Paralarval gonatid squids (Cephalopoda: Oegopsida) from the Mid-North Atlantic Ocean

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Abstract.—Ninety six gonatid cephalopod specimens (Oegopsida: Gonatidae) from the University of Amsterdam Mid-North Atlantic Plankton Expeditions were analyzed and two species were identified: *Gonatus steenstrupi* (Kristensen 1981) and *Gonatus fabricii* (Lichtenstein 1818). Gonatids were collected only in spring and summer, despite sampling in autumn and winter. This paper describes aspects of their development and reports their geographical distribution in the central North Atlantic Ocean. Chromatophore patterns were the most consistently useful characters for distinguishing between the species. Among 34 measurements, Tentacle Length (TtL) relative to Dorsal Mantle Length (ML) and number of suckers on Arms I–IV were useful for distinguishing specimens >13 mm ML. Both species develop hooks from suckers on the arms and tentacular clubs at ML >20 mm. Subtle differences were noted in the morphology of the funnel pads except in the smallest specimens. Specimens of *G. steenstrupi* >20 mm ML were collected at greater depths (250 to 995 m) than the smaller specimens (found at depths <200 m). Our data suggest that 20 mm ML is the point of transition between paralarvae and juveniles of *G. steenstrupi,* because specimens larger than 20 mm ML have well defined hooks, and a juvenile vertical distribution is established.

Knowledge of early-life-history stages is required for comprehensive understanding of the ecology of squids. These stages presumably are most vulnerable to starvation and predation and they occupy a separate niche from older conspecifics (Vecchione 1987). Because of controversy about use of the term "larva" for early life history stages in cephalopods, Young & Harman (1988: 202) introduced the term "paralarva" for "a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctly different mode of life from that of older conspecific individuals." The paralar-val concept includes both morphological and ecological features, in contrast to the definition of a "larva", which is based on morphological differences from the adults.

The University of Amsterdam, Netherlands, conducted four research expeditions in the North Atlantic Ocean between 55°N and 24°N approximately along 30°W longitude. This research was designed to "elucidate the patterns of latitudinal diversity, taxonomical variation below species level, vertical variation and interaction of climate, hydrographic features and ecology on morphological variation of marine plankton" (Van der Spoel 1981:1). The expeditions
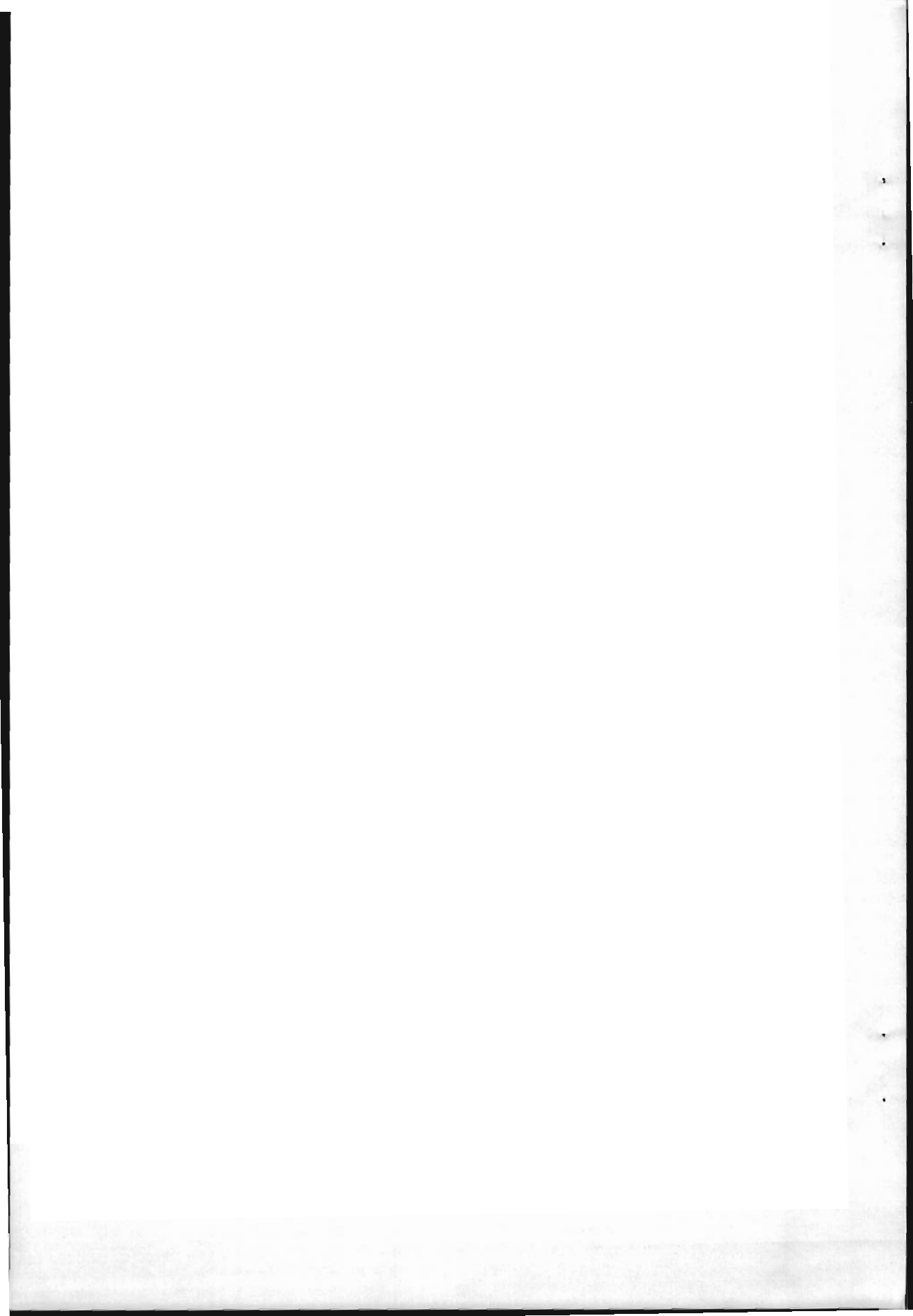
were conducted during four consecutive years (1980–1983), each during a different season (Van der Spoel 1981, 1985; Van der Spoel & Meerding 1983). Discrete-depth samples were collected using opening/closing nets. Cephalopod paralarvae sorted from the samples were donated to the National Museum of Natural History, Smithsonian Institution for systematic and ecological studies. Shea (1995) sorted the material into families in preparation for subsequent studies. The present paper reports on paralarval development and distribution of the squid family Gonatidae in these samples.

