

1 **Reproduction among protobranch bivalves of the family Nuculidae from**
2 **sublittoral, bathyal, and abyssal depths off the New England coast of North**
3 **America**

4
5 Rudolf S. Scheltema^{a*}, Isabelle P. Williams^a

6
7 ^a*Biology Department, MS #34, Woods Hole Oceanographic Institution, Woods Hole, MA, 02543, USA*

8
9 *Corresponding author.

10
11 E-mail addresses: rscheltema@whoi.edu (R.S. Scheltema); iwilliams@whoi.edu (I.P. Williams).
12 Telephone: (508) 289-2337; FAX (508) 457-2134

13
14 *“I should have thought that I had committed*
15 *a serious sin against common sense*
16 *if because I approved of something at one time*
17 *I was obliged to regard it similarly at a later time...”*
18 René Descartes, Discourse on Methods

19
20 **Abstract**

21
22 Protobranch bivalve species of the family Nuculidae pass either through a planktonic
23 lecithotrophic larval stage or a direct non-planktonic development. Oogenesis of the three
24 sublittoral species examined is synchronous. Deposition of egg masses by *Nucula delphinodonta*
25 and spawning by *Nucula annulata* and *Nucula proxima* occurs only during summer months.
26 Among the four bathyal and abyssal species, *Ennucula similis*, *Ennucula granulosa*, *Deminucula*
27 *atacellana*, and *Brevinucula verrilli*, oogenesis is asynchronous and there is no discernable
28 pattern of periodicity of spawning. Absence of periodicity in reproduction in these deep-sea
29 species is confirmed by examination of individuals from dredge samples taken at different times
30 of year. The median apparent fecundity among both sublittoral and deep-sea species is directly
31 related to size (i.e., shell length) and age. Among the Nuculidae the median apparent fecundity is
32 greater among sublittoral than bathyal and abyssal species. The geographic distribution of a
33 species depends on its capacity to disperse. The dispersal of the planktonic lecithotrophic larvae
34 of the sublittoral species *Nucula annulata* and *Nucula proxima* is limited to the continental shelf
35 of the northwestern Atlantic by inshore bottom circulation and because these very small
36 planktonic larvae (<2.5 mm) lack the capacity to move vertically upward through the water

37 column into the offshore currents. On the other hand, the bathyal and abyssal species having
38 lecithotrophic larvae have a very wide amphi-Atlantic distribution extending from 60°N to 40°S
39 latitude along the North and South American coasts and from 55°N to ca. 19°S from off Europe
40 southwards to the coast of West Africa as a consequence of dispersal by planktonic
41 lecithotrophic larvae along the seafloor. The amphi-Atlantic dispersal must occur stepwise
42 between deep-sea populations (e.g., off Greenland). Such a geographic distribution indicates a
43 widespread dispersal and is supported by the genetic similarity that has been described between
44 North American and western European populations of *Deminucula atacellana*.

45

46 *Keywords:* oogenesis, periodicity, fecundity, geographic distribution

47

48 **1. Introduction**

49

50 Protobranch bivalve molluscs are ubiquitous infaunal components of silt-clay sublittoral
51 and deep-sea benthic communities off the New England coast of North America (Sanders, 1958;
52 Sanders et al., 1965; Allen, 1954; Rhind and Allen, 1992). For example, a single sublittoral
53 species, *Nucula annulata* Hampson, 1971, accounts numerically for 59% of all infaunal
54 organisms in silt-clay sediments in Buzzards Bay on Cape Cod, Massachusetts and can reach
55 concentrations up to 22,325 individuals m⁻² (as *Nucula proxima* Say, 1822 in Sanders, 1960,
56 Station 1RA, pp. 141 and 146, tables 2 and 4). Likewise, Nuculidae are a significant infaunal
57 part of the deep-sea fauna having concentrations of 90 to 200 individuals m⁻² at bathyal depths
58 and between 1 to 30 individuals m⁻² in the abyss (Sanders et al., 1965).

59 There are seven Nuculidae species in four genera between the New England coast and the
60 island of Bermuda (Table 1). The three sublittoral species (<200 m depth) include *Nucula*
61 *proxima* Say, 1822, *Nucula annulata* Hampson, 1971, and *Nucula delphinodonta* Mighels and
62 Adam, 1842. Among the four deep-sea species (>200 m depth), *Ennucula similis* Rhind and
63 Allen, 1992, *Ennucula granulosa* (Verrill, 1884), *Deminucula atacellana* (Schenck, 1939), and
64 *Brevinucula verrilli* (Dall, 1886), all occur at bathyal depths. But two species, *D. atacellana* and
65 *B. verrilli*, extend into the abyss (Table 1).

66

67 **2. Methods**

68

69 *2.1 Sampling procedures*

70

71 The results described here are from examination of 16 deep-sea bottom samples dredged
72 along a transect between Gay Head on Martha's Vineyard, Massachusetts and Bermuda (Sanders
73 et al., 1965, text and fig. 1) and 11 sublittoral samples collected at "Station R" by Sanders (1958,
74 p. 246, fig. 1) in Buzzards Bay, Massachusetts (41°30'N, 70°53'W) at 19 m depth and
75 characterized as a "muddy silt-clay" bottom. Two additional samples were collected in nearby
76 Quissett Harbor on the eastern shore of Buzzards Bay near Woods Hole on Cape Cod.

77 Deep-sea samples were obtained using an epibenthic sled described by Hessler and
78 Sanders (1967) or a large anchor dredge. To concentrate macro-organisms, sediment samples
79 were elutriated and sieved through a 0.42 mm screen (Sanders et al., 1965, pp. 850-851). The
80 retained sediment and fauna were fixed for two days in 10% buffered formalin and subsequently
81 stored in 70% ethyl alcohol. Sublittoral samples were taken with a small Forester anchor dredge
82 (Sanders, 1958) and treated in the same manner as that described for deep-sea samples.

83

84 *2.2 Laboratory procedures*

85

86 Protobranch Nuculidae bivalves were separated from the samples by sorting under a
87 stereoscopic microscope (Wild M-5). The method of fixation and preservation, although not
88 ideal for histological work, was dictated by the necessity of preserving the calcareous shell for
89 later taxonomic identification and photography (Figs. 1, 2).

90 Histological preparations were made from whole specimens embedded in paraffin.
91 Before embedding, each specimen was identified to species and its shell length determined from
92 calibrated *camera lucida* drawings made at 25x using a Wild M-5 stereomicroscope. The shell
93 was then decalcified using a chelating agent, ethylenediaminetetraacetic acid (EDTA). The
94 minimum size at sexual maturity was determined by relating shell-length to the first appearance
95 of ova as determined by gross anatomical examination prior to sectioning. Specimens were
96 sectioned serially at 10 µm on a rotary microtome. Diameters of ova were determined with an
97 ocular micrometer at 100x. Since ova seen in histological section are usually not spherical, as
98 found after extrusion from their gonad under natural conditions, it was necessary to make two

99 measurements, one along the longest axis and a second normal to it. The average of the two
100 measurements was then recorded as the approximate diameter of the ovum. Photographs of
101 histological sections were all made at the same magnification with a Zeiss compound microscope
102 (Figs. 3–5). Scanning electron photography of prodissoconchs was with a JOEL-JSM Electron
103 Microscope (Figs. 1, 2).

104

105 **3. Results**

106

107 Three attributes of interest for understanding the demography of benthic marine
108 invertebrate species are: (1) the kind or *mode of development*; (2) the *periodicity of reproduction*,
109 i.e., whether oogenesis is asynchronous and continuous, or synchronous and periodic, the period
110 restricted to certain times of year (i.e., seasonal); and (3) *fecundity*, the number of ova produced
111 over time.

112

113 *3.1 Mode of development*

114

115 Among the Nuculidae, two modes of larval development are known: (1) a lecithotrophic
116 non-feeding planktonic larva, and (2) non-planktonic direct development. Development of two
117 sublittoral species, *Nucula proxima* and *Nucula delphinodonta*, were described by Drew (1899,
118 1901). *Nucula proxima* ova developed into lecithotrophic, free-swimming, "barrel shaped"
119 pericalymma larvae in three days at ambient laboratory temperatures. However, specimens of *N.*
120 *proxima* examined by Drew were collected from the coast of Maine, and the development he
121 described probably was that of *Nucula annulata*, rather than that of *N. proxima* whose northern
122 limit is reported to be Buzzards Bay, Massachusetts (Hampson, 1971). The evidence offered here
123 indicates that the two species, *N. proxima* and *N. annulata*, have similar lecithotrophic larvae
124 (Fig. 1A, B). The second species observed by Drew (1901), *N. delphinodonta*, has a non-
125 planktonic direct development that occurs within a sand-encrusted egg capsule often found
126 attached to the shell of an adult; development is completed in the laboratory in 10 to 14 days
127 (Fig. 2A; Table 2).

128

129 Where development cannot be directly observed, as among deep-sea protobranchs, the
mode may be inferred by an indirect method described by Ockelmann (1965). From the

130 examination of more than 200 species of northeastern Atlantic and Baltic bivalve molluscs,
131 Ockelmann demonstrated that a quantitative relationship exists among egg diameter,
132 prodissoconch size and mode of development. Webb (1987, p. 446, table I) has summarized data
133 of egg diameter for six protobranch species. The values of Webb for eastern North Atlantic
134 bivalves correspond closely to those of Ockelmann (1965). Though very useful, Ockelmann's
135 method must be used with caution because size categories sometimes overlap. Using
136 Ockelmann's methods, it has been possible for us to infer the mode of development of the four
137 deep-sea nuculid species (Table 2).

138 No species belonging to the family Nuculidae are known to have larvae that feed on
139 phytoplankton. Accordingly, their egg diameters and prodissoconch lengths are greater than
140 those found among bivalve species with a phytoplanktotrophic development. The range in egg
141 diameters for the five species considered here to have a lecithotrophic planktonic development
142 falls approximately between 85 and 140 μm , and for those species with non-planktonic direct
143 development, between 193 and 288 μm (Table 2). Prodissoconch length always exceeds egg
144 diameter. The range of prodissoconch length falls approximately between 150 and 223 μm in
145 those species examined that have a lecithotrophic planktonic development and between 230 to
146 >500 μm in species with a non-planktonic direct development (Figs. 1, 2). These values compare
147 well with those of Ockelmann (1965) and Webb (1987).

148 The average length of the prodissoconchs and diameter of ova for sublittoral and deep-
149 sea species are summarized in Table 2 and illustrated in Figures 1–5. The deep-sea species
150 *Ennucula granulosa*, *Deminucula atacellana* and *Brevinucula verrilli* are inferred from their
151 prodissoconch and ovum size to have a lecithotrophic planktonic development similar to that of
152 *N. annulata*. The bathyal species *Ennucula similis* has an exceptionally large ovum with a mean
153 diameter of 288 μm and mean prodissoconch length of 380 μm , exceeding that of the directly
154 developing sublittoral species *Nucula delphinodonta* which has a mean ovum diameter of 193
155 μm and a mean prodissoconch length of 324 μm . The diameter of ova and length of
156 prodissoconchs generally are greater among bathyal and abyssal species than found in sublittoral
157 Nuculidae. The percentages of the deep-sea Nuculidae with a lecithotrophic planktonic
158 development (75%) and those with direct non-planktonic development (25%) are similar to the
159 results of Knudsen (1979) and Schein (1989), who found among 92 species of bathyal and

160 abyssal bivalve mollusca, 60% with lecithotrophic planktonic larvae and 34% with a direct non-
161 planktonic development.

162 The mode of development may affect the life history of deep-sea molluscs in two ways:
163 (1) by influencing patterns of colonization and recruitment and, consequently, the geographic
164 distribution of a species; (2) by affecting the amount of genetic exchange between disjunct
165 populations of the species.

166

167 *3.2 Periodicity of reproduction*

168

169 Periodicity is "the quality or character of being periodic; a tendency to reoccur
170 (especially at regular intervals)". A period is "any length of time occupied by a reoccurring
171 process or are inferred marked by the regular reoccurrence of a phenomenon" (OED).

172 Two kinds of evidence from histological examination of individual gonads can be used to
173 infer periodicity of oogenesis among protobranchs. (1) The absence of gametes will indicate that
174 oogenesis was synchronous and that spawning has occurred. In specimens collected sequentially
175 from the same population at relevant intervals, the timing of spawning can be determined. (2) If
176 the gonad of a female contains only ova, a synchronous oogenesis and periodic spawning is
177 indicated. If instead, both ova and oocytes of various sizes are present, oogenesis is
178 asynchronous and gametes are not released simultaneously. When gametes are synchronously
179 produced and at the same stage of development, all ova necessarily will be spawned
180 simultaneously. If gametes are asynchronously produced, and are at various stages of
181 development, they will not be spawned simultaneously.

