THE LIFE CYCLE OF A GORGONIAN: *EUNICELLA SINGULARIS* (ESPER, 1794)

by

STEVEN WEINBERG & FRANCISCA WEINBERG

Institute of Taxonomic Zoology, University of Amsterdam, The Netherlands

ABSTRACT

The life cycle of the gorgonian *Eunicella singularis* has been studied with emphasis on larval behaviour, metamorphosis and annual growth. Planulae are found to have a mobile phase lasting from several hours to several days. Once settled, they metamorphose into a complete primary polyp in approximately four days. In the first year, budding will yield colonies of a height between 10 and 30 mm. Subsequently, average growth rates range from 14 to 33 mm year^{-1}. Death may be due to several causes. Predators may partly denude the gorgonian branches, thus facilitating the settlement of epibionts, which in turn may invade the entire skeleton, slowly pushing back the living tissue of the gorgonian. Colonies may also be torn off their substratum by wave or current action, this process sometimes being speeded up when tall epibionts such as fast growing bryozoans enhance resistance to water movement. Once toppled, the gorgonians die by necrosis of their living tissues, or by being buried under sediment. Colonies of *E. singularis* are estimated to reach an age of approximately 25 to 30 years. Some data have been obtained on growth rates and life spans of two other Mediterranean gorgonians, *Lophogorgia ceratophyta* and *Paramuricea clavata*.

RÉSUMÉ

Dans cette étude le cycle de vie de la gorgone *Eunicella singularis* est abordé, et plus particulièrement le comportement larvaire, la métamorphose et la croissance annuelle. Les larves planula ont une phase mobile qui dure de quelques heures à quelques jours. Après s'être fixées sur un substrat favorable, elles se métamorphosent en un polype primaire complet en l'espace de quatre jours environ. Pendant la première année, les jeunes colonies atteindront entre 10 et 30 mm de hauteur par bourgeonnement. Ensuite, les vitesses de croissance moyennes seront de 14 à 33 mm an^{-1}. La mort peut survenir par plusieurs causes. Certains prédateurs peuvent partiellement dénuder les branches des gorgones, facilitant ainsi l'installation d'organismes épibiontiques, qui à leur tour, peuvent envahir le squelette entier, repoussant lentement les tissus vivants de la gorgone. Les colonies peuvent également être arrachées de leur substrat par l'action des vagues ou du courant. Ce phénomène est parfois précipité lorsque de grands organismes épibiontiques, tels des bryozoaires, augmentent la résistance à l'eau. Une fois renversées, les gorgones meurent par nécrose des tissus vivants, ou par recouvrement par le sédiment. Les colonies d'*E. singularis* atteignent un âge de 25 à 30 ans environ. Quelques données sur les vitesses de croissance et la durée de vie de deux autres gorgones méditerranéennes, *Lophogorgia ceratophyta* et *Paramuricea clavata*, ont été obtenues également.

1. INTRODUCTION

The biology of members of the subclass Octocorallia (Anthozoa) is still poorly known. Although the development of the gonads, as well as some aspects of larval behaviour, have been studied rather well, very little is known about the further life of these animals, their growth rates, or the causes leading to their death.

In an attempt to draw a picture of the life cycle of a typical octocoral, we examined the fate of gorgonians from the Mediterranean Sea during some critical phases. Most observations were carried out on the White Sea Fan, *Eunicella singularis* (Esper, 1794), although some data were also obtained for the Orange Sea Fan, *Lophogorgia ceratophyta* (Linnaeus, 1758) and the Purple Sea Fan, *Paramuricea clavata* (Risso, 1826). Recent descriptions of these gorgonians can be found in Carpine & Grasshoff (1975) and Weinberg (1976).

Wherever our own observations were insufficient, we consulted previous authors for additional information. We feel that studies of this type are necessary for a better understanding of the ecology of these animals.

2. MATERIAL AND METHODS

Field observations were invariably carried out by means of SCUBA diving in the region of Banyuls-sur-Mer (southern France). Ripe female colonies of *Eunicella singularis* were recognized under water (pl. I A) by scratching away a small portion of coenenchyme with a finger nail, thus revealing the bright pink eggs or planulae when present. These colonies were collected and kept in seawater aquaria until spawning of the larvae took place. Larvae were collected by means of a suction flask (fig. 1).

Metamorphosis was observed in aquaria with running seawater, either by direct observation or by means of time-lapse cinematography. Tagging of gorgonian branches was done with numbered tags of label tape, which were attached by means of thin, plastic coated electrical wire.