The identification of paralarval cephalopod stages is difficult because of insufficient collections which often come from inadequate sampling devices and methods, and because of poorly understood taxonomy, even in adults (Vecchione 1987). This is true for the genus *Gonatus* in the North Atlantic Ocean in which only one arctic/boreal species was recognized, *Gonatus fabricii* (Lichtenstein 1818), until Kristensen (1981) described *Gonatus steenstrupi* from boreal waters. At least five *Gonatus* species are found in the North Pacific Ocean and one in the Southern Ocean (Kristensen 1981). The primary morphological characters used to separate adults of the two North Atlantic species are (a) the presence or absence of chromatophores on the ventral surface of the head, (b) the shape of the funnel organ, and (c) the patterns of hooks and suckers on the tentacular clubs. The onset of formation of hooks from suckers both on the tentacular clubs and arms I–III seems a good character to define the differences between paralarvae and juveniles in gonatids (Young 1972, Kristensen 1977a). The presence of hooks presumably indicates a change in feeding and therefore in the squid's role in the oceanic trophic structure.

The main goals of the present study were to identify the species of paralarval gonatids in the Mid-North Atlantic collections, to analyze early-life-history features that could separate paralarvae from juveniles, and to determine the distribution of the two species in these samples.

Methods

Gonatid specimens were arranged by size and their taxonomic identification began with the largest specimens, then proceeded sequentially to the smallest specimens. We looked in particular for previously unrecognized taxonomic characters for these paralarvae, in addition to using various taxonomic guides (Kristensen 1981, Nesis 1987, Roper et al. 1984). Fifteen specimens were damaged and were excluded from some of the quantitative analysis. Characters were measured or counted on each of the 81 undamaged gonatids following Roper & Voss (1983), including:

ML (Dorsal Mantle Length); MW (Mantle Width); HL (Head Length); HW (Head Width); ED (Eye Diameter); FL (Fin Length); FW (Fin Width); TL (Total Length); TtL (Tentacle Length); CL (Club Length); AHI-IV (number of hooks on Arms I-IV); ASI-IV (Arm I-IV Sucker counts); ALI-IV (Arm I-IV Length); AWI-IV (Arm I-IV Width).

We also measured the following characters: D (Dactylus Length); M (Manus Length); C (Carpus Length); CS (Club Sucker Length); ForgL (Funnel Organ Length); ForgW (Funnel Organ Width); ForgL1 (Funnel Organ Dorsal Pad Length); ForgW1 (Funnel Organ Dorsal Pad Width). Characters on damaged specimens were measured when their condition permitted.

Three specimens of different sizes from each of the two species were selected based on condition, and their third arms and tentacular clubs (left for *G. fabricii* and right for *G. steenstrupi,* because of specimen damage) were removed for scanning electron microscopical (SEM) analysis. The specimens had been fixed in formalin and preserved in 45% isopropanol. Tissue for SEM was transferred through a dehydration series to 100% ETOH prior to critical-point drying, which was conducted using a Den-

ton Vacuum-1₁ Critical-Point Dryer. The arms and tentacular clubs were examined using a Leica 440 SEM to find morphological features that could separate the species.