182

183 *3.2.1 Synchronous oogenesis among sublittoral species*

184

185 Sublittoral species, namely, *Nucula annulata*, *Nucula proxima*, and *Nucula*
186 *delphinodonta*, have a readily demonstrable periodicity of reproduction. Synchronous oogenesis
187 is restricted to summer and fall months (Fig. 4A, C) and does not occur during the winter or
188 early spring (Fig. 4B, D) as confirmed by bottom samples (Table 3). For the first two species, the
189 ova develop into lecithotrophic planktonic larvae. *Nucula delphinodonta* has direct development
190 without planktonic larvae and produces eggs only during the summer and early fall (Table 3).

191 Periodic seasonal oogenesis and spawning during summer months is correlated with seasonal
192 environmental changes of temperature, and with primary productivity occurring during spring
193 and summer months.

194

195 3.2.2 *Asynchronous oogenesis among deep-sea species*

196

197 In contrast to sublittoral species, the deep-sea species *Ennucula similis* (Fig. 5A, B) with
198 direct non-planktonic development and *Ennucula granulosa*, *Deminucula atacellana* (Fig. 4E, F)
199 and *Brevinucula verrilli* with lecithotrophic planktonic development show asynchronous
200 oogenesis. Fixation of deep-sea specimens frequently is not good enough to allow determination
201 of the stages of oogenesis in histological sections, but asynchronous development within the
202 gonad can be recognized by the presence of ova as well as oocytes of different sizes.
203 Asynchronous development of gametes in all examined deep-sea species contrasts strikingly
204 with that of sublittoral species where synchronous oogenesis is periodic and seasonal. Results
205 from dredge samples support the conclusion that oogenesis and spawning are not seasonally
206 periodic among the deep-sea species studied here (Table 3).

207

208 3.2.3 *Comparison of temporal patterns of reproduction between sublittoral and deep-sea species*

209

210 Periodicity of reproduction among sublittoral species is correlated with warm summer
211 temperature and biological productivity. The temperature at bathyal and abyssal depths is
212 approximately constant throughout the year and therefore cannot provide a cue for oogenesis or
213 spawning. The only relevant connection between the sea surface and the deep-sea is the flux of
214 particulate matter. However, the amount of flux into the deep-sea from oligotrophic offshore
215 surface water is variable and only ca. 1% of the surface primary productivity reaches the seafloor
216 (Scheltema, 1994, pp. 46-48).

217 Wherever the primary productivity at the surface is high and markedly periodic as occurs
218 in deep water near continental landmasses, there is a possibility that some deep-sea benthic
219 species will perceive the seasonal changes in the amount of particulate organic material to reach
220 the bottom. However, under regions where surface productivity is low, it is unlikely that
221 seasonal differences in particulate flux will be discerned. In oligotrophic waters of the open

222 ocean and in low latitude tropical regions surface productivity is very low and, accordingly,
 223 particulate flux to the bottom also will be extremely low. Periodicity in the flux of particulate
 224 matter also may be masked by horizontal bottom currents and by reworking of bottom sediment
 225 by infaunal deposit feeders (Scheltema, 1994, pp. 46-48). Periodicity in reproduction among
 226 deep-sea species is rarely encountered and only near coastal regions where primary productivity
 227 is high such as in the region of Rockall Trough (e.g., *Ledella pustulosa* and *Yoldiella jeffreysi*,
 228 Lightfoot et al., 1979; Gage et al., 1986; Giles et al., 1991).

229

230 3.3 Fecundity

231

232 Fecundity is "the potential reproductive capacity of an organism or population as
 233 measured by the number of the potential gametes produced" during a given interval of time
 234 (Lincoln et al., 1982).

235 *Semelparous* species are those that reproduce only once during their lifetime (Cole,
 236 1954). In this instance, fecundity can readily be determined by counting the number of ova in the
 237 ovary of a gravid female. Semelparity, insofar as is known, is rare among bivalves in the deep
 238 sea and occurs only among those that live in ephemeral habitats, for example, a deep-sea
 239 *Xylophaga* species that bores into wood (Turner, 1973). Semelparity is not known to occur
 240 among infaunal, sediment-dwelling, deep-sea bivalves.

241 *Iteroparous* species may have seasonal reproductive cycles or, alternatively, reproduce
 242 more or less irregularly throughout their sexually mature lifetime. If a species spawns at regular
 243 intervals it is possible to compute the number of gametes produced by a female over its lifetime
 244 from the relationship that exists between age, shell length and number of gametes.

245 The number of ova present in the gonad shows an approximately linear relationship to
 246 shell length according to the equation:

247

$$248 \mathbf{Y} = \mathbf{bX} - \mathbf{a}$$

249

250 where **Y** equals the number of ova and **X** the shell length; **a** is the minimum length at sexual
 251 maturity and **b** is a coefficient that defines the increase in number of ova with increasing shell
 252 length (Fig. 6). Larger older individuals produce more ova than smaller young ones.

253 Accordingly, the cumulative sum of the number of gametes produced at regular and discreet
 254 predictable intervals during the lifetime of an individual will equal its effective lifetime
 255 fecundity.

256

257 3.3.1 Fecundity of sublittoral species

258

259 Reproduction in *Nucula annulata* is known to be periodic and to occur only during the
 260 summer and early autumn months. Consider now, as an example, *N. annulata* in which the
 261 average shell length of an individual increases about 1 mm per year after reaching sexual
 262 maturity (as *Nucula proxima* in Blake and Jeffries, 1971; Craig, 1994). In the first year of sexual
 263 maturity at 2.1 mm, it produces 300 ova (Fig. 6A); during the following summer, the shell length
 264 will be between 2.5 to 3 mm and approximately 1100 ova will be produced. During the
 265 succeeding third summer, after attaining at a shell length of 4 mm, about 1500 ova will be
 266 produced. Then **F**, the cumulative production of ova, will equal:

267

$$268 \mathbf{F} = \sum \mathbf{f}_1 + \mathbf{f}_2 + \mathbf{f}_3, \dots, \mathbf{f}_x$$

269

270 where **f**₁, **f**₂, **f**₃ are the fecundities for three successive unique spawning events over the course
 271 of three summers and **F** is the cumulative total of the realized fecundity over the number of years
 272 since reaching sexual maturity. Therefore, in the three years after reaching sexual maturity, **F** for
 273 *N. annulata* will equal 2900 ova.

274 *Nucula proxima* becomes sexually mature at about 4.5 mm in length (Fig. 6B) and
 275 reaches a maximum shell length of approximately 7 mm. If the annual growth increment equals 1
 276 mm per year, then the production of ova over the first three years after sexual maturity would
 277 equal approximately 16,000 gametes.

278 *Nucula delphinodonta* has a direct non-planktonic development and a shell length of ca. 2
 279 mm (Fig. 6F) when becoming sexually mature. Its ova, however, are ca. 192 μm in diameter
 280 (Table 2), about twice as large as those of the other two sublittoral species that have
 281 lecithotrophic larval development. When first sexually mature at ca. 2 mm, *N. delphinodonta*

282 produces ca. 55 ova (Fig. 6F). If we assume a shell increase of 1 mm per year, then the
283 cumulative number after three years will equal 183 ova.

284 The calculations above illustrate that both size and number of ova produced by a species
285 are related to mode of development, but the lifetime fecundities illustrated here are only
286 estimates based upon an assumed rate of 1 mm growth per year. If the precise growth is known
287 from field data, the lifetime fecundity can then be derived from Figure 6. Unfortunately, the
288 growth rate for most species is unknown.

289

290 3.3.2 *Fecundity of bathyal and abyssal species*

291

292 Among deep-sea species of Nuculidae protobranches, oogenesis is asynchronous and the
293 periodicity of spawning cannot be inferred indirectly. Consequently, a value for the actual
294 effective lifetime fecundity, as described for sublittoral species, cannot be derived. However, a
295 measure of the differences in fecundity between species can be made using the linear
296 relationship of shell length and number of ova in sexually mature females, as shell length
297 approximates age and time; the resulting regression lines (Fig. 6) have high correlation
298 coefficients with r values ranging from 0.79 to 0.91 in species with lecithotrophic larvae. The
299 values chosen for comparing apparent fecundity, or number of ova at one particular point in
300 time, among species (Table 4) are those on the median, or mid-point, of the x -axis of the
301 regression lines, that is, shell lengths that are halfway between the largest and smallest sexually
302 mature females. Such a comparison shows that median apparent fecundities of the deep-sea
303 species with lecithotrophic larvae, *Ennucula granulosa*, *Deminucula atacellana* and *Brevinucula*
304 *verrilli*, are greater than that of the directly developing *Ennucula similis* that has fewer (Table 4)
305 and larger ova (Table 2).

306

307 3.3.3 *Comparison of fecundity between populations of a sublittoral and a deep-sea species*

308

309 An estimate of the population fecundity between populations of the sublittoral species
310 *Nucula annulata* and the deep-sea species *Deminucula atacellana* can be derived by dividing the
311 respective populations into one-half mm size-class categories, determining the median fecundity
312 for each size class, and then summing the apparent fecundities of all size classes (Table 5). Both

313 species have lecithotrophic larvae and are approximately the same length, with sexually mature
314 females from 2 to 5 mm for *N. annulata* and 2 to 4.5 mm for *D. atacellana*. Although the number
315 of individuals in populations of the two species differed greatly, the character of the length-
316 frequency distribution of *D. atacellana* closely paralleled that of *N. annulata*. The large
317 difference in apparent fecundity in the two species, more than twenty times greater in *N.*
318 *annulata* as in *D. atacellana*, results not only from the difference in population size but also from
319 differences in the median number of ova per individual in each size-class (Table 5). Ova of *N.*
320 *annulata* are about 89 μm in diameter, much smaller than those of *D. atacellana* that are
321 approximately 125 μm in diameter and accordingly as a result larvae of *N. annulata* (157 μm)
322 are smaller than those of *D. atacellana* (205 μm) (Table 2). The larger size of the lecithotrophic
323 larvae of *D. atacellana* may be an adaptation for a longer planktonic existence.

324 In both species, more than 95% of the fecundity is contributed by the three size classes
325 between 2 and 3.5 mm; larger individuals contribute only 5% to the total population fecundity
326 even though they have more ova per individual than the smaller individuals (Fig. 6; Table 5).

327

328 *3.4 Geographic distribution*

329

330 The extent of large-scale geographic distribution of a species depends upon its capacity
331 to disperse. Among most benthic infaunal bivalve species, widespread spatial distribution is most
332 likely to be accomplished by the passive dispersal of planktonic larvae.

333

334 *3.4.1 Geographic distribution of sublittoral species*

335

336 The geographic distribution of *Nucula proxima*, with a planktonic lecithotrophic larval
337 development, is restricted to the east coast of North America from Quissett Harbor,
338 Massachusetts, southward to Tampa Bay, Florida (Hampson, 1971). It is most abundant inshore
339 in shallow bays. *Nucula annulata* also has a lecithotrophic planktonic larval development and
340 has a known geographic distribution from Nova Scotia south to Virginia (Hampson, 1971), but
341 since it has been only recently described and is easily confused with *N. proxima*, will probably
342 prove to have a greater geographic range along the western Atlantic continental shelf than

343 presently known. *Nucula delphinodonta* has direct non-planktonic larval development and a
 344 geographic distribution ranging from Labrador to the coast of Maryland.

345 A ten-year study of coastal circulation over the continental shelf of the United States and
 346 part of Canada has shown that a shoreward bottom drift exists between 25° and 45° north latitude
 347 (Bumpus, 1973; Bumpus and Lauzier, 1965). Its effect on the offshore dispersal of invertebrate
 348 larvae is summarized by Scheltema (1975, fig. 3, p. 377).

349 The sublittoral species with planktonic lecithotrophic larval development, *Nucula*
 350 *annulata* and *Nucula proxima*, are restricted to the continental shelf because of the shoreward
 351 bottom circulation. Small Nuculidae larvae are limited in their swimming ability $<2 \text{ cm s}^{-1}$ (e.g.,
 352 Chia et al., 1984), and, therefore, are restricted in their upward vertical movement into the
 353 offshore surface current. *Nucula delphinodonta* with direct development lacks a dispersal stage
 354 and also has a restricted geographic distribution.

