archipelago areas, also carries ova under the scales.

The syllids are known through at least 40 species in 15 genera; species are most frequent in Subantarctic regions, in moderate to shallow depths. Five species in the Autolytinae undergo alternation of generations in which the benthic stock buds off modified individuals which become natatory and go to the plankton. The Exogoninae, with six species, generally release large, yolky ova which they attach to the body segments, and carry the developing larvae to an advanced stage. At least two, Brania rhopalophora (Ehlers) and Exogone heterosetosa McIntosh, acquire modified setae at sexual maturity, but it is not known that they become planktonic. Three species of Antarctic Sphaerosyllis acquire swimming setae. The giant Antarctic syllid, Trypanosyllis gigantea (McIntosh) grows until it acquires 200 or more body segments; then buds off a linear series of four or five tetraglene stolons, each of which breaks away as a spawning individual. Tetraglenes have been taken in the Ross Sea in September (MONRO, 1936, p. 126), in Mc-Murdo Sound in February and March (EHLERS, 1912, p. 17) and off the Antarctic Peninsula in January (ELTANIN Sta. 439). Pionosyllis nutrix (Monro) carries developing ova attached to the dorsum in February (MONRO, 1936, p. 128). Mystides notialis Ehlers deposits a mass of large ova which the female surrounds (GRAVIER, 1911, p. 60).

Nereidae frequently become epitokous when mature. *Platynereis magalhaensis* Kinberg *Eunereis patagonica* (McIntosh) and *Neanthes kerguelensis* (McIntosh) abundant in the Magellanic-Kerguelen regions, occur in moderate to shallow depths, where they transform to epitokes in January and February (ELTANIN Sta. 435, 436, 932, 974). *Eunereis patagonica* (McIntosh) has been observed once as an epitoke, in September (ELTANIN Sta. 222). *Perinereis falklandica* Ramsay, in the Falklands Islands, becomes subepitokous (FAUVEL, 1941, p. 281) and thus perhaps also epitokous. *Namanereis quadraticeps* (Blanchard) is a hermaphroditic euryhaline species in the Magellan area (FAUVEL, 1941, p. 283) and thus not planktonic.

Among the nephtyids, *Aglaophamus* sp. was taken once from the Pacific Antarctic Basin, in January, in 2562 m over 4118 m (ELTANIN Sta. 941). *Flabel-ligera mundata* Gravier, from the South Shetland Islands, in 420 m, carries ova in the cephalic cage in December (GRAVIER, 1911, p. 110).

These examples illustrate the diversity of larval development among some of the Antarctic polar polychaetes. It can be concluded that epitoky is more or less limited to Subantarctic regions in shallow to moderate depths.

One of the most successful polychaete families in moderate to great depths of Antarctica is the Onuphidae, represented by at least 15 species in six genera, all tubicolous. They have been recovered in samples of the ELTANIN in great numbers, especially from deep to abyssal samples. Three of these onuphids are more or less cosmopolitan, known from world-wide areas and extend south into Subantarctic seas; none shows any indication of brood care. They are:

Hyalinoecia tubicola (Muller), Nothria conchylega (Sars) and Nothria iridescens (Johnson). Each of these has been traced south into Subantarctic regions. H. tubicola is one of the giants of the onuphids; it occurs in greatest abundance in the Falkland Islands in depths to 353 to 462 fms. In its abundance it may be compared with the longest of all known polychaetes, Onuphis teres (Ehlers), which in southeastern Australia attains a length of up to 200 cm and numbers countless of millions in some sandy beaches (DAKIN, 1960, p. 148). Nothing is known of the reproduction of these aggregating giants.

Another onuphid, Onuphis dorsalis (Ehlers) occurs in the Magellan and Falkland areas in shallow depths; its development is unknown. Four other species are known through single records, all from abyssal Antarctic depths; they are Nothria abranchiata McIntosh, Onuphis armandi (McIntosh), Paronuphis antarcticus (Monro) and Paronuphis benthaliana (McIntosh). Five other abyssal species have been identified in samples taken by the ELTANIN; they are Nothria from deep water off Chile, another from Drake Passage in 4200 m, one from south of the Falkland Islands in 2452 m, and one from north of the Shetland Islands in 3678m. An unknown Paranorthia comes from the Weddell Sea, in 3250 m. Onuphis paucibranchis (Ehlers) is an abyssal form throughout deep basins of the Antarctic, into south Pacific regions,

Two species, Nothria notialis Monro and Paronuphis antarcticus (Monro) both abundant but not limited to the Bransfield Strait north of the Antarctic Peninsula, in 800 to 900 m, have been found to exhibit a highly evolved pattern of incubation in January. Nothria notialis constructs long, cylindrical tubes internally chitinized and externally covered lightly with silt and scattered pebbles attached along its exposed, distal end. The tube of the female has as many as six to fourteen lateral capsules, in alternate series; each capsule contains two (seldom three) deposited ova or developing larvae. The oldest or most developed have 24 segments, at the lowermost end of the series. Successive capsules contain less developed individuals, and the distalmost have yolky masses which are undifferentiated. The time lapse in developing larvae in a single tube strand may thus represent a period of weeks during which oviposition occurs. The two larvae in a capsule are in about the same stage of development; there is no indication of cannibalism wherein the stronger individuals subsist on weaker ones. Each capsule is partly shut off from the parent tube by a web-like membrane which may permit exchange of water currents or nutrients, but the larvae are unable to flow back into the parent tube. The youngest segmented larvae resemble grubs in which a large yolk mass overlies a platform consisting of partly developed cephalic region and ten or more embryonic segments. The oldest larvae consist of a well developed cephalic region and 24 parapodial segments; the alimentary tract is complete and the pharyngeal armature well developed; they resemble adults in all respects but size and number of segments.

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Another onuphid, *Paronuphis antarcticus* (Monro) has been taken in samples with *Nothria notialis*. It constructs long, cylindrical, silt-covered tubes in which ova are deposited along the inner walls. The ova flush freely away from the tube. Larvae up to an advanced, 24-segmented stage have been observed partly emerging from the tube. There is no indication that the developing larvae are partitioned off from the adult. The adult tube is open at either end, permitting escape from anterior or posterior ends. It is not known how the young or developing ova maintain their position in the tube unless there is some mechanism whereby they are either retained in parapodial grooves or in a weakly retaining membrane of the tube-lining.

The available evidence indicates that Subantarctic species are not incubating, whereas their Antarctic relatives display a greater or lesser degree of brood-care.

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