Results

In total, 96 specimens of the family Gonatidae were collected during the spring (1980) and summer (1983) cruises. No gonatids were found in samples from the other two cruises. The presence of two chromatophores on the ventral side of the head in *G. fabricii* and their absence in *G. steenstrupi,* the shape of the funnel organ and the development and pattern of hooks and suckers on the tentacular club were the basic features that we used to distinguish these two species. The 96 gonatids were separated into 43 *G. fabricii* and 38 *G. steenstrupi,* the remaining 15 specimens were too damaged to determine species with certainty. The 81 undamaged specimens ranged in size from 1.6 to 31.6 mm ML in *G. steenstrupi,* 3.3 to 24.1 mm in *G. fabricii* and 3.0 to 10.8 mm for the damaged specimens.

Gonatus fabricii paralarvae are characterized by the presence of a pair of round or oblong chromatophores on the ventral surface of the head slightly anterior to the ocular axis (see Kristensen 1981:67, fig. 3 for specimens larger than those reported here). The dorsal pad of the funnel organ in this species has an inverted V-shape with very straight lateral sides (Fig. 1; cf. Kristensen 1981:69, fig. 5). After the largest specimen of *G. fabricii* (24.1 mm ML) was identified, published taxonomic characters could then be recognized in progressively smaller specimens. The presence of chromatophores was the primary character used to identify the smallest specimens of *G. fabricii.* The funnel organ is so small in specimens <3.6 mm ML that its shape can not be determined confidently. Scanning electron microscopy on specimens of 24.1, 14.6, and 7.2 mm ML revealed that the patterns of hooks and suckers on the tentacular clubs of the largest *G. fabricii* were similar

to those described by Kristensen (1977a, 1981). The largest specimen (24.1 mm ML) had one large hook, with three small hooks and a sucker proximal to the large hook. A concentration of small suckers occurs on both dorsal and ventral sides of the club, especially on the proximal end, where the suckers form a large cluster (Fig. 2d).

The largest specimens of *G. steenstrupi* (e.g., 31.6 mm ML) were identified following the description of the holotype (Kristensen 1981). The shape of the funnel organ is characterized by a slight curve on the lateral edges of the dorsal pad (Kristensen 1981: 83, fig. 20). This character can be seen in our largest specimens (Fig. 3). The absence of chromatophores on the ventral surface of the head is the primary distinguishing character of the smallest *G. steenstrupi* paralarvae available, which could not be identified based on funnel-organ morphology. Scanning electron microscopy was used to examine specimens of 31.6, 19.2 and 9.6 mm ML. The tentacular club of the largest specimen under SEM had the pattern of hooks and suckers described by Kristensen (1981) in which one large hook is preceded proximally with four small hooks and no suckers (Fig. 2c). At <20 mm ML the hooks are not yet well developed (Fig. 2a, b). *Gonatus steenstrupi* and *G. fabricii* smaller than 20 mm ML have similar sucker patterns in this central series on their tentacular clubs.