355

356 3.4.2. Geographic distribution of bathyal and abyssal species

357

358 Three deep-sea species considered here, *Ennucula granulosa*, *Deminucula atacellana*
 359 and *Brevinucula verrilli* have planktonic lecithotrophic development and an amphi-Atlantic
 360 distribution (Fig. 7). *Deminucula atacellana* is distributed in the western Atlantic from 60°N to
 361 40°S in the Argentine Basin, in the mid-Atlantic at about 48°N, 38°W, and in the eastern
 362 Atlantic from 55°N to 10°S off the west coast of Africa. *Brevinucula verrilli* distribution in the
 363 western Atlantic extends from 40°N to 12°S, in the eastern Atlantic from 50°N to the equator,
 364 and on the equator at about 28° west longitude in the mid-Atlantic. Such a geographic
 365 distribution must be the consequence of larval dispersal. But, until now, no deep-ocean larvae of
 366 Nuculidae have been recovered from the deep sea because of the difficulty of sampling larvae
 367 close to the sea floor and the relatively large mesh-size of nets used in the collection of
 368 zooplankton. The larvae of *E. granulosa*, *D. atacellana* and *B. verrilli*, as shown by
 369 prodissoconch measurements, are quite small, between ca. 150 and ca. 225 μm (Figs. 1C, 2B,D;
 370 Table 2), smaller than the mesh of zooplankton nets (#6 mesh = 239 μm).

371 The extent of geographical dispersal by larvae is limited by the duration of their
 372 development and their ability to delay settlement. However, some non-feeding lecithotrophic
 373 larvae of invertebrates have been shown to have a remarkably long planktonic life (Pearse,

1994). Stepwise dispersal across ocean basins by successive populations between two points presents a possible explanation. For one example, individuals of *Deminucula atacellana* have been recorded from off North America (ca. 40°N, 72°W), southeast and southwest of Greenland, and commonly off Ireland (Fig. 7). *Brevinucula verrilli* that has been collected from several stations along the equator provides another example. It is perhaps possible that larvae may be transported in a cross-axis flow across the mid-Atlantic Ridge (Mullineaux et al., 2002).

380

381 4. Conclusions

382

383 The results presented here help support a previous conclusion (Scheltema, 1994, p. 56)
384 that approximately two-thirds of all known species of protobranch bivalve species have
385 planktonic lecithotrophic development. The remaining species have direct non-planktonic
386 development. Both modes of development are seen in the seven species of nuculid bivalves
387 found along the New England coast and extending into the northwestern Atlantic Ocean to
388 Bermuda. Two sublittoral species, *Nucula annulata* and *Nucula proxima*, and three bathyal
389 species, *Brevinucula verrilli*, *Deminucula atacellana* and *Ennucula granulosa* have planktonic
390 lecithotrophic development. One sublittoral species, *Nucula delphinodonta*, and one bathyal
391 species, *Ennucula similis*, have direct non-planktonic development.

392 Fecundity is the potential capacity of a species or the populations of a species to produce
393 gametes. Among sublittoral species, oogenesis is synchronous (Fig. 4A, B). Field observations
394 confirm that spawning occurs only once a year during summer months and that reproduction is
395 periodic; this distinct period of spawning is characteristic and the effective lifetime fecundity can
396 be derived from the cumulative values for each period of reproduction.

397 Among deep-sea species, oogenesis is asynchronous and various stages of developing
398 oocytes and ova co-occur (Fig. 4E,F). Field data confirm that oogenesis is a continuous process
399 and no periodicity or seasonal reproduction is discernable. Fecundity over a lifetime cannot be
400 determined in a deep-sea species with asynchronous oogenesis as the timing and number of ova
401 produced at each spawning is unknown and only the apparent fecundity at the time of collection
402 can be determined.

403 Apparent fecundity is linearly related to shell length and age (Fig. 6) and excludes the
404 dimension of time. The median apparent fecundity during sexual maturity allows a comparison

405 to be made between individuals of different species. In making such a comparison it is apparent
406 that the median number of ova is much greater among the sublittoral than bathyal and abyssal
407 species (Table 4).

408 A comparison of fecundity between populations of *Nucula annulata* and *Deminucula*
409 *atacellana* illustrates characteristics and differences between sublittoral and deep-sea
410 populations (Table 5). The size of the two populations differs widely and reflects the difference
411 in population density that can be expected between the sublittoral and the deep sea. The two
412 species fall within the same size range. (1) In both species more than 90 percent of the apparent
413 fecundity can be accounted for in the first three (one-half millimeter) size classes, i.e., between
414 2.0 and 3.5 mm. (2) The larger individuals in both species, (>3.5 mm) have a greater number of
415 ova per individual, but contribute only little to the apparent population fecundity of either
416 species. (3) In each size class the median number of ova per individual is greater in the
417 sublittoral than in the deep-sea species. The median apparent population fecundity (sum of the
418 median number of ova per individual for each size class) is greater in the sublittoral species *N.*
419 *annulata* than in the deep-sea species *D. atacellana*. The ova are larger in the deep-sea species
420 (125 μm) than in the sublittoral species (89 μm). In summary, the deep-sea species has fewer and
421 larger ova and larvae than the sublittoral species (Table 2).

422 In both sublittoral and deep-sea species, mode of reproduction and fecundity are closely
423 related. Ovum diameter is smaller (Table 2) and median apparent fecundity greater (Table 4) in
424 species with lecithotrophic development than in species with direct non-planktonic development.

425 The geographical distribution of the sublittoral species *Nucula annulata* and *Nucula*
426 *proxima* is limited to the North American continental shelf. The onshore bottom circulation of
427 the North American continental shelf is likely to retain the sublittoral species to coastal water.

428 The deep-sea species *Deminucula atacellana*, *Ennucula granulosa* and *Brevinucula*
429 *verrilli* are amphi-Atlantic in their geographic distribution. Genetic similarity between eastern
430 and western North Atlantic populations of *D. atacellana*, as demonstrated by Zardus et al.
431 (2006), suggests a genetic continuity between eastern and western North Atlantic populations.
432 Lecithotrophic larvae of the deep-sea species may have the ability to delay metamorphosis
433 because of energy provided by large ova.

434

435 **Acknowledgments**

436

437 Deep-sea dredge samples were collected using an epibenthic sled designed by Robert
438 Hessler and constructed under the guidance of George Hampson. The technique of elutriating
439 samples through fine screens was devised by Howard Sanders. Protobranch bivalves were sorted
440 from dredge samples by numerous colleagues and laboratory technicians. Captains Dick Colburn
441 and Emerson Hiller and crews of the Woods Hole Oceanographic Institution's research vessels,
442 *Atlantis*, *Atlantis II* and *Chain*, made the dredging operations possible. John Allen clarified the
443 distinction between nuculid bivalves included in the present study. Amelie Scheltema was very
444 helpful in the accomplishment of the manuscript. The critique of an anonymous reviewer was
445 useful. For all these persons we tender our thanks. Some financial support was provided by
446 research grants from the National Science Foundation.

447 We thank Rich Lutz for inviting us to participate in the symposium held in honor of Fred
448 Grassle and to contribute to this volume of Deep-Sea Research.

449

450 **References**

451

- 452 Allen, J.A., 1954. A comparative study of the British species of *Nucula* and *Nuculana*. Journal of the
453 Marine Biological Association of the U.K. 33, 457-472.
- 454 Allen, J.A., Sanders, H.L., 1996. Studies on the deep-sea Protobranchia (Bivalvia): the family
455 Neilonellidae and the family Nuculanidae. Bulletin of the Natural History Museum, London
456 (zoology) 62, 101-132.
- 457 Blake, N.J., Jeffries, H.P., 1971. The structure of an experimental infaunal community. Journal of
458 experimental marine Biology and Ecology 6, 1-14.
- 459 Bumpus, D.F., 1973. A description of the circulation on the continental shelf of the east coast of the
460 United States. Progress in Oceanography 6, 11-157.
- 461 Bumpus, D.F., Lauzier, L.M., 1965. Surface circulation on the continental shelf off eastern North
462 America between Newfoundland and Florida. Serial Atlas of the Marine Environment,
463 American Geographical Society Folio 7, 4 pp, 8 pl.
- 464 Chia, F.S., Buckland-Nicks, J., Young C.M., 1984. Locomotion of marine invertebrate larvae: a
465 review. Canadian Journal of Zoology 62, 1205-1222.

- 466 Cole, L.C., 1954. The population consequences of life history phenomena. *Quarterly Review of*
467 *Biology* 29, 103–137.
- 468 Craig, N.I., 1994. Growth of the bivalve *Nucula annulata* in nutrient-enriched environments.
469 *Marine Ecology Progress Series* 104, 77-90.
- 470 Dall, W.H., 1886. Reports on the results of dredging under the supervision of Alexander
471 Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80) by its coast
472 survey steamer 'Blake', Lieut-Commander C.D. Sigsbee, U.S.N. and Commander J. R.
473 Bartlett, U. S. N. commanding. XXIX Report on the Mollusca, Part I, Brachiopoda and
474 Pelecypoda. *Bulletin of the Museum of Comparative Zoology Harvard* 12,171-318.
- 475 Drew, A.G., 1899. Some observations on the habits, anatomy and embryology of members of the
476 Protobranchia. *Anatomischer Anzeiger* 15, 493-519.
- 477 Drew, A.D., 1901. The life history of *Nucula delphinodonta* (Mighels) *Quarterly Journal of*
478 *microscopical Science* 44, 313-391.
- 479 Gage, J.D., Tyler, P.A., Davies, G., Harvey, R., 1986. Life history studies on deep-sea
480 protobranch bivalves from Rockall Trough (N.E. Atlantic). In: Heppell (Ed) Ninth
481 International Malacological Congress, Edinburgh, Scotland, 31 August–6 September
482 1986. National Museums of Scotland, Edinburgh (Abstract) p. 27.
- 483 Giles, L.A., Tyler, P.A., Gage, J.D., 1991. Diet and reproduction in the deep-sea protobranchs
484 *Ledella pustulosa* and *Malletia cuneata*. Sixth Deep-sea Biological Symposium,
485 Copenhagen, Abstract. P. 84.
- 486 Hampson, G.R., 1971. A species pair of the genus *Nucula* (Bivalvia) from the eastern coast of
487 the United States. *Proceedings of the malacological Society, London* 39, 333-342.
- 488 Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep sea. *Deep-Sea Research* 14, 65-
489 78.
- 490 Knudsen, J., 1979. Deep-sea bivalves. In: Spoel, S.v.d., Bruggen, A.D.v., Lever, J. (Eds)
491 *Pathways in Malacology, Utrecht*, pp. 195-224.
- 492 Lightfoot, R.H., Tyler, P.A., Gage, J.D., 1979. Seasonal reproduction in deep-sea bivalves and
493 brittle stars. *Deep-Sea Research* 26A, 967-973.
- 494 Lincoln, R.J., Boxshall, G. A., Clark, P.F., 1982. A dictionary of ecology, evolution and
495 systematics. Cambridge University Press, Cambridge.

- 496 Mighels, J.W., Adams, C.B., 1842. Description of 24 species of the shells of New England.
497 Boston Journal of Natural History 4, 37-54.
- 498 Mullineaux, L.S., Speer, K.G., Thurnherr, H.M., Maltrud, M.E., Vangriesheim, A., 2002.
499 Implications of cross-axis flow for larval dispersal along mid-ocean ridges. Cahiers de
500 Biologie Marine 43, 281-284.
- 501 Ockelmann, K.W., 1965. Developmental types in marine bivalves and their distribution along the
502 Atlantic coast of Europe. In: Cox, L.R., Peake, J. (Eds) Proceedings of the first European
503 Malacological Congress, London 1962, pp. 25-35.
- 504 Pearse, J.S., 1994. Cold-water echinoderms break "Thorson's Rule". In: Young, C.M., Eckelbarger,
505 K.J. (Eds.), Reproduction, larval biology, and recruitment of the deep-sea benthos. Columbia
506 University Press, New York, pp. 26-43.
- 507 Rhind, P.M., Allen, J.A., 1992. Studies on the deep-sea Protobranchia (Bivalvia): the family
508 Nuculidae. Bulletin of the British Museum of Natural History (Zoology) 58(1), 61-93.
- 509 Sanders, H.L., 1958. Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships.
510 Limnology and Oceanography 3(3), 245-258.
- 511 Sanders, H.L., 1960. Benthic Studies in Buzzards Bay. III. The Structure of the Soft-bottom
512 Community. Limnology and Oceanography 5(2) 138-153.
- 513 Sanders, H.L., Hessler, R.R., Hampson, G.R., 1965. An introduction to the study of deep-sea
514 benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-Sea Research
515 12, 845-867.
- 516 Say, T., 1822. An account of some marine shells of the U.S. Journal of the Academy of Natural
517 Sciences of Philadelphia, 1st series 2, 270.
- 518 Schein, E., 1989. Pectinidae (Mollusca, Bivalvia) bathyaux et abyssaux des campagnes BIOGAS
519 (Golfe de Gascogne) systématique et biogéographie. Annales de l'Institut
520 Océanographique, Nouvelle Série, Paris 65 (2), 59-125, 9 pls.
- 521 Scheltema, R.S., 1972. Reproduction and dispersal of bottom dwelling deep-sea invertebrates: A
522 speculative summary. In: Brauer, R.W. (Ed), Barobiology and Experimental Biology of
523 the Deep Sea, University of North Carolina, North Carolina Sea Grant Program, pp. 58-
524 66.
- 525 Scheltema, R.S., 1975. Relationship of larval dispersal, gene-flow and natural selection to geographic
526 variation of benthic invertebrates in estuaries and along coastal regions. In: Cronin, L.E. (Ed.),