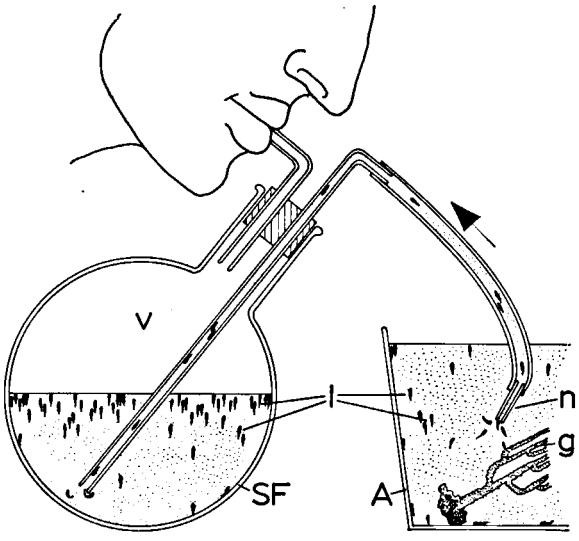

Fig. 1. Ripe female gorgonian colonies (g) are kept in a seawater aquarium (A) until spawning of the larvae (l) takes place. Suction produces a vacuum (v) in the suction flask (SF), causing the larvae to be drawn in (arrow) by directing the nozzle (n) at them.

3. THE GONADS

The development of octocorallian gonads has been studied by several authors (De Lacaze-Duthiers, 1864; Von Koch, 1887; Kükenthal, 1919; Moser, 1919; Suzuki, 1971; Vighi, 1972).

Octocoral colonies are either male or female, the sperm vesicles and eggs developing on the six non-siphonoglyphal septae (Kükenthal, 1925). This development takes several months, in the case of the female gonads of *Corallium rubrum* (Linnaeus, 1758) even two years (Vighi, 1972). Although we have not attempted to follow the development of the gonads of *E. singularis* throughout a yearly cycle, we have only seen ripe gonads towards the end of spring (May). A detailed study of the gonads of *Eunicella cavolinii* (Von Koch, 1887), a closely related species, was carried out by Von Koch (1887). Some micrographs of gonads of *Eunicella* appear in pl. I B-E. The eggs are polylecithal, spherical and bright pink in colour.

The spermatozoids, released into the seawater, enter via the oral apertures into the body cavities of polyps of female colonies, where fertilization takes place. Segmentation of the zygote is holoblastic (Kowalewsky, 1873; Von Koch, 1887) and takes place in the body cavity of the female polyp. Although this is the mechanism encountered in most Octocorallia, some exceptions exist, e.g. in *Clavularia crassa* (Milne Edwards, 1848) where the cleavage of the zygote takes place on the outside of the polyps (Kowalewsky & Marion, 1882, 1883; d'Hondt & Tixier-Durivault, 1975; Weinberg, 1978), as is the case for *Cornularia sagamiensis* Utinomi, 1955 (see Suzuki, 1971).

4. THE PLANULA LARVA

The cleavage of each zygote eventually leads to the planula larva, a description of which follows. The planula of *E. singularis* is bright pink in colour, due to the vitelline reserve which is its only food source during the mobile phase. It is pear- to worm-shaped, being at average 2.5 mm long and 0.5 mm wide (fig. 2a-d).

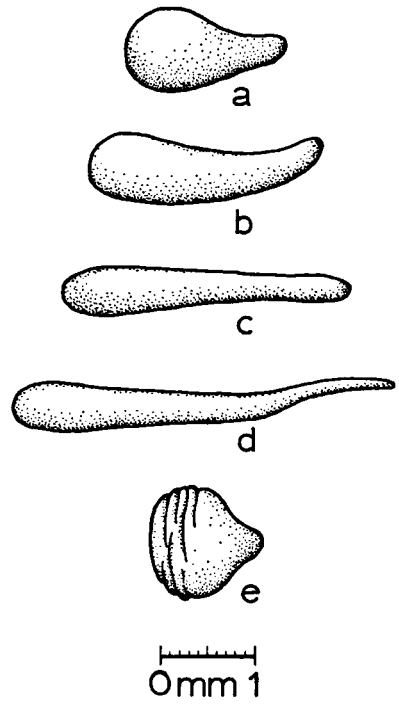

Fig. 2. Variable shapes and sizes of planulae of *Eunicella singularis* (a-d). Anterior side of the larvae is left in the figures. Certain stimuli cause the larvae to contract (e).