The scatterplot of the relation between TtL and ML for all the undamaged specimens indicates a growth curve for *G. steenstrupi* that diverges from that of *G. fabricii* at ML >13 mm (Fig. 4). The relation between TtL and ML is more linear for *G. fabricii* than for *G. steenstrupi,* perhaps because of the lack of large *G. fabricii* specimens. However, all *G. steenstrupi* >13 mm ML had tentacles that were longer than those of similar-sized *G. fabricii.* Extension of a quadratic function line fitted to the *G. fabricii* data indicates that the difference in TtL between species likely continues at larger sizes, although a shift in growth pa-
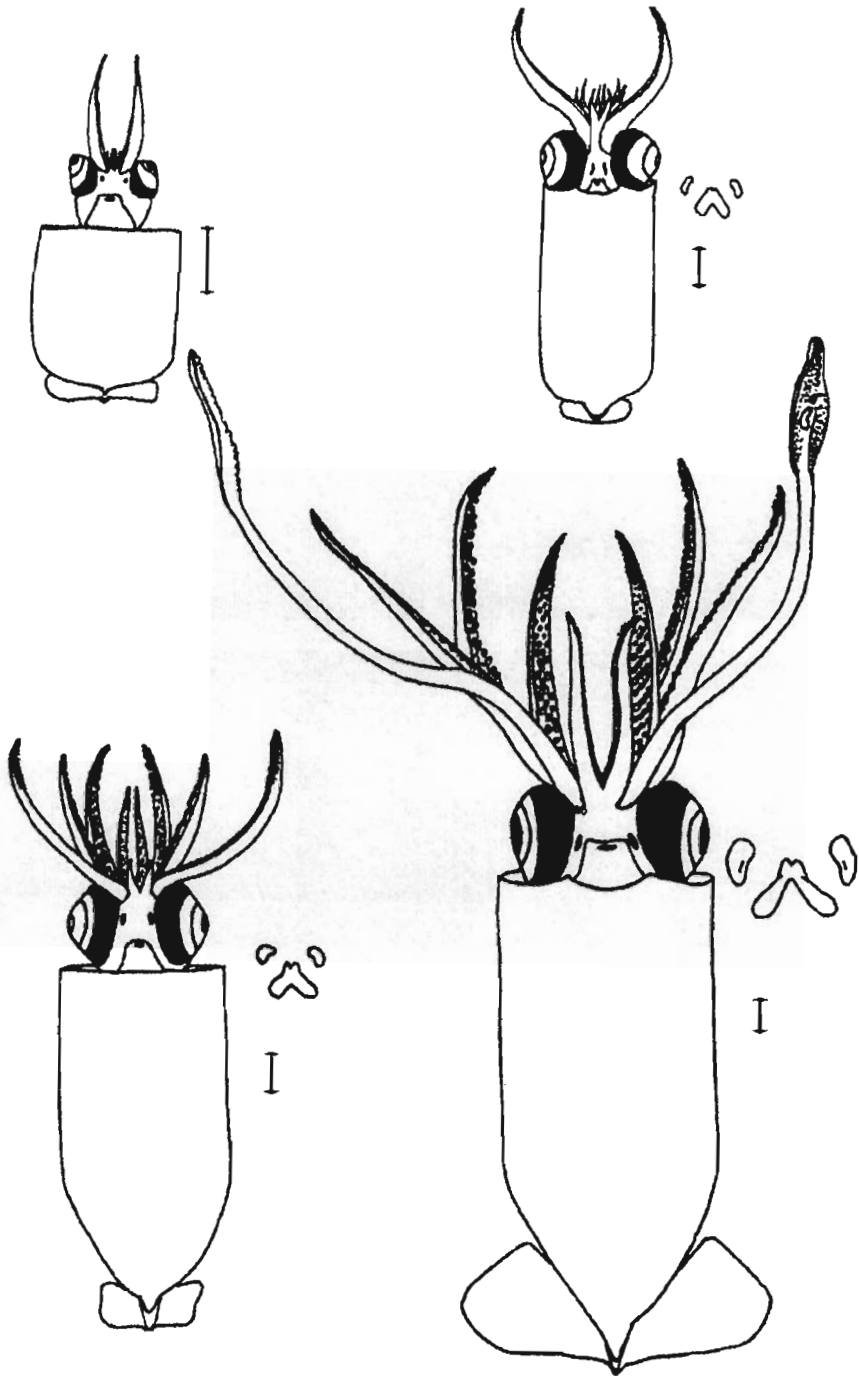
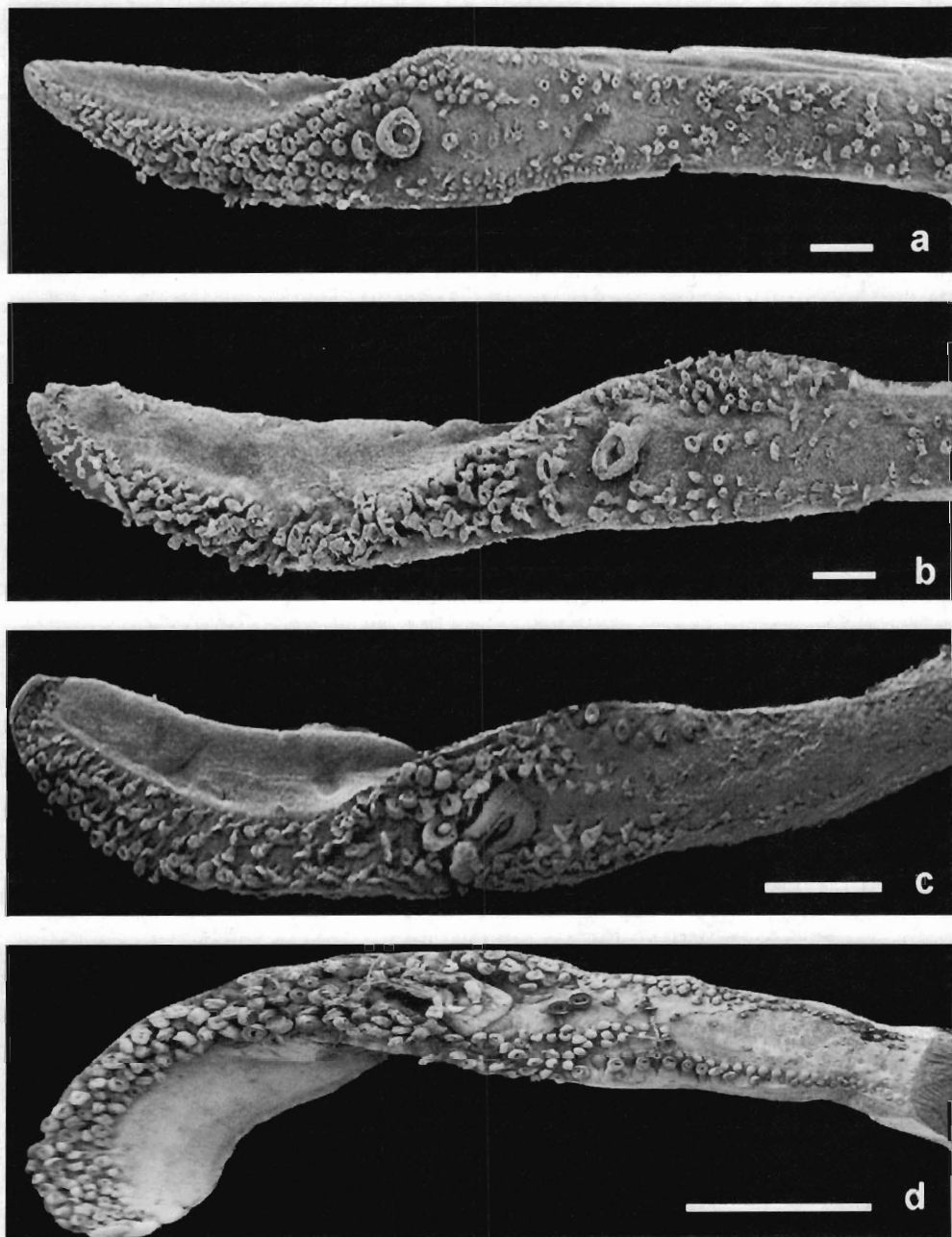Fig. 1.   Growth series of *G. fabricii*. Scale bar = 1 mm.