- 527 Estuarine Research: Volume 1: Chemistry, Biology, and the estuarine System, Academic
528 Press, New York, pp. 372-391.
- 529 Scheltema, R.S., 1994. Adaptations for reproduction among deep-sea benthic molluscs: An appraisal
530 of the existing evidence. In: Young, C.M., Eckelbarger, K.L. (Eds.), Reproduction, Larval
531 Biology, and Recruitment of the Deep-sea Benthos. Columbia University Press, New York,
532 pp. 44-75.
- 533 Schenck, H.G. 1939. Revised nomenclature for some nuculid pelecypods. Journal of
534 Paleontology 13, 21-41.
- 535 Turner, R.D., 1973. Wood-boring bivalves, opportunistic species in the deep sea. Science 180,
536 1377-1379.
- 537 Verrill, A.E., 1884. Second catalogue of Mollusca recently added to the fauna of the New
538 England coast and the adjacent parts of the Atlantic consisting mostly of deep-sea
539 species, with notes on others previously recorded. Transactions of the Connecticut
540 Academy of Arts and Science 6, 395-452.
- 541 Webb, C.M., 1987. Post-larval development of the bivalves *Nucula turgida*, *Venus striatula*,
542 *Spicula subtruncata* and *S. elliptica* (Mollusca: Bivalvia), (with reference to the late
543 larva). Journal of the marine biological Association of the United Kingdom 67,441-460.
- 544 Zardus, J.D., Etter, R.J., Chase, M.R., Rex, M.A., Boyle, E.E., 2006. Bathymetric and
545 Geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula*
546 *atacellana* (Schenck, 1939) Molecular Ecology 15, 639-651.
- 547
- 548

549 Table 1. Nuculidae species examined from sublittoral, continental shelf, bathyal, and abyssal depths off the New
 550 England coast of North America to Bermuda.

551

Species	Vertical Distribution
<i>Nucula proxima</i> Say, 1822	Shallow sublittoral
<i>Nucula annulata</i> Hampson, 1971	Shallow sublittoral
<i>Nucula delphinodonta</i> Mighels & Adams, 1842	Shallow sublittoral to 200 m
<i>Ennucula similis</i> Rhind & Allen, 1992 [as <i>Nucula subovata</i> in Scheltema, 1972; <i>Nuculoma similis</i> Rhind & Allen 1992]	Continental slope, 400–2,000 m ^a
<i>Ennucula granulosa</i> (Verrill, 1884) [as <i>Nucula granulosa</i> in Scheltema, 1972; <i>Nuculoma granulosa</i> in Rhind and Allen, 1992]	Continental slope 500–2,000 m ^a , most abundant at ~1,500 m
<i>Deminucula atacellana</i> (Schenk, 1939) (= <i>Nucula cancellata</i> Jeffreys, 1881)	Continental slope to abyss 1,000–4,800 m ^a , most abundant at 2,000 m
<i>Brevinucula verrilli</i> (Dall, 1886) [as <i>Nucula verrilli</i> in Scheltema, 1972]	Continental slope to abyss, 1,900–4,800 m ^a

552 ^a Rhind and Allen, 1992

553

554 Table 2. Mean prodissoconch length, mean ovum diameter, and inferred mode of reproduction among species of
 555 Nuculidae from sublittoral, continental slope, and abyssal depths of the New England coast of North America.
 556

Species ^a	Mean prodissoconch length μm^b	Mean ovum diameter μm^c	Inferred mode of reproduction
<u>Sublittoral species</u>			
<i>Nucula proxima</i> ^d	153.4 \pm 2.4	84.5 \pm 1.1	Pelagic, lecithotrophic ^d
<i>Nucula annulata</i>	157.1 \pm 4.2	89.4 \pm 2.0	Pelagic, lecithotrophic
<i>Nucula delphinodonta</i> ^e	323.5 \pm 8.2	192.6 \pm 2.1	Non-pelagic, direct ^e
<u>Bathyal and abyssal species</u>			
<i>Ennucula granulosa</i>	150.0 \pm 3.1	100.5 \pm 1.1	Pelagic, lecithotrophic
<i>Deminucula atacellana</i>	204.6 \pm 6.2	125.2 \pm 8.4	Pelagic, lecithotrophic
<i>Brevinucula verrilli</i>	223.1 \pm 6.4	138.2 \pm 4.0	Pelagic, lecithotrophic
<i>Ennucula similis</i>	379.6 \pm 5.6	288.1 \pm 5.6	Non-pelagic, direct

557 ^a Underscore = direct development

558 ^b Ten specimens measured; one standard error indicated.

559 ^c Values computed from the 10 largest of 20 "full-sized" ova measured in two different specimens (i.e., total of 20
 560 ova). Value for *B. verrilli* comes from 2 individuals originating from different localities. Value for *E. similis* comes
 561 from 3 specimens collected from 2 localities and is based on 30 measurements. Values for all other species from
 562 specimens collected at a single location. One standard error indicated.

563 ^d Mode of reproduction and larva described by Drew (1899, pp. 513–514) who reported egg size as 0.09 mm (p.
 564 506); Drew could make no distinction between *N. proxima* and *N. annulata*.

565 ^e Mode of reproduction and development of *N. delphinodonta* described by Drew (1901), who reported egg size as
 566 0.21 mm (p. 316).

567

568 Table 3. Time of reproduction of protobranch molluscs off the northeast coast of New England.

569

Species	Months sampled	Months with mature ova
<u>Coastal Sublittoral</u>		
<i>Nucula proxima</i>	Feb., Aug., Dec.	Aug.
<i>Nucula annulata</i>	Jan., July, Nov.	July, Nov.
<i>Nucula delphinodonta</i>	April, July, Nov.	July, Nov.
<u>Bathyal and Abyssal</u>		
<i>Ennucula similis</i>	Feb., May, July, Aug.	Feb., May, July, Aug.
<i>Ennucula granulosa</i>	Feb., July	Feb., July
<i>Deminucula atacellana</i>	May, Dec.	May, Dec.
<i>Brevinucula verrilli</i>	Feb., June, Aug.	Feb., June, Aug.

570

571

572 Table 4. Median apparent fecundity of sublittoral and
 573 deep-sea species of Nuculidae from the northwest Atlantic.
 574

Species ^a	Median length mm ^b	Median no. ova ^b
Sublittoral species		
<i>Nucula proxima</i>	5.5	4500
<i>Nucula annulata</i>	3.0	1200
<i>Nucula delphinodonta</i>	2.6	100
Bathyal and abyssal species		
<i>Ennucula granulosa</i>	2.0	170
<i>Deminucula atacellana</i>	2.7	270
<i>Brevinucula verrilli</i>	3.7	150
<i>Ennucula similis</i>	2.8	57

575 ^a Underscore = direct non-planktonic development.

576 ^b Data derived from Figure 6; mid-point of regression lines.

577

578 Table 5. Comparison of apparent fecundity of sublittoral *Nucula annulata* and deep-sea *Deminucula atacellana*
 579 populations.

580

Size class mm	Number of individuals	Median number of ova per individual ^c	Total ova per size class: apparent fecundity
<i>Nucula annulata</i> ^a			
2.00–2.49	3168	400	130 X 10 ⁴
2.50–2.99	1667	900	150 X 10 ⁴
3.00–3.49	415	1200	50 X 10 ⁴
3.50–3.99	91	1550	10 X 10 ⁴
4.00–4.49	24	1850	4 X 10 ⁴
4.50–4.99	2	2000	0.4 X 10 ⁴
Totals	5367	—	344.4 X 10 ⁴
<i>Deminucula atacellana</i> ^b			
2.00–2.49	234	160	3.7 X 10 ⁴
2.50–2.99	272	250	6.8 X 10 ⁴
3.00–3.49	132	340	4.5 X 10 ⁴
3.50–3.99	26	400	1.0 X 10 ⁴
4.00–4.49	1	550	0.05 X 10 ⁴
Totals	665	—	16.05 X 10 ⁴

581 ^a Total sample 16,449: juveniles and males 67.4%. Buzzards Bay, Station R, August 18, 1965, depth 19 m.

582 ^b Total sample 1017: juveniles and males 34.6%. Atlantis II, Station 131, December 18, 1966, depth 2178 m.

583 ^c Based on values derived from Figure 6.

584

585 **Figure captions**

586

587 **Fig. 1.** Prodissoconchs of three species of Protobranchia belonging to the family Nuculidae with
 588 lecithotrophic planktonic development (A) *Nucula proxima* (cf. Fig. 3A), (B) *Nucula annulata*
 589 (cf. Fig. 3B), (C) *Ennucula granulosa* (cf. Fig. 3D). Bars = 100 μ m.

590

591 **Fig. 2.** Prodissoconchs of four species of Protobranchia belonging to the family Nuculidae. (A)
 592 *Nucula delphinodonta* with non-planktonic direct development (cf. Fig. 3F), (B) *Deminucula*
 593 *atacellana* with planktonic lecithotrophic development (cf. Fig. 3E), (C) *Ennucula similis* having
 594 direct non-planktonic development (cf. Fig. 3G), (D) *Brevinucula verrilli* with planktonic
 595 lecithotrophic development (cf. Fig. 3C). Bars = 100 μ m.

596

597 **Fig. 3.** Ova in seven species of Protobranchia belonging to the family Nuculidae. (A) *Nucula*
 598 *proxima*, (B) *Nucula annulata*, (C) *Brevinucula verrilli*, (D) *Ennucula granulosa*, (E)
 599 *Deminucula atacellana*, (F) *Nucula delphinodonta*, (G) *Ennucula similis*; arrows refer to sperm
 600 present in this apparently hermaphroditic species. Scale bar refers to all images.

601

602 **Fig. 4.** Condition of the ovaries of species belonging to the protobranch family Nuculidae in
 603 relation to season. (A) *Nucula annulata*, 41°30'N, 70°53'W, Buzzards Bay, 19 m, gonads filled
 604 with ova; summer. (B) *Nucula annulata*, same location as A, gonads emptied of ova, with
 605 oocytes (arrowheads); winter. (C) *Nucula proxima*, 41°32.5'N, 70°39.7'W, 3 m, gonads filled
 606 with ova, oocytes not evident; summer. (D) *Nucula proxima*, same location as C, gonads appear
 607 empty of ova but with oocytes of various sizes; winter. (E) *Deminucula atacellana*, 39°43'N,
 608 70°37'W, 2022 m, gonad with mature ova (e.g., arrow) and oocytes of various sizes; summer. (F)
 609 *Deminucula atacellana*, 39°39'N, 70°37'W, 2178 m, mature ova (e.g., arrow), oocytes of various
 610 sizes, winter. d, digestive gland; s, stomach. Scale bar refers to all images.

611

612 **Fig. 5.** Condition of the ovaries of *Ennucula similis* in the bivalve family Nuculidae with direct
 613 non-larval development in relation to season. (A) 39°48'N, 70°41'W, 1102 m, gonads with ova
 614 (arrows); summer. (B) 39°48'N, 70°50'W, 1501 m, gonads with ova (arrows); winter. d, digestive
 615 gland; s, stomach.