In microscopic sections (pls. I F, II A-B) it can be seen that the larva consists of an ectodermal and an entodermal layer separated by a mesogloea. The entoderm contains zooxanthellae in the case of larvae of *E. singularis singularis*, the most common form and the only one infested with these commensal algae. In young planulae the entoderm is continuous with the central yolk material, which is gradually digested in older larvae, leaving a void, the primitive coelenteron. The entoderm also contains some contractile fibres, which enable the larvae to bend to one side or the other, or to contract upon certain stimuli, such as head-on collision with other larvae, or contact with chemicals (e.g. formaldehyde) (fig. 2e). The ectoderm is a ciliated epithelium, which confers mobility to the larvae.

Each polyp emits several larvae. Théodor (1967b) has estimated that a medium-sized female colony of *E. singularis* emits some 6000 planulae during the spawning season, which begins in June (in Banyuls-sur-Mer we recorded the first planulae on 19 June 1976, 8 June 1977 and 13 June 1978, respectively), and may last till the end of July. Surface colonies (warmer water) will spawn earlier in the season than deeper ones, a phenomenon also observed by Grigg (1977).

Among the thousands of larvae obtained when keeping ripe female colonies in aquaria, several dozens will show malformations (see also Von Koch, 1887), mainly of the "siamese twin" type, as a result either of incomplete fusion of two eggs, or a separate development (without complete separation) of each cell of the initial doublet (fig. 3).

Once the planula is expulsed by the polyp it will start to fall down in a vertical position (fig. 4a), its density being slightly superior to that of seawater. In presence of even the slightest current the larvae will be carried away, adopting the same passive position, although with increasing current speed they tend to be swept away in a horizontal position. Once a larva reaches the bottom, it will start crawling over the substratum by means of its cilia, either in a perfect translation (fig. 4b) or accompanied by a dextrogyrous rotation along its main axis (fig. 4c). The maximal speed we measured over short distances in larvae of *E. singularis* is 18 cm min^{-1}, thus 50% faster than the values found by Théodor (1967b).

However, a larva will often stop, remaining motionless, or exploring the substratum at a given spot by a rapid, mostly counterclockwise rotation (fig. 4d) before resuming its initial course. Moreover, it will hardly ever travel along a straight line, and the resulting mean speed we measured over a distance of 120 cm was at most about 2.5 cm min^{-1}. We obtained this result by liberating about 300 larvae at one spot of a large (diam. ca. 75 cm) ring-shaped basin used for experiments on larval

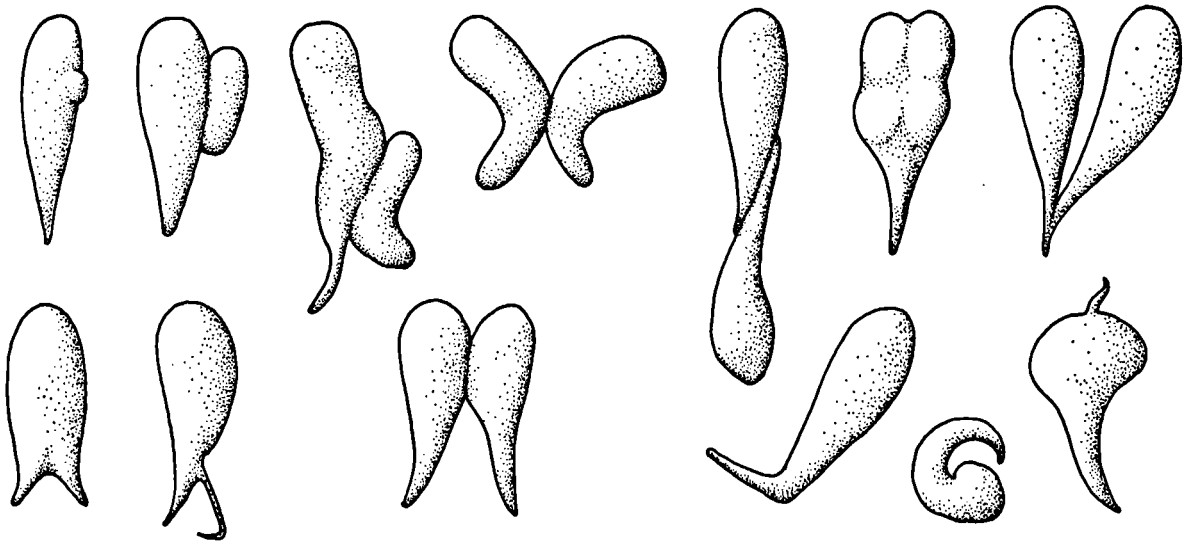

Fig. 3. Malformations occurring among planulae, mostly of the "siamese twin" type.

phototaxis (Weinberg, in preparation). This basin was divided into 16 sectors, the average distance from one sector to the next being ca. 15 cm. After 55 minutes the first larvae released in sector 1 reached sector 9 (the opposite sector), either by following the left or the right half of the annular basin, and the number of larvae present in each sector was counted. Numbers of planulae present in the left sector 2 and the right sector 2 were added together (they had travelled at the same speed); the same was done for sectors 3 through 8. This yielded a speed spectrum for this group of larvae; fig. 5 shows the percentage of larvae corresponding to each speed interval after a time of 55 minutes. Although these velocities are rather low, they will enable the larvae during the several hours to several days [1]) of their mobile phase to explore a vast surface before settling down.

