Sigmoidal growth in the brittle star *Amphiura filiformis* (Echinodermata: Ophiuroidea)

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**Abstract** The post-larval growth pattern and dynamics of *Amphiura filiformis* (Echinodermata: Ophiuroidea) were investigated in 1991 at the sill of the Gullmarnsöfjord. A total of 201 specimens were examined in detail by video-techniques to analyse the growth patterns of disks, arms and arm segments. Maximum settling was recorded in October, with 7,100 ± 7,400 (mean ± SD) ind. m⁻², after which settlement rapidly declined. The initial size of the settlers was around 300 μm in disk diameter with one arm segment developed. Specific growth rates during August–November were 0.42% day⁻¹ for disk diameter and 1.76% day⁻¹ for mean arm length. Growth of the oral width between 1.5 and 3 mm (3.6–9.7 mm disk diameter) shows a von Bertalanffy growth pattern, and the best fit for early growth was a model in which disk size increased exponentially with time. When combining the juvenile growth curve with adult growth curves from the literature, an asymptotic sigmoidal pattern appeared, which was best described by a Gompertz curve, suggesting that adult size and sexual maturity (ca. 4 mm disk diameter) are attained around 2 years after settlement. The inflexion point in the sigmoidal growth curve occurs ca. 1 year after settlement, at an approximate disk diameter of 2 mm. The higher growth rate after the early phase of life is suggested to be attributable to the attained capability of suspension feeding at this size, which in this species may be a more efficient means of acquiring energy than other modes of feeding. Predictions of disk diameter (up to 6 mm) from the reconstructed growth curve correspond well with measurements from the North Sea and elsewhere.

**Introduction**

The ophiuroid *Amphiura filiformis* (O.F. Müller) has been considered a key species of Northeast Atlantic silt-mud bottoms below 2 m (Petersen 1915). Abundance of adults range from 90 ind. m⁻² (W Scotland; Pearson 1970) to 4,000 ind. m⁻² (N Kattegat; Josefson and Jensen 1991). Populations of *A. filiformis* have often been characterised as structurally stable in time, and adults comprised of several year classes dominate populations (Ockelmann and Muus 1978; O’Connor et al. 1986; Sköld et al. 1994). This accumulation of year classes combined with a low level of recruitment makes it difficult to separate cohorts and consequently to determine age. Life span estimates from different areas show great variation: 2–25 years (summarised in O’Connor et al. 1983). *A. filiformis* has an even sex ratio (Ockelmann and Muus 1978; Bowmer 1982), and Ockelmann and Muus (1978) reported that *A. filiformis* is polytelic and that spawning occurs in an epidemic way, with males maturing a little earlier than females. Thorson (1961) found *A. filiformis* larvae in the plankton of the Öresund mainly from the beginning of August to the end of November, and in the southern North Sea newly settled *Amphiura* larvae were first found in July and disappeared by the end of August (Duineveld and van Noort 1986).

Despite accumulating information over the years on the biology and population dynamics, the growth pattern for the entire benthic phase has not yet been described. Especially the role of the juvenile stages in the population dynamics of *A. filiformis* is poorly understood; one reason for this is the method used to sort fauna, i.e. only using a sieve with a mesh size of 1 mm (Muus 1981). We are aware of only one study of growth dynamics of the juvenile phase of this species (Muus 1981). Among few studies that have attempted to model somatic growth in this species (Gage 1990; Sköld et al.
1994; Josefson 1995, 1998) none included the juvenile phase. Therefore, the amount of time the species requires to attain adult size is still unclear. Information on when maturity is reached is, for instance, important in the evaluation of the recovery capacity of the *A. filiformis* community, which is one of the quantitatively most important communities in coastal areas of the northeastern Atlantic.

The aim of the present study was to describe the post-larval population dynamics of *A. filiformis* and somatic growth during the first year of life. We also aimed at constructing a growth curve for *A. filiformis*, covering the entire benthic part of the life cycle. Because of the long life span we have combined the present data on early growth with data from the literature on adult growth in various parts of the same geographical area.

**Materials and methods**

**Station description**

The station where early growth was studied is situated at the sill of the Gullmarnsfiord, on the Swedish west coast (58°14'72 N; 11°25'80 E; Fig. 1) at a water depth of 40 m. The salinity at this depth varies between 30 and 34, and the temperature between 4.6°C and 13.8°C (Fig. 2). Oxygen concentrations at the adjacent station “Slaggö” were not observed to reach critical levels during the study period. The sediment consisted of unsorted, clayey mud, with a water content varying between 55% and 63% wet weight. The organic matter and organic carbon content of the sediment was relatively constant during the sampling period, with annual means (±SD) of 3.5±0.3% and 2.37±0.28%, respectively, based on sediment dry weight (Sköld et al. 1994).

**Sampling**

Quantitative benthic samples were collected in 2–3 week intervals over the period from 23 March 1991 to 4 November 1991. Two samples were taken with a box-corer (0.1 m²) on each occasion. The overlying water in the core was siphoned off, and three replicate sub-samples were taken in each core with a plexiglass tube (5 cm internal diameter) pressed down to 4 cm in the sediment. After the samples had been conserved in 96% ethanol they were washed in seawater on a 200 μm sieve, and sorted under a dissecting microscope. All ophiuroids were videotaped, disk diameter and mean arm length were measured by image analysis, using the software NIH Image 1.50, and the number of arm segments was counted.

**Statistics**

Temporal changes in densities of individuals were analysed in a two-factor, nested ANOVA, with time as the fixed orthogonal factor and core as a random factor nested in time. Cochran’s test for homogeneity of variance (Underwood 1981) showed significant heterogeneity (*P* < 0.05); thus, the data were log + 1 transformed.