616

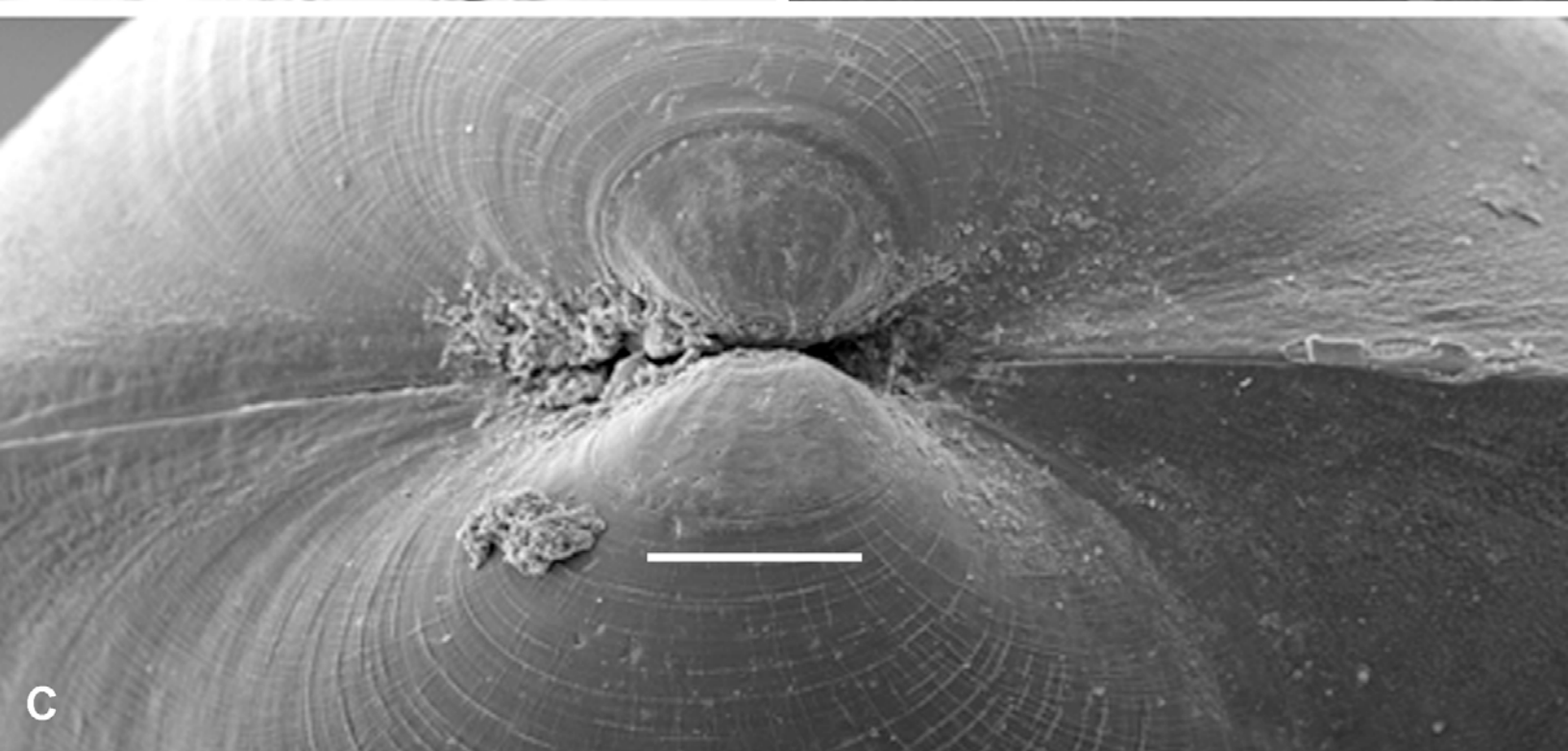
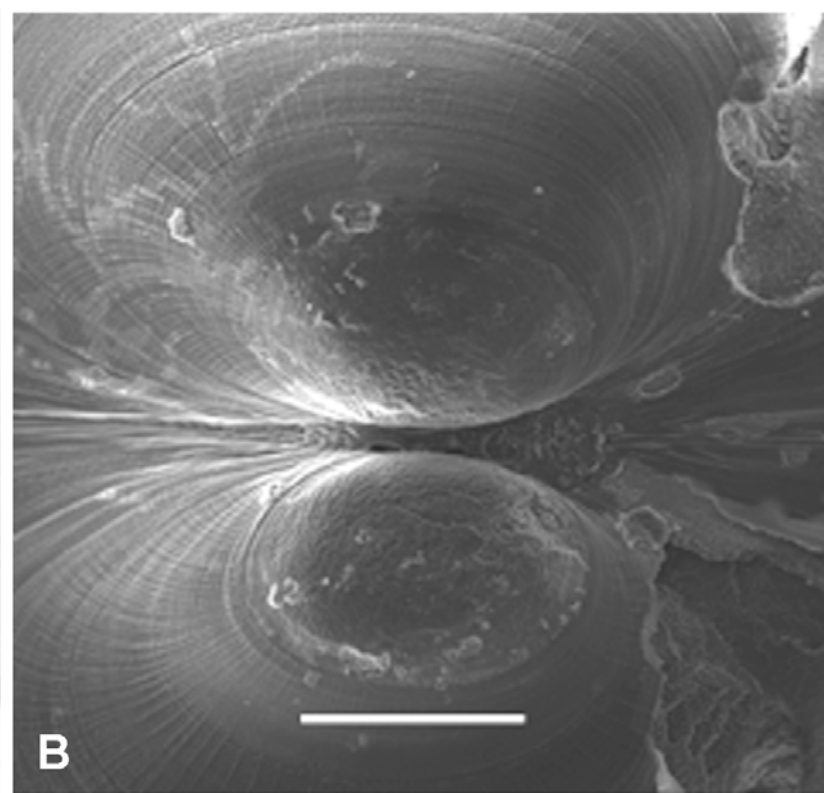
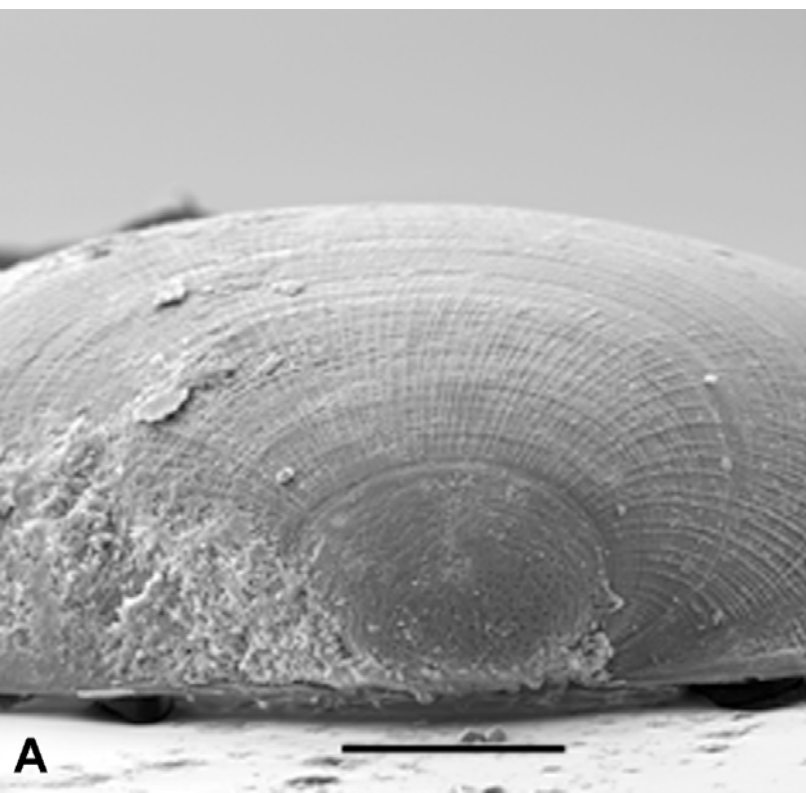
617 **Fig. 6.** The relationship of shell length in sexually mature females and the number of ova in
618 seven species of Nuculidae from sublittoral, bathyal, and abyssal depths off the western North
619 Atlantic coast. (A) *Nucula annulata*, shallow sublittoral; (B) *Nucula proxima*, shallow
620 sublittoral; (C) *Ennucula granulosa*, continental slope to 2,000 m; (D) *Brevinucula verrilli*,
621 continental slope to abyss; (E) *Deminucula atacellana*, continental slope to abyss; (F) Open
622 circles: *Nucula delphinodonta*, continental shelf; closed circles: *Ennucula similis*, continental
623 slope 400–2,000 m. A–E, species with lecithotrophic larvae; F, species with direct development
624 without planktonic larvae.

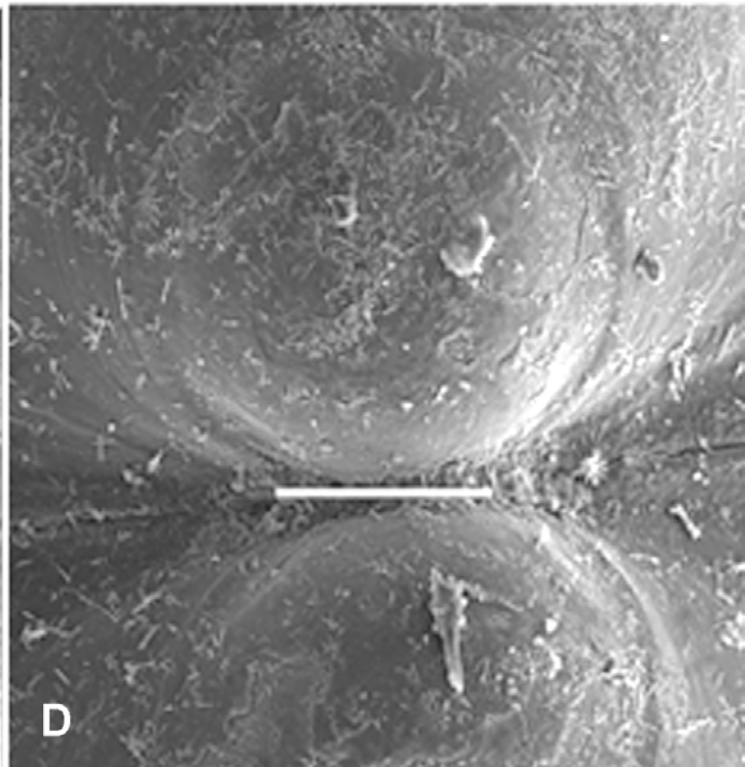
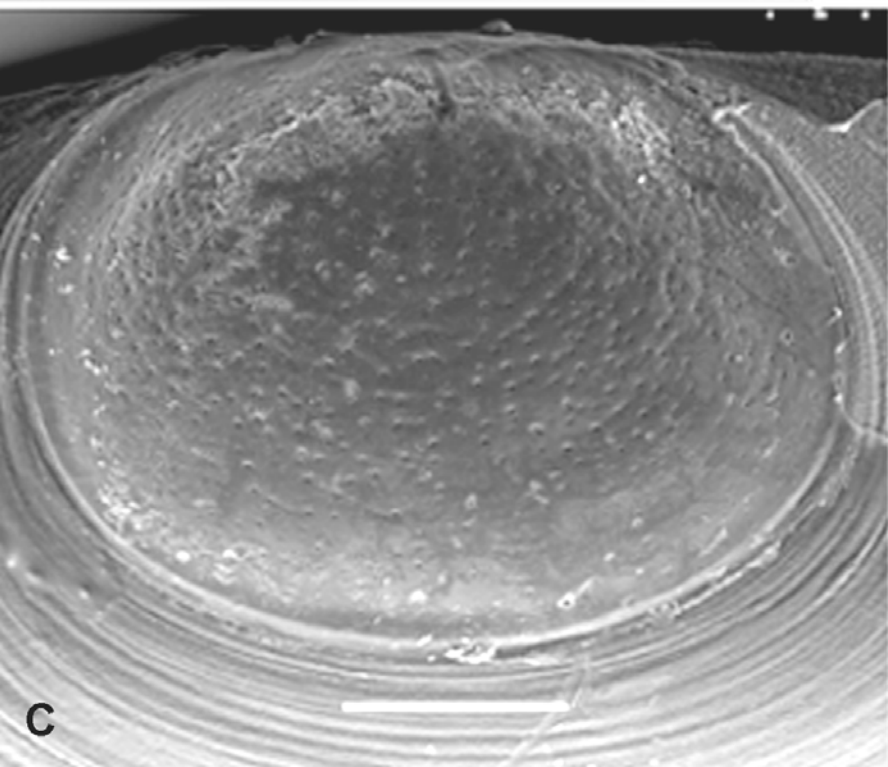
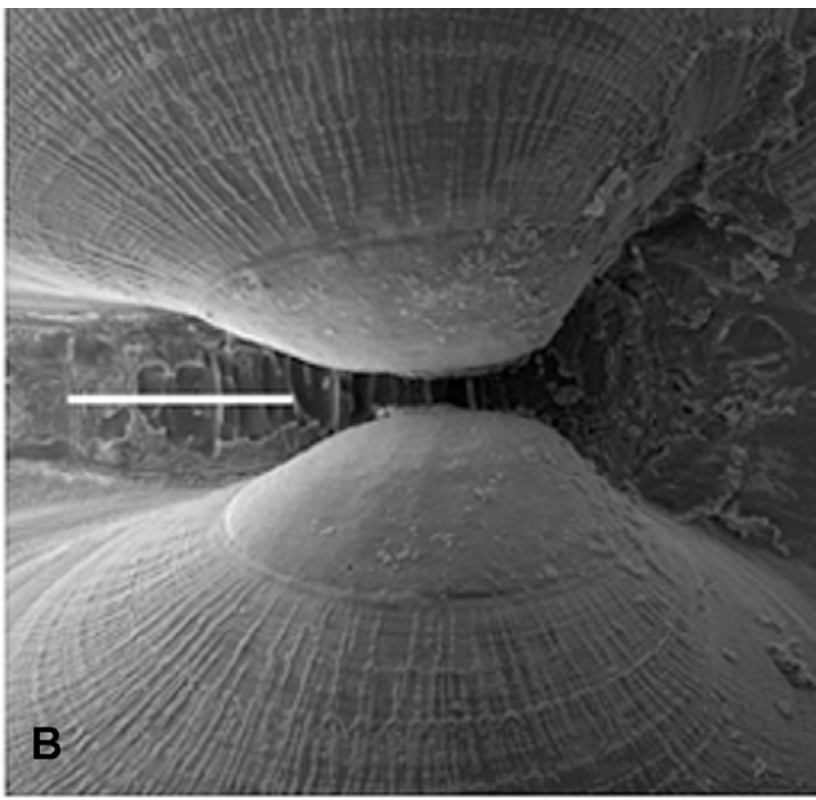
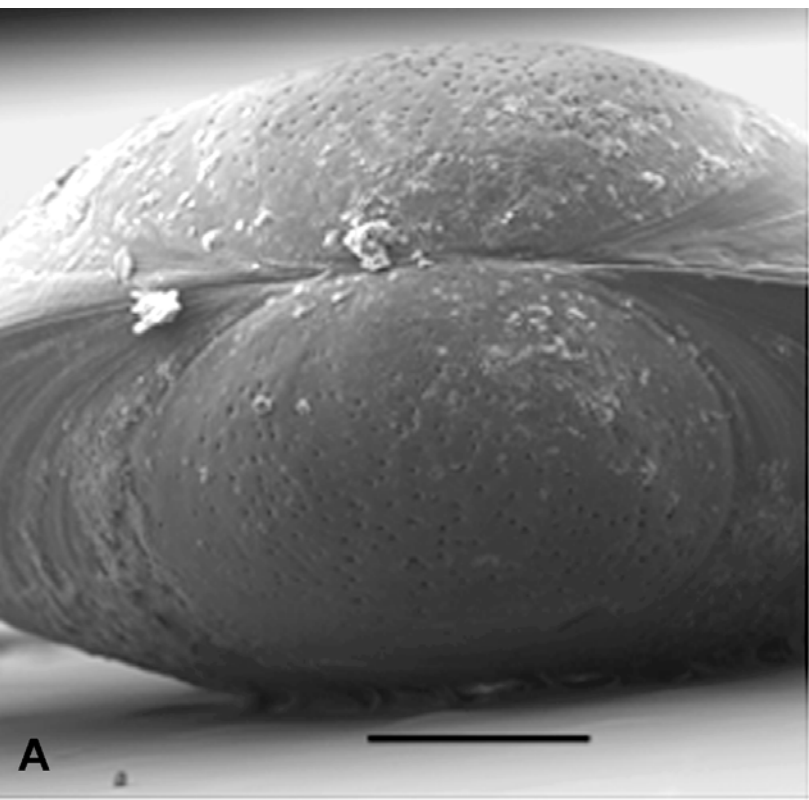
625