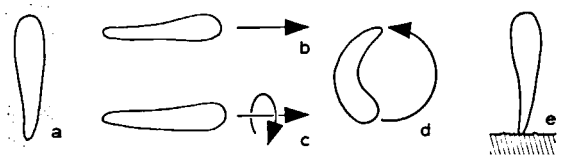

Fig. 4. Planula behaviour. a, Passive vertical floating position upon expulsion from the polyp. b, Crawling: translation over substratum by means of cilia. c, Do., accompanied by dextrogyrous rotation. d, Exploratory behaviour: quick (mostly counterclockwise) rotation on the same spot. e, Pre-settlement behaviour: upright standing on substratum, sometimes accompanied by slow rotation.

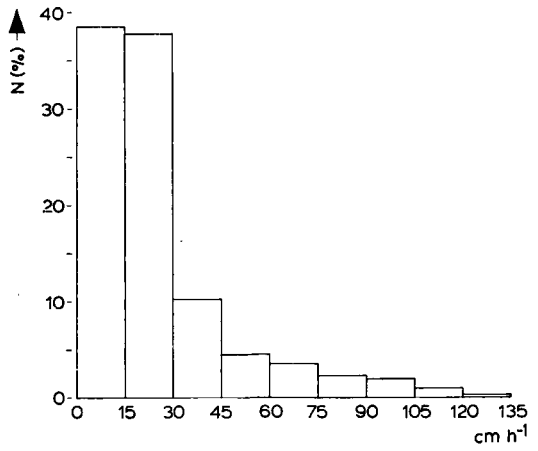

Fig. 5. Spectrum of average speed (in cm h^{-1}) of a group of 300 larvae (see text). Ordinate is number of larvae N (in %) for each speed class.

1) Théodor (1967b) reports a maximum life span of 122 days in vitro, which must be considered exceptional.

We observed that in presence of a favourable substratum (the underside of gorgonian holdfasts), settlement takes place within approximately 30 hours. During this period, the slowest larvae can explore the substratum over a distance of ca. 2 m, the fastest over a distance of ca. 40 m. The triggering factors for settlement are a suitable roughness of the substratum (Cary, 1914; Gohar, 1940; Théodor, 1967b; personal observations), absence of other organisms (Théodor, 1967b; personal observations) and optimum illumination (Weinberg, in preparation).

Once such a place has been selected after the exploratory behaviour of fig. 4d, the larva adopts an upright position, its posterior end touching the substratum (fig. 4e). Possibly, the cement necessary for attachment is secreted during this phase, while sometimes a slow rotation is observed. This settlement behaviour involving several successive explorations of the substratum is typical of many larvae of marine invertebrates (Meadows & Campbell, 1972). As a whole, octocoral larvae and their behaviour (see also De Lacaze-Duthiers, 1864, 1900; Von Koch, 1887; Théodor, 1967b; Suzuki, 1971; Grigg, 1977) do not differ very much from those of Hexacorallia (Atoda, 1947a & b, 1951a, b & c, 1953; Lewis, 1974; Vandermeulen, 1974) except for the fact that the latter develop a mouth during their pelagic phase.

5. SETTLEMENT AND METAMORPHOSIS

We have never been able to witness the actual settling of a larva. We know that some 30 hours after emission, several planulae are found firmly attached to a suitable substratum. In the terminology of Mileikovsky (1971) the larvae of *E. singularis* exhibit a demersal lecithotrophic development. Whereas during the pre-settlement behaviour the larvae touched the substratum with their tapered (posterior) end, attached larvae have their thickest part adhered to the bottom. Whether the larvae have inverted position or simply changed shape during attachment we do not know.