Fig. 2.   Tentacular clubs. a–c) *G. steenstrupi,* 9.6, 19.2, and 31.6 mm ML respectively, d) *G. fabricii,* 24.1 mm ML. Scale bars: a) 200 μm, b) 300 μm, c) 1 mm, d) 1 mm.

rameters at the transition between paralar-
vae and juveniles (Shea 1995) could either
reduce or increase interspecific differences.

Well-developed hooks on arms and ten-
tacular clubs and well-differentiated tentac-
ular clubs are found in specimens of both
species larger than 20 mm ML. Kristensen
(1981) described major differences between
these species on specimens larger than 37
mm gladius length, which is equivalent to
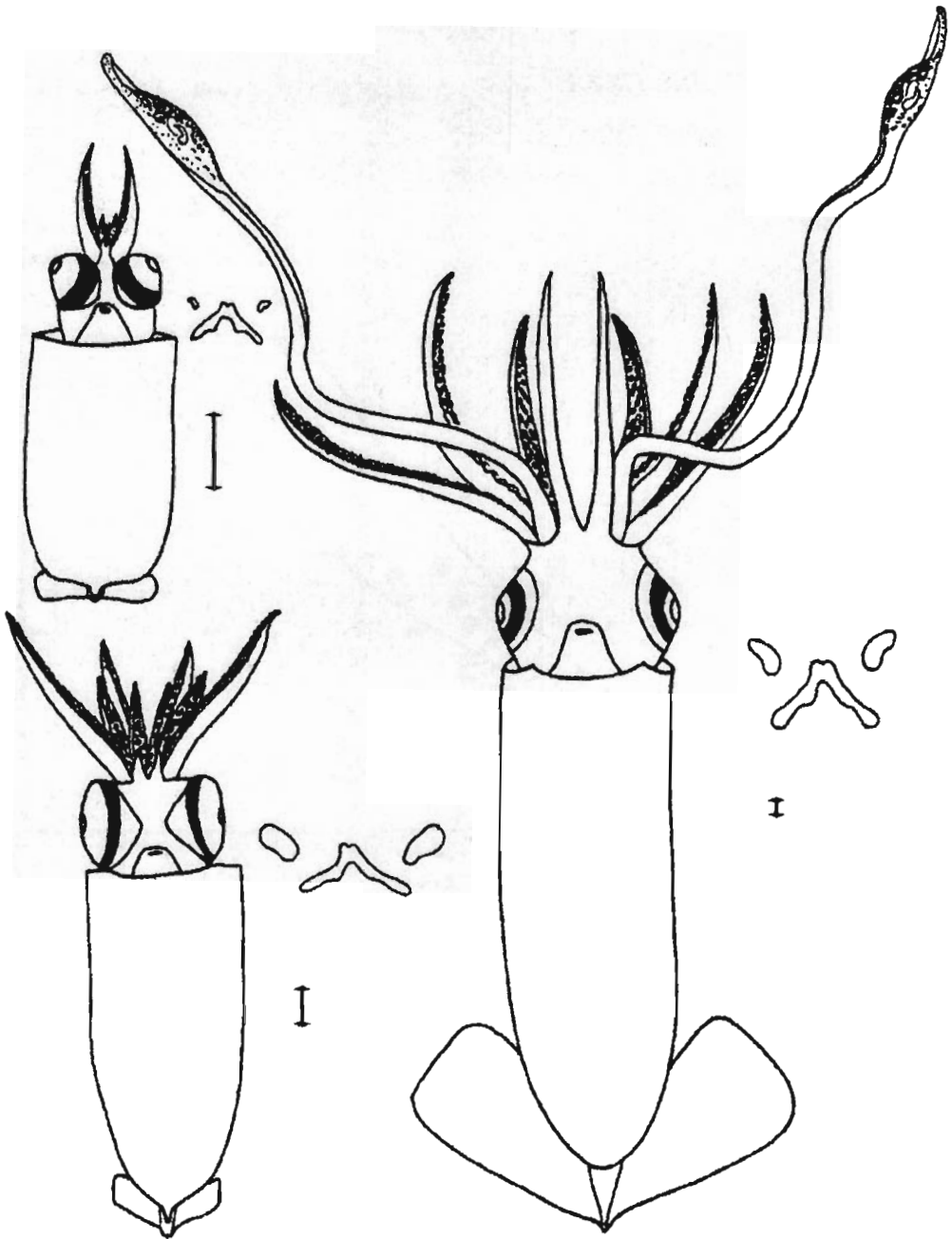
Fig. 3.   Growth series of *G. steenstrupi*. Scale bar = 1 mm.