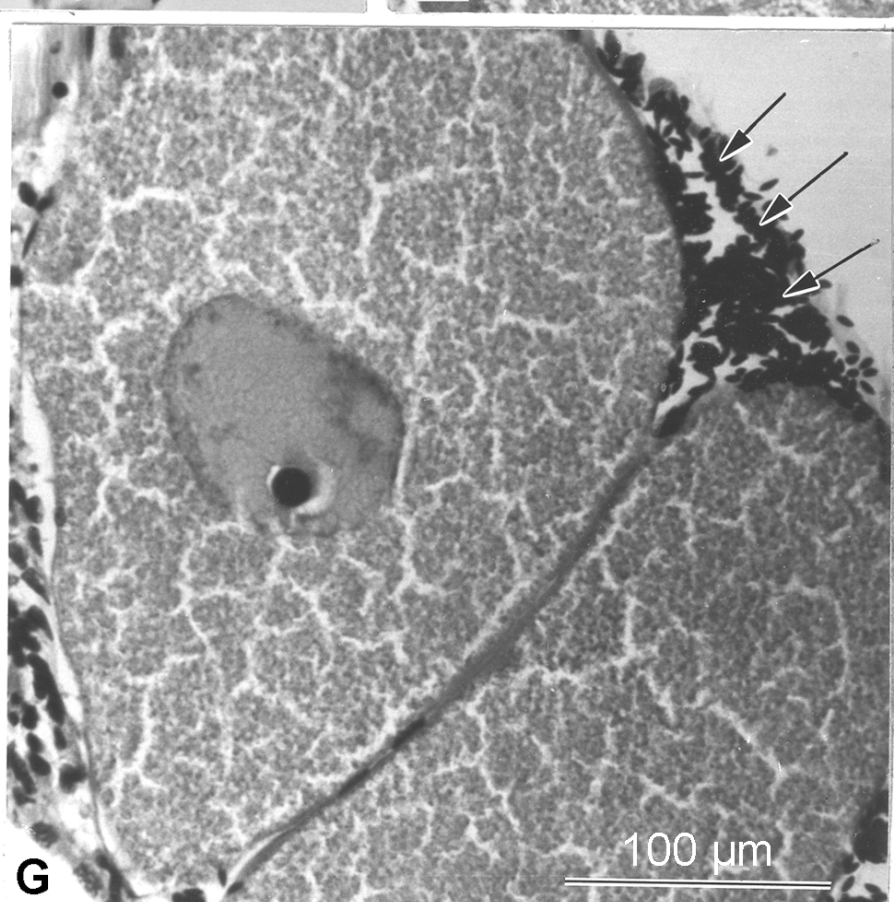
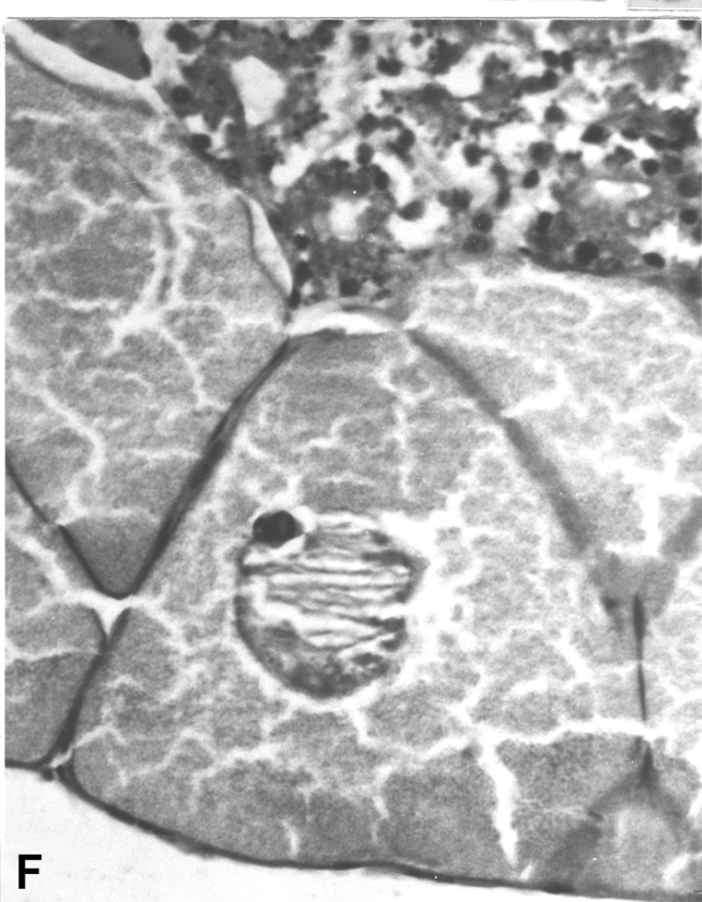
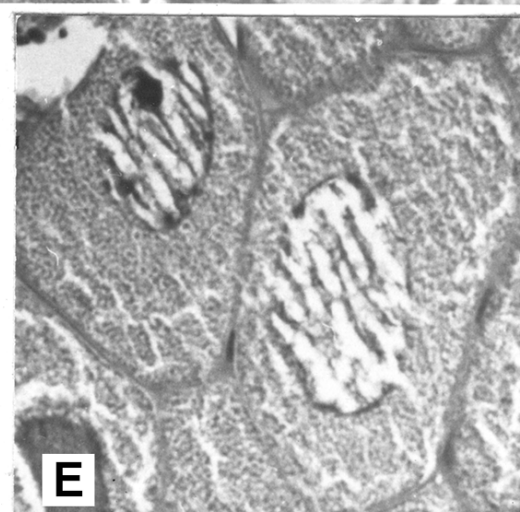
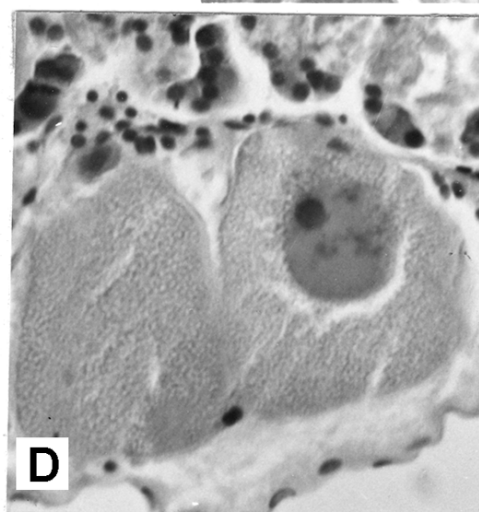
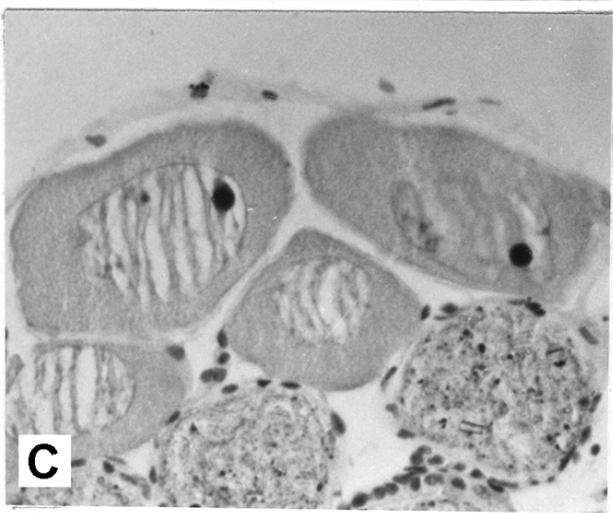
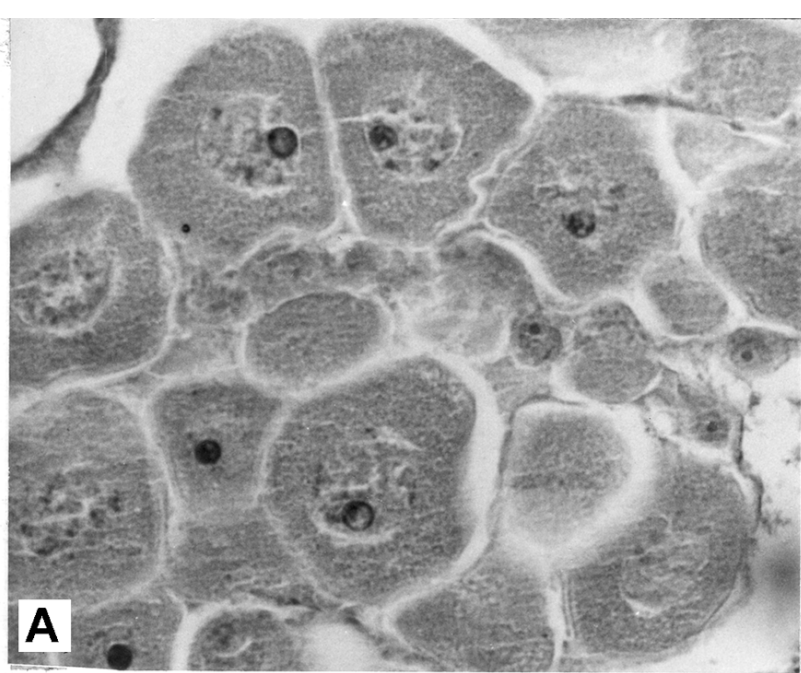
626 **Fig. 7.** Geographic distribution in the Atlantic Ocean of deep-sea Nuculidae bivalves known to
627 have lecithotrophic larvae. Data compiled from dredging expeditions of the Woods Hole
628 Oceanographic Institution's ships, *R/V Atlantis*, *R/V Atlantis II*, *R/V Chain*, and *R/V Knorr*, and
629 from published records of the *Albatross*, *Valdivia* and *Galathea* as well as records from the
630 biological literature including Allen and Sanders (1996). Some localities indicated represent
631 more than one sample.