The subsequent phases of metamorphosis have been studied by time-lapse cinematography of 14 settled larvae over a period of four days, and

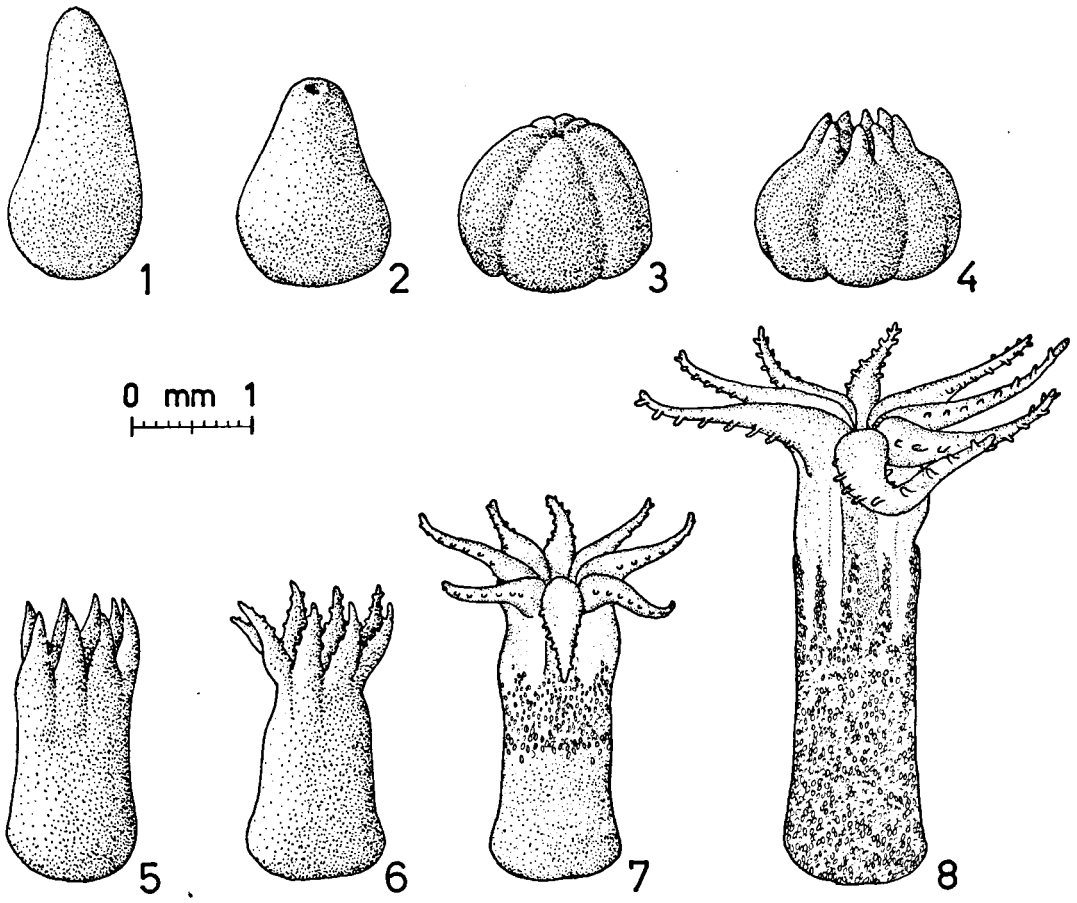

Fig. 6. Metamorphosis of the planula: 1 = settlement; 2 = invagination; 3 = septation; 4, 5 = development of primordial tentacles; 6 = appearance of primordial pinnules; 7 = pinnules clearly visible, appearance of sclerites; 8 = complete primary polyp.

additional observations on several other larvae (figs. 6 & 7). Five to ten hours after attachment the larvae start to invaginate, accompanied by a shortening and thickening of their body. After another five to ten hours interval, the septae are formed (pl. II C), and the metamorphosing larvae reach their minimum length at this point. Their structure is entirely hollow now, with a primitive mouth and internal septae. After a period of rest of ten to twenty hours, the primordial tentacles start developing, being clearly visible two days after settlement, and the lateral pinnules start growing on each tentacle. One day later, the pinnules are well developed, and the first sclerites appear as white dots on the translucent pink polypean walls. They start forming eight vertical rows, one under each tentacle, and the spicular sheath gradually invades the proximal part of the polyp. Four days after settlement the primary polyp is complete (pl. II D).