ML in gonatids. Our SEM analysis of arm III suckers for *G. steenstrupi* of 31.6 mm ML (Fig. 5a) and *G. fabricii* of 24.1 mm ML (Fig. 5c) shows that no obvious differences occur, although the chitinous teeth of the internal ring of the suckers are sharper in *G. steenstrupi*. There is no difference between species in this character on smaller specimens (Fig. 5b, d).
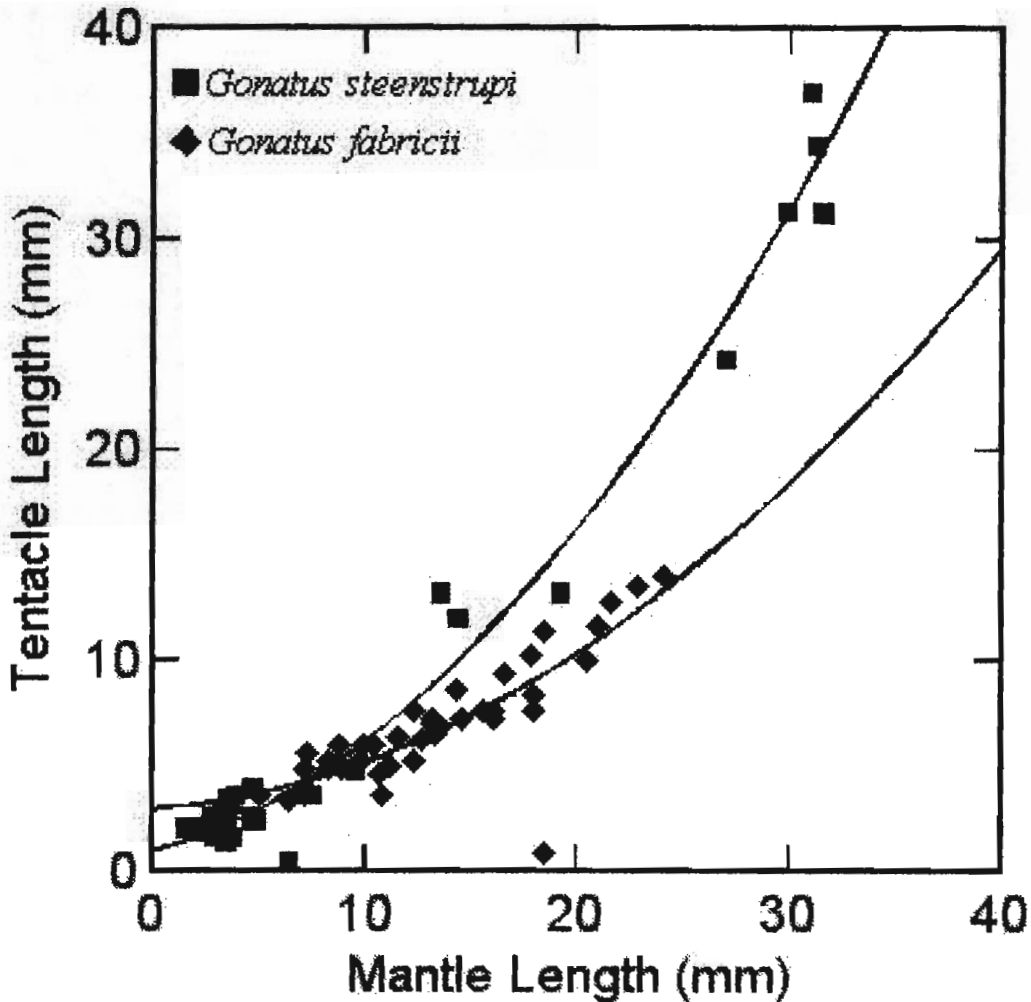
The vertical distribution of the paralar-