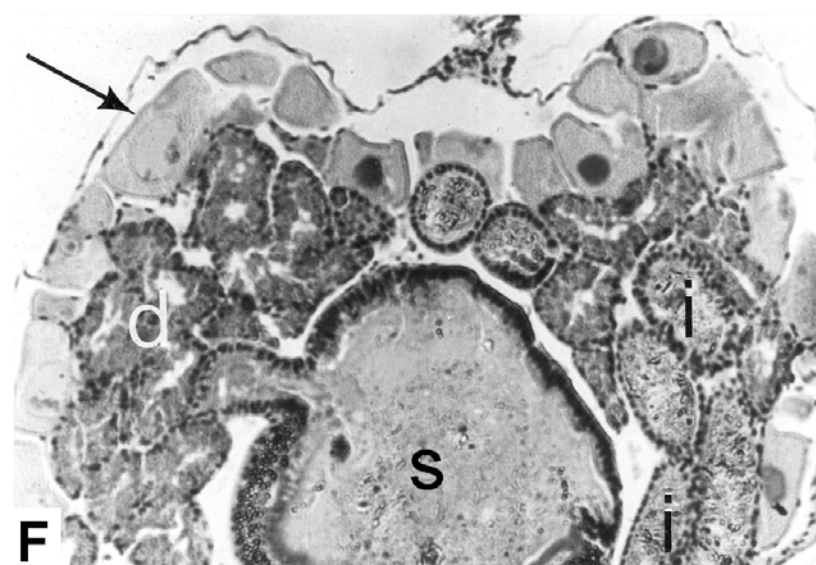
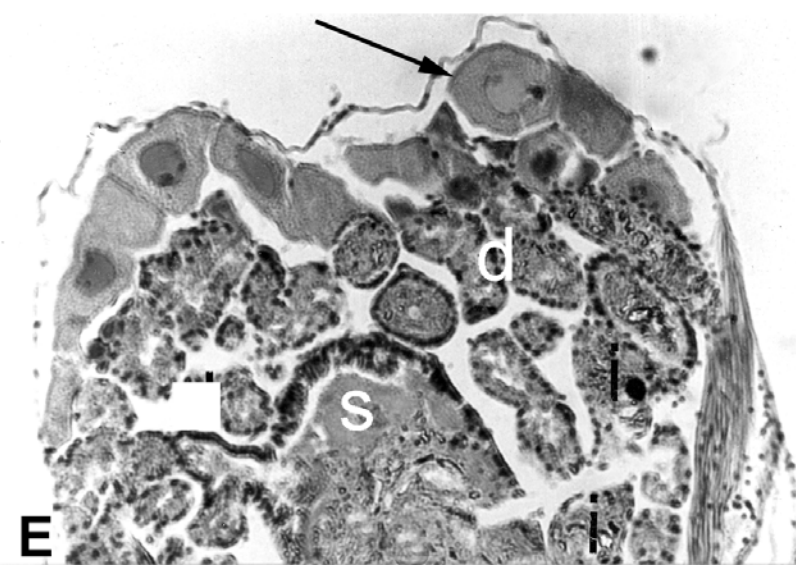
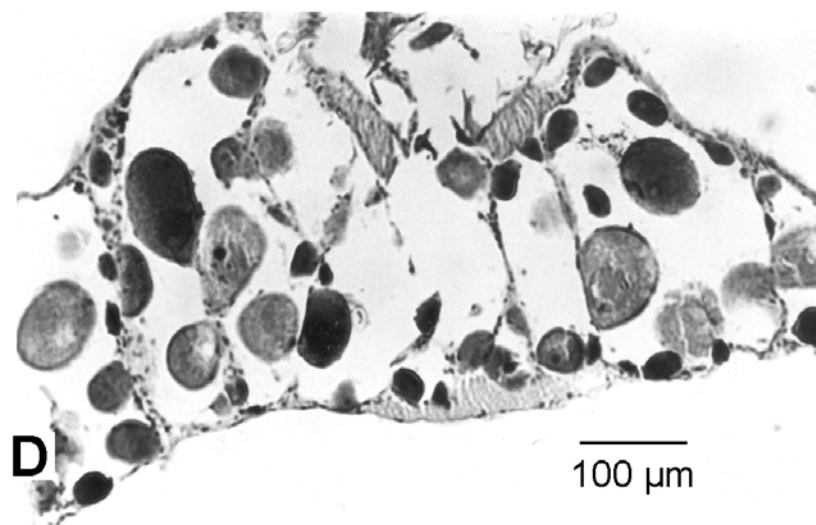
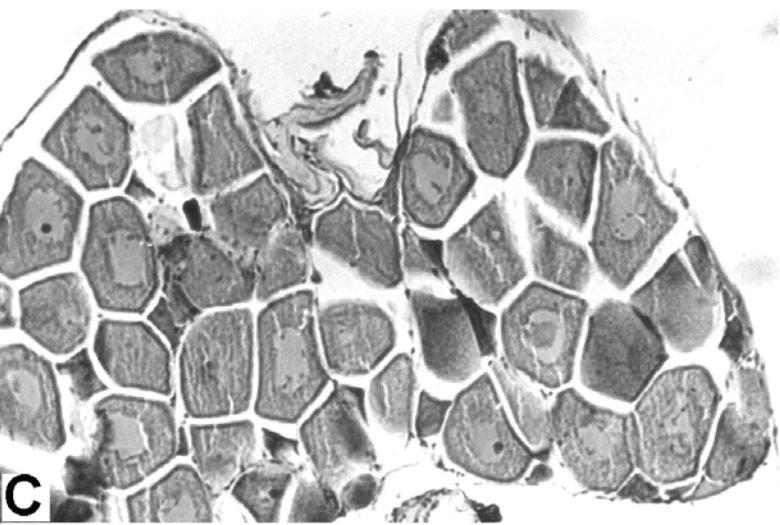
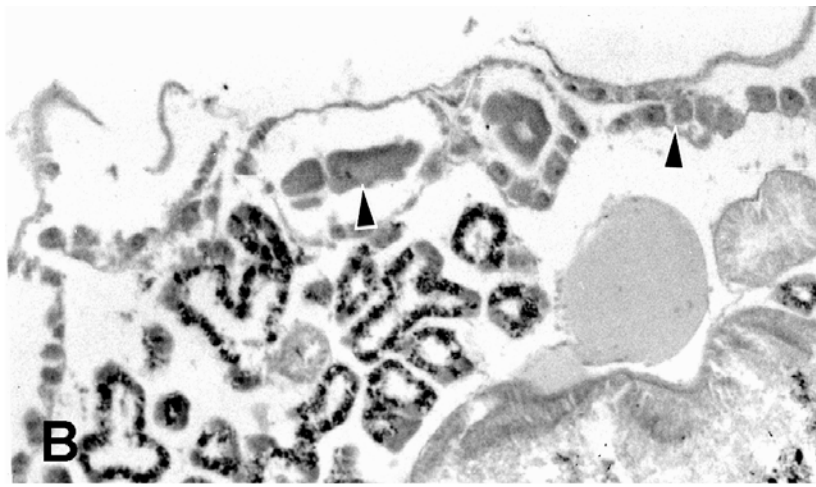
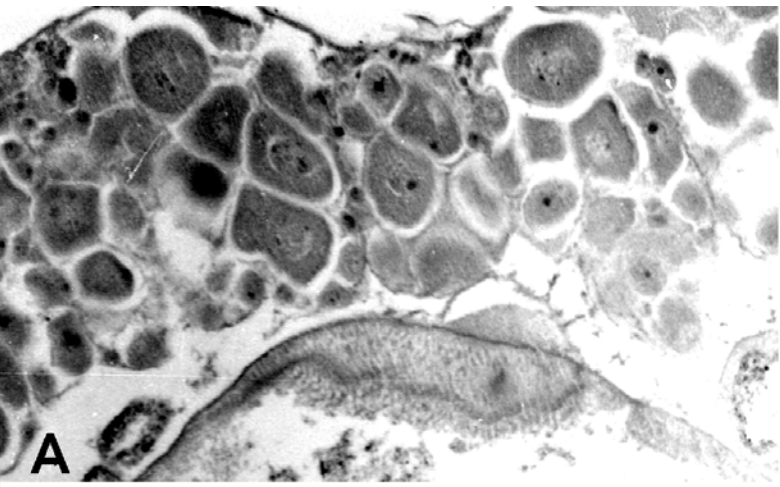
632

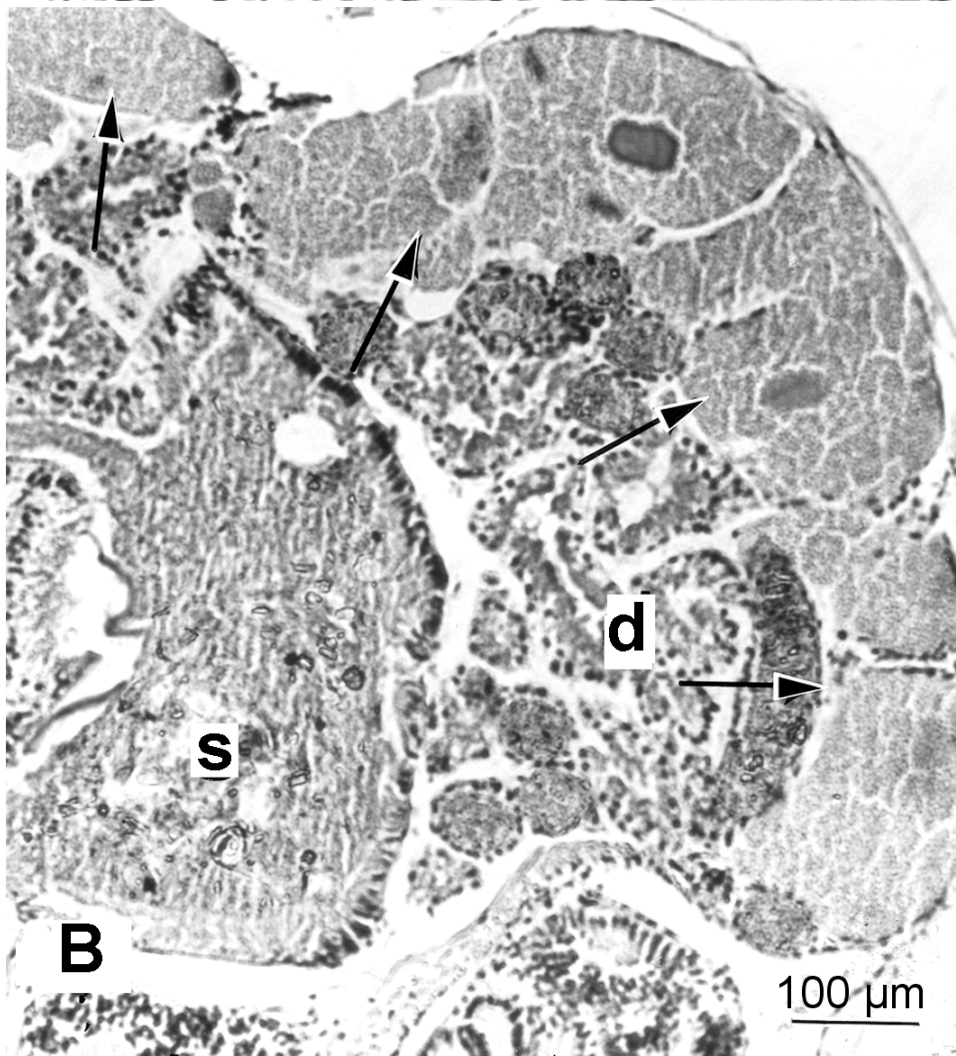
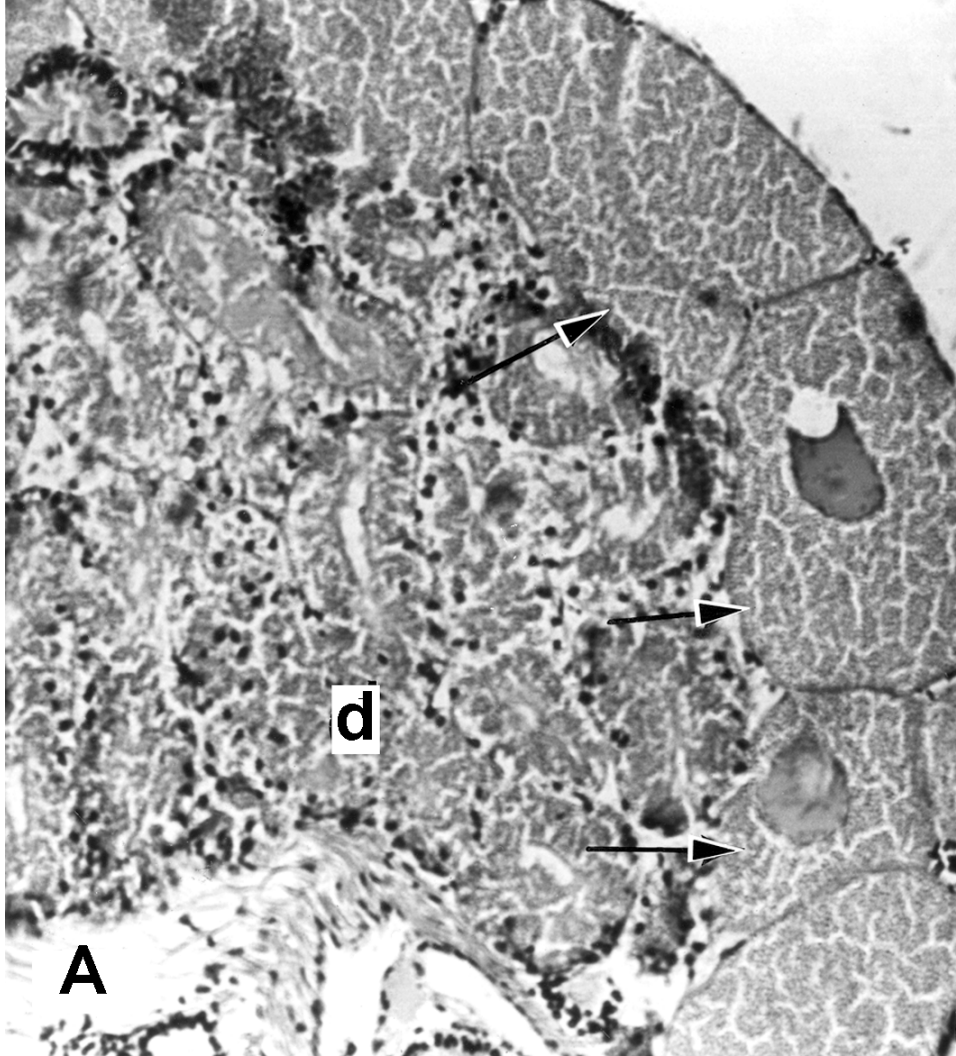
633