This chronology (fig. 7), based on a limited number of polyps, is only approximate, but corresponds remarkably well with the one given by Suzuki (1971) for *Cornularia sagamiensis*, and the data presented for several Hexacorallia by Atoda (1947a & b, 1951a, b & c, 1953). Variations occur from one individual to another. A complete histological description of the changes involved in Octocorallia of the genus *Xenia* can be found in Gohar (1940), whereas Von Koch (1887) gives a description for *E. cavolinii.*

6. THE FIRST YEAR

Only a very small fraction of the larvae reaches the primary polyp stage. Many are lost by alighting on unfavourable substrata (soft bottoms, animal or

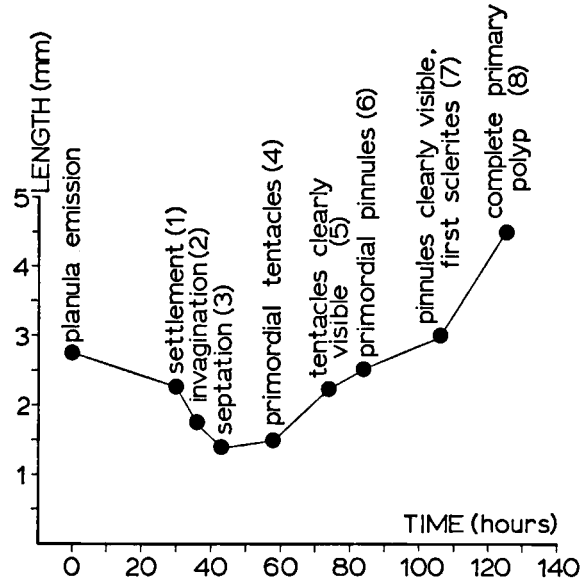

Fig. 7. Average chronology of metamorphosis, with average larval length, based on time-lapse cinematography of several polyps. Numbers between brackets refer to stages in fig. 6.

plant surfaces), probably many are eaten by fishes or other organisms, although we have never actually witnessed the capture of a planula. Thorson (1950) assumes depredation to be the most important cause of death of planktonic larvae. In situ observations over several months of primary polyps in several underwater stations near Banyuls-sur-Mer have convinced us that only about one or two polyps out of a hundred will survive the first year. Abrasion and/or smothering by sediment or algae are among the main death causes at this stage. Théodor (1967b) has estimated that of 60000 larvae emitted, only one will survive the first year.

We have tried to raise primary polyps in vitro. Secondary polyps formed by budding sometimes occurred as soon as a fortnight after completion of the primary polyp. After four months, budding had yielded colonies of 2-5 polyps, with a maximum height of 8 mm (pl. II E). Shortly after, these experimental colonies died due to a technical accident, making further observations impossible.

Young colonies measured at 18 and 26 m depth near the harbour pier of Port Vendres in December 1977 fall into three size classes (fig. 8), presumably three different generations: one with a size from 2 to 10 mm (ca. 5 months old), one with a size from 10 to 40 mm (ca. 17 months old) and one with a size from 30 to 70 mm (ca. 29 months old). These data suggest a growth rate of 8 to 30 mm year^{-1} at least during the first year(s). A number of one year old colonies (summer 1978) at 20 m depth at Cap Rédéris (Banyuls) measured between 13 and 21 mm (mean: 17 mm).

One might expect, however, that with increasing size, food capture becomes more efficient, and abrasion or smothering by sediment causing necrosis of living tissues becomes less important, so that growth rates may increase with age.

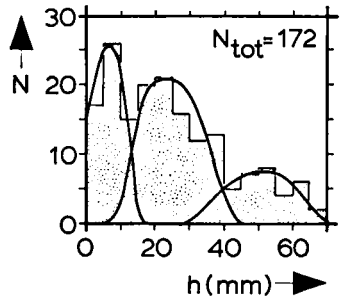

Fig. 8. Histogram of number of young colonies (N) of *Eunicella singularis* found at Port Vendres in December 1977, in height (h) classes of 5 mm each. Curves show (tentatively) three different generations.

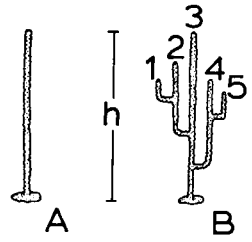

Fig. 9. Comparison of two young colonies, one unbranched (A) and one ramified (B). Although total length differs in both, they have the same age, as colony A and the third branch of colony B took the same time (approximately) to reach height h.

7. ANNUAL GROWTH

Before attempting to determine annual growth, we have to define what annual growth in a gorgonian is. Cary (1914) and Grigg (1974) measured increase in colony height, whereas Velimirov (1975) measured increase in total length, i.e. the sum of the lengths of all the branches of a colony. Colonies are formed by budding sequences, some

buds starting lateral branches. If we compare the unbranched colony of fig. 9A with the ramified one of fig. 9B, we would say they were of equal age when taking colony height as a criterium, whereas on the basis of total length the second colony would be considered much older than the first.