Fig. 4. Dorsal Mantle Length (ML) vs. Tentacle Length (TtL). Quadratic function lines are fitted to the scatterplots of the two species simply to identify trends in the data, rather than to test hypotheses of differences.

vae was analyzed for each cruise (Fig. 6). During the spring cruise (1980), *G. steenstrupi* larger than 20 mm ML were captured at the deepest sampling stations (250 to 995 m). The specimens smaller than 20 mm ML were collected in the upper 200 m, although one specimen of 2.8 mm ML was caught between 390 and 510 m. *Gonatus fabricii* differed in spring vertical distribution, exhibiting greater variability in depths for all sizes. All *G. fabricii* specimens were captured shallower than 400 m although samples were collected from

depths as great as 1750 m. The summer cruise (1983) showed a similar distribution for *G. steenstrupi* where specimens larger than 20 mm ML were caught between 490 and 995 m and those smaller than 20 mm ML were found in the upper 50 m. *Gonatus fabricii* were again found with greater variability in their vertical distribution, as specimens with 7.2 mm and 15.6 mm ML were collected at the deepest stations (1750 to 1000 m), while the rest of the sampled population was found in the upper 100 m.
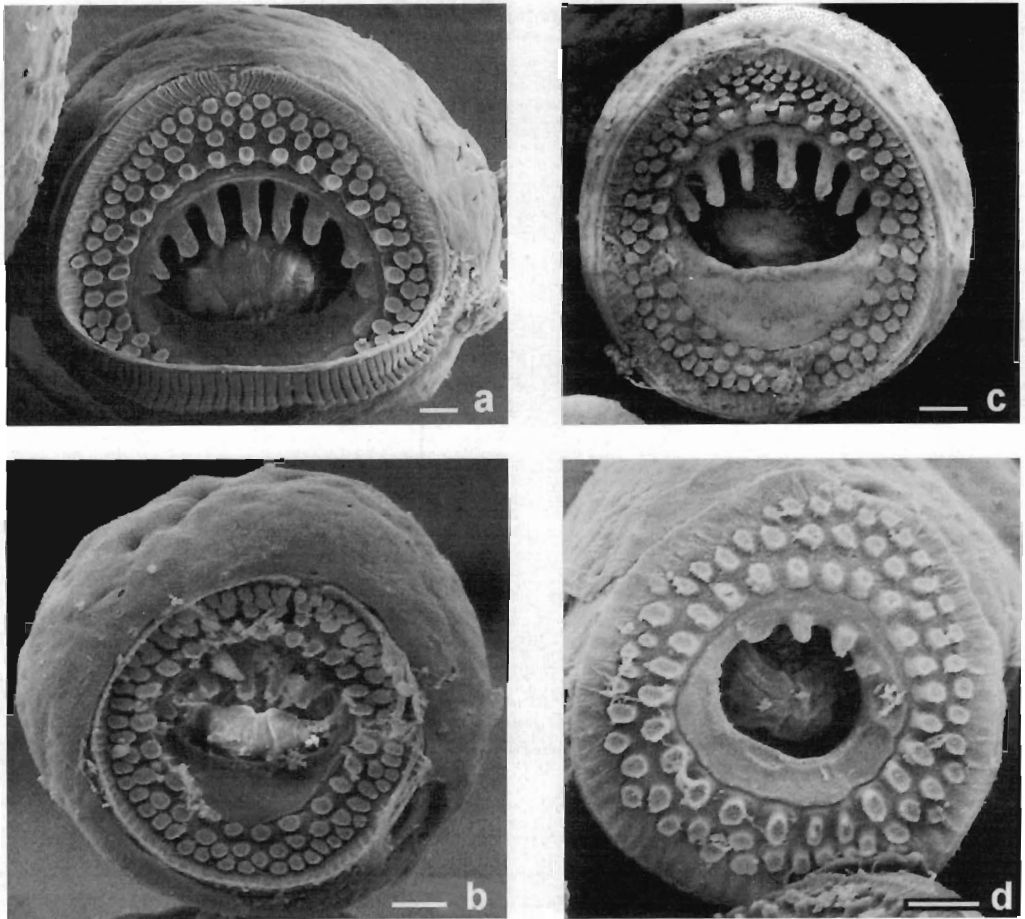
Fig. 5. Suckers in Arm III. a) *G. steenstrupi,* 31.6 mm ML, b) *G. steenstrupi,* 19.2 mm ML, c) *G. fabricii,* 24.1 mm ML, d) *G. fabricii,* 14.6 mm ML. Scale bars: a) 20 μm, b) 20 μm, c) 30 μm, d) 10 μm.