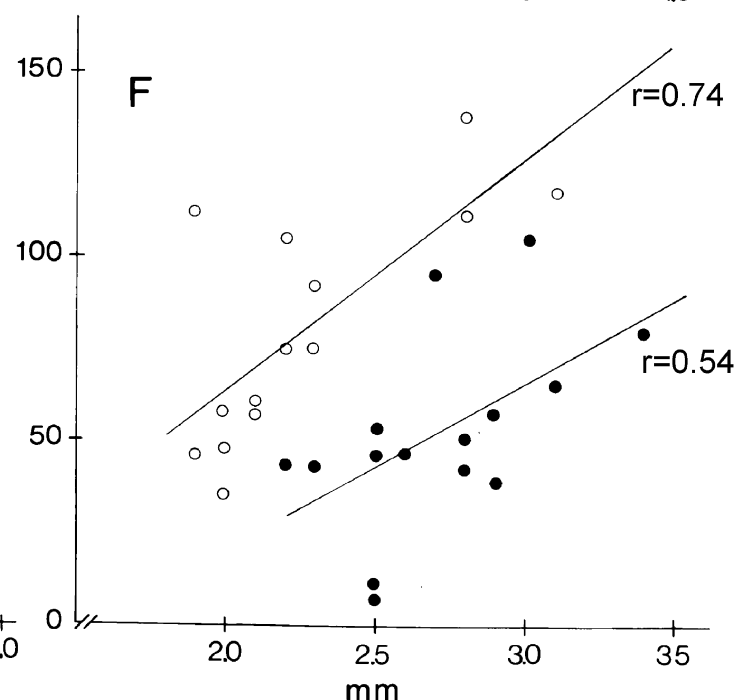
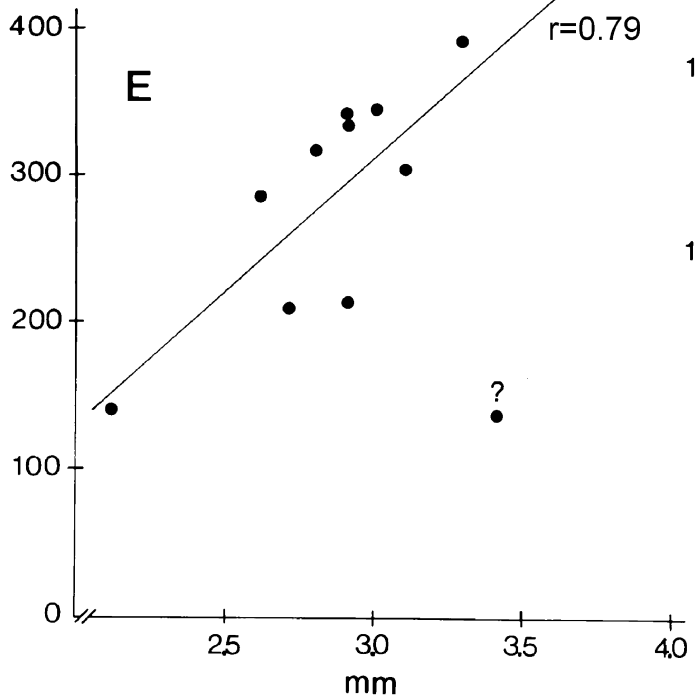
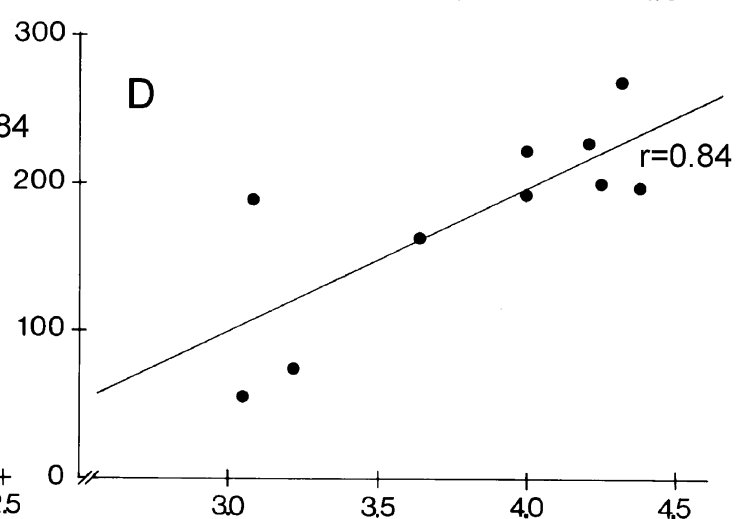
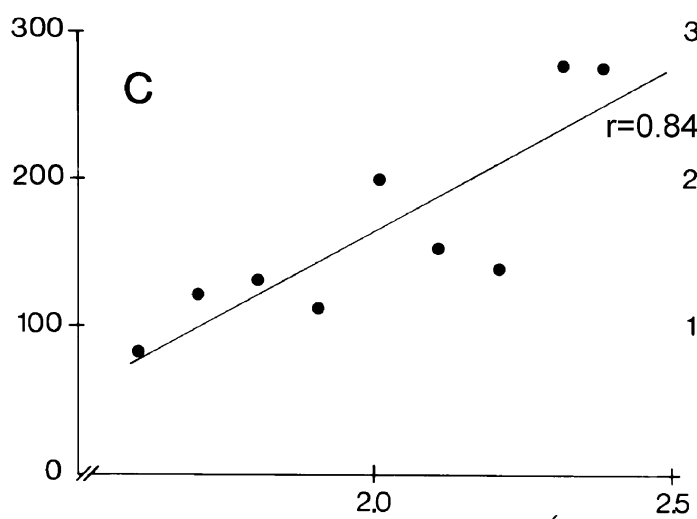
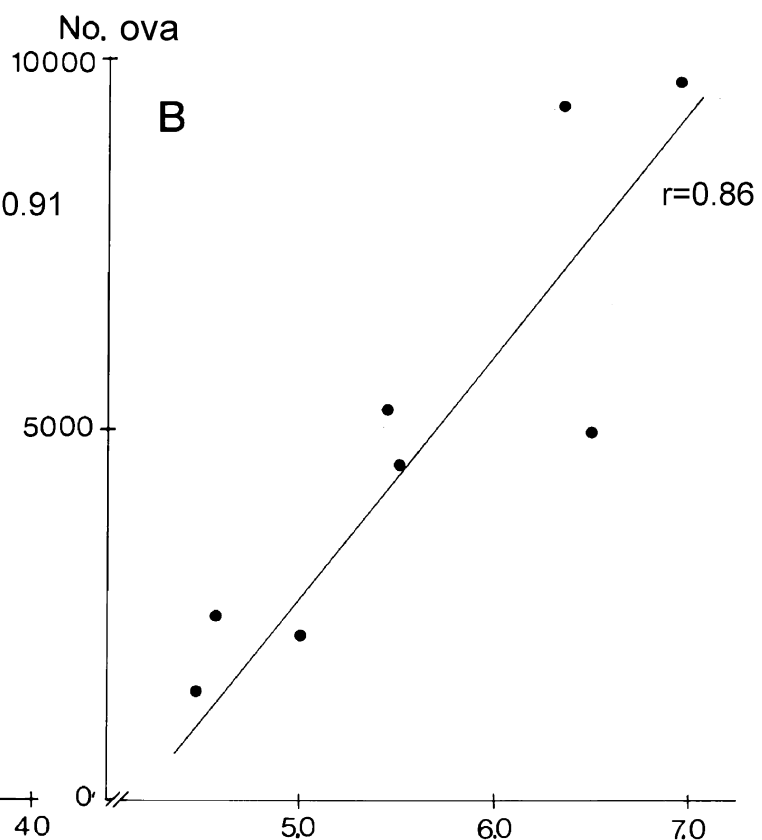
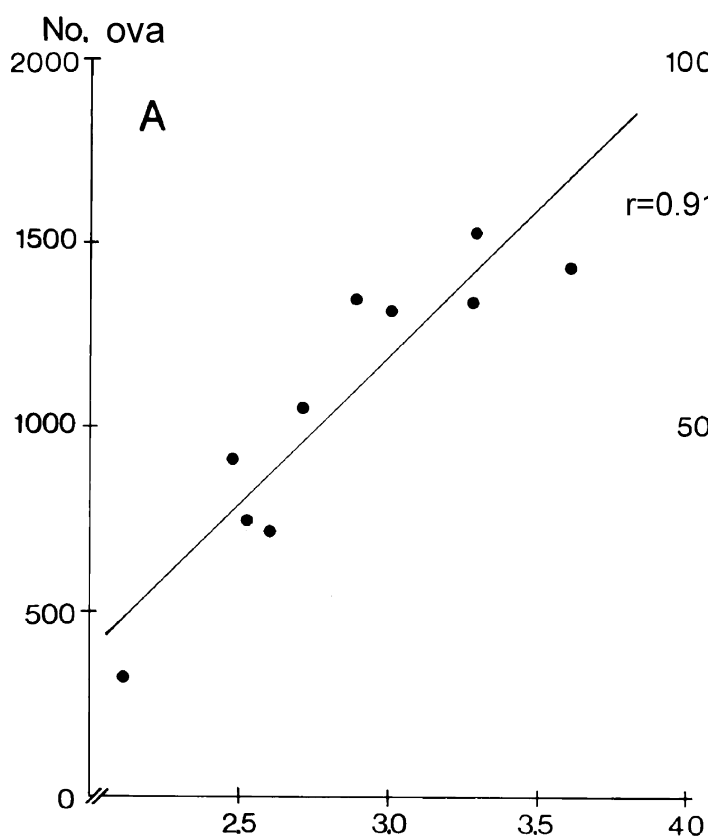












Length