Our field observations have shown that each branch grows independently from the others. Hence, assuming equal growth rates, colonies A and B have the same age, as branch 3, growing independently from branches 1, 2, 4 and 5, took as long as colony A to reach height *h*. For age estimates it is better therefore to measure colony height than total length. This method is an approximation, however, as in most cases colony height is smaller than the real maximum size for colony growth, i.e. the longest budding sequence in a colony, as shown in fig. 10A & B. The latter figure represents the case of a colony that is wider than its height, in which case colony height yields a poor estimate of its age. It is even more accurate to count growth rings, which have annual periodicity (Grigg, 1974), especially since growth rates may differ considerably from one individual to another, as will be shown later on. However, for practical reasons, and since counting growth rings is a destructive method, we measured length from a gorgonian foothold to the most distant branch tip.

Our first attempt to measure growth rates of *E. singularis* consisted in the tagging of 47 branchlets near Ile Grosse, Banyuls-sur-Mer. The first experiment consisted of two series, 10 branchlets at 15 m depth and 11 at 10 m depth, which started November 28th, 1976. The first series was soon interrupted, as the tags nearly all disappeared. Another series of 26 tagged branchlets replaced the initial 15 m experiment on April 12th, 1977. Although a number of tags were lost here too, branches of both the 10 m and 15 m series were measured with intervals until July 1978 when 7 and 11 tagged branches subsisted, respectively (fig. 11).

Due to intrinsic and external factors individual growth rates can vary to a large extent, a fact also reported by Grigg (1974). Some branchlets showed negative growth, probably due to abrasion and/or predation. These few branchlets were left out of our calculations. The others showed individual growth rates ranging from 0 to 49 mm year^{-1}. This is faster than the 5.2 to 21.5 m year^{-1} reported by Velimirov (1975) for the Mediterranean species *E. cavolinii*, but slower than the growth rates observed for *Gorgonia flabellum* Linnaeus, 1758 (0-83 mm year^{-1}) and *Plexaura flexuosa* Lamouroux, 1821 (5-55 mm year^{-1}) near Florida (Cary, 1914) or the Californian *Muricea californica* (Aurivillius, 1931) (0-60 mm year^{-1}) reported by Grigg (1974). Kükenthal (1909) undertook growth experiments with *E. singularis*. He cut off branch tips of colonies maintained in an aquarium, and measured a growth of 60 mm in 22 days (= 995 mm year^{-1})! This

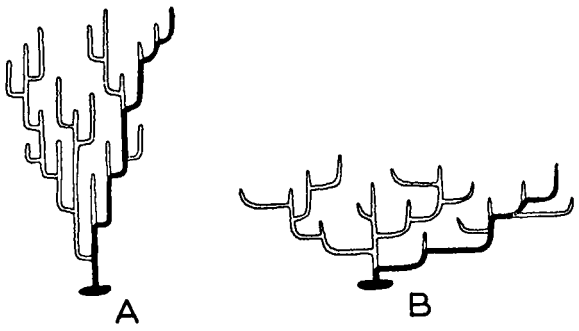

Fig. 10. Length of longest budding sequence (black) is a better dimension for colony size than its height, especially in the case of colonies that are broader than their height, like colony B.

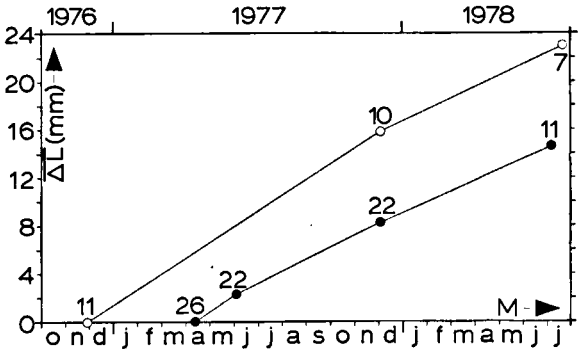

Fig. 11. Average increase in length ($\overline{\Delta L}$) as a function of time in months (M) for a number of tagged branches of *Eunicella singularis* at 10 m depth (open circles) and 15 m depth (black dots) near Ile Grosse, Banyuls-sur-Mer. Numbers indicate number of tagged branches found back at time of each measurement. Increase is linear; $\overline{\Delta L}$ = 14.6 mm year^{-1} at 10 m, 12.1 mm year^{-1} at 15 m.

growth rate is obviously exceptional, and caused by the cutting, if the observation is reliable at all, which we doubt.

Curves based on average growth of all given branches in each spot (fig. 11) strongly suggest a linear growth and no seasonal influences such as observed for *E. cavolinii* by Velimirov (1975). Linear regression yields very high correlation coefficients (0.996 for the 10 m experiment and 0.998 for the 15 m experiment) and the obtained average growth rates are 14.6 mm year^{-1} in the first case and 12.1 mm year^{-1} in the second [2]). These values seem a little low when compared to those obtained by observation of young colonies (preceding paragraph). We suspected that damage caused by the tagging itself, which forced the branchlets to repair wounds inflicted by friction of the wire, might have slowed down growth rates.