Discussion

Van der Spoel (1981) reported that during the 1980 spring cruise subarctic polar water was present at depths greater than 500 m north of 50°N. The 1983 summer cruise also may have sampled subarctic water north of 53°N, as well as an isothermal layer above the thermocline at depths greater than 90 m near 55°N. Both the spring (1980) and summer (1983) cruises found a well marked northern branch of the North Atlantic Drift, although the southern branch was much more marked in 1983 (Van der Spoel 1985). The presence of *Gonatus* in these samples likely resulted from the presence of cold subarctic water in the area.

Both *Gonatus fabricii* and *Gonatus steenstrupi,* occurred in a previously unreported distribution (54°53'54"N 029°55'48"W to 48°58'54"N 030°01'18"W). Earlier reports (Kristensen 1977b, 1981: 62, fig. 1) listed their distribution as nearer to the coast and much more northerly, especially *G. fabricii.* This new distribution extends the known occurrence of both species far offshore towards the Central North Atlantic Ocean and more southerly.

The change in vertical distribution by *G. steenstrupi* larger than 20 mm ML and the coincident presence above that size of well-developed hooks on the arms and tentacular clubs of both species may define the tran-
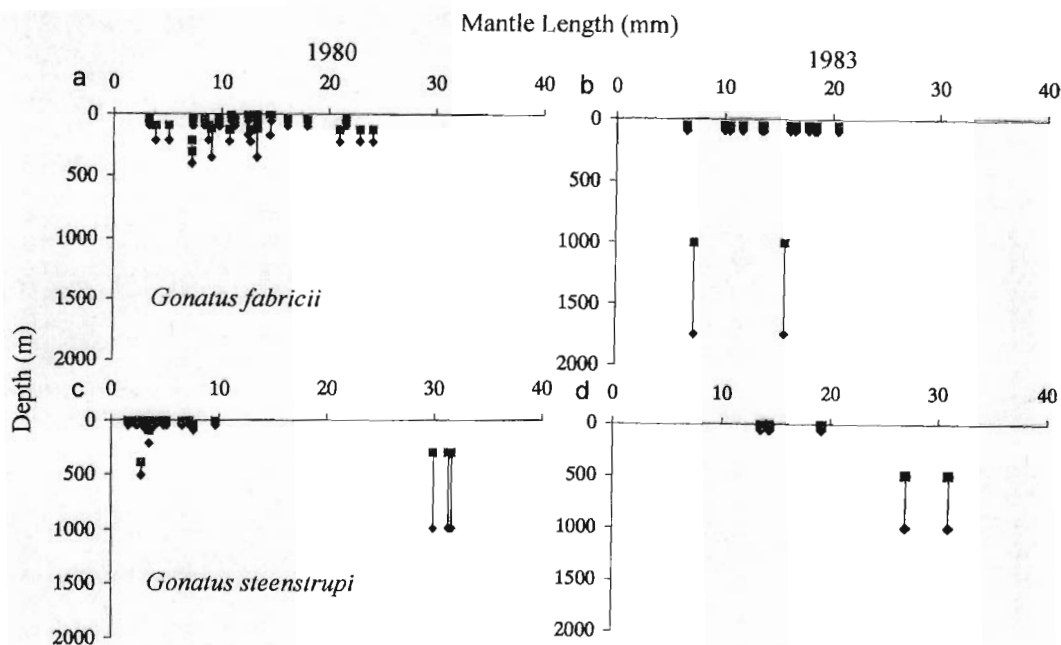
Fig. 6.   Depth of capture vs Dorsal Mantle Length (ML). a) *G. fabricii* in spring 1980, b) *G. fabricii* in summer 1983, c) *G. steenstrupi* in spring 1980, b) *G. steenstrupi* in summer 1983. Diamonds indicate depth at opening of net, squares depth at closing of net, vertical lines, depth range sampled.

sition between paralarvae and juveniles. Differences between the species on specimens larger than 20 mm ML include the pattern of hook development from suckers both on the tentacular clubs and the arms. Additional specimens are needed to confirm the apparent transition point between early-life-history stages for *G. steenstrupi* and to delineate such stages for *G. fabricii*. The results reported here, however, do indicate changes in both the morphological and ecological characteristics at sizes about 20 mm ML, particularly for *G. steenstrupi*.

Acknowledgments

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