We therefore undertook a second attempt, i.e. measuring colony size on substrata of known age, a method used by several investigators of coral growth (Grigg, 1974; Buddemeier & Kinzie, 1976). In December 1977 we counted 142 gorgonians at 20 m depth on a section of the sewer pipe of Port Vendres. Ten of these gorgonians measured 160-180 mm. As this concrete pipe was installed in March 1972, the oldest colonies had settled in the summer of 1972, and were therefore 5.5 years old when we measured them. This yielded a maximal growth rate (over longer periods) of 33 mm year^{-1} [3]).

The discrepancy between these data and the preceding ones led us to undertake a third attempt. On December 9th, 1977, a number of stones bearing gorgonians were installed on a metal rack at 20 m depth at Cap Béar. Instead of tagging, each colony was carefully drawn and all branches measured. The same was repeated on June 22nd, 1978. In these undisturbed branches growth rates varied from 0-32 mm in 195 days, i.e. 0-60 mm year^{-1}. The average growth rate obtained for 25 branchlets of *E. singularis* was 22.4 mm year^{-1}, whereas 4 branchlets of *Lophogorgia ceratophyta* yielded an average growth rate of 28.5 mm year^{-1}. A similar experiment carried out at 26 m depth at Cap Rédéris with a young colony of *Paramuricea clavata* (6 branches) yielded an average growth rate of 12.5 mm year^{-1}.

Table I summarizes the data obtained by the different methods. Whereas tagging seems to have a negative effect on the growth of branches of *E. singularis, P. clavata* with its much thicker branches is not affected by this method.

TABLE I

Growth rates (in mm year^{-1}) of three Mediterranean gorgonians as determined by three different methods. A = average growth rates of tagged branches; B = average growth rates of branches of untagged colonies; C = estimated maximal growth rates after observation of gorgonians on sewer pipes of known age.

	Eunicella singularis	*Lophogorgia ceratophyta*	*Paramuricea clavata*
A	14.5	—	18.3
B	22.4	28.5	12.5
C	33.0	24.0	—

8. AGEING AND DEATH

Years of observation on gorgonians never led us to witness obvious signs of ageing in these animals. In small and large colonies alike, the tissues and polyps at the base (the oldest part of the colony) always look as healthy and active as those at the newly formed branch tips. Whereas individual polyps may age and die, the regeneration capacity of the colonies (Kükenthal, 1909; Cary, 1914; Lang da Silveira & Van 't Hof, 1977) will lead to quick healing or replacement of lost individuals. It is obvious, on the other hand, that for each species there is a maximum colony size never exceeded. Two possible causes, determinate growth or death at this size, are unlikely. Whereas death is hard to conceive if no ageing takes place, the very nature of these colonial, branching animals makes the hypothesis of determinate growth equally improbable. As integration of the colony is very poor, there seems to be no reason for budding to stop at the branch tips, especially since the colony is probably not able to "tell" it has reached a certain size. Many workers on Hexacorallia have also assumed or proved indeterminate growth in

[2]) For comparison: tagging of 26 colonies of *Paramuricea clavata* at 24 m depth yielded an average growth rate of 18.3 mm year^{-1} (range: 1.6-36.9 mm year^{-1}).

[3]) Likewise, counting 48 gorgonians at 31 m depth on the sewer pipe of Banyuls-sur-Mer, which was installed spring 1965, yielded a maximal growth rate of 24 mm year^{-1} for the species *Lophogorgia ceratophyta.*

most colonial corals (e.g. Buddemeier & Kinzie, 1976). If we assume indeterminate growth and if death is not the result of ageing, only one possibility remains: destruction of the colonies by external agents.

One such agent could be predation. We never witnessed, however, any important damage due to predation. We know of no larger organism (e.g. fish) feeding on Mediterranean gorgonians. The only predator of *E. singularis* that we have observed is a small ovulid gastropod, *Neosimnia spelta spelta* (Linnaeus, 1758), capable of denuding small portions of the branches of their living tissue (pl. III A) (see also Théodor, 1967a). A similar behaviour is displayed by *Pseudosimnia carnea carnea* (Poiret, 1789), feeding on deep-water gorgonians (e.g. *Eunicella verrucosa* (Pallas, 1766)) in the Mediterranean. In the Caribbean, related ovulid gastropods, *Cymbula acicularis* (Lamarck, 1810) and *Simnialena uniplicata* (Sowerby, 1848) feed on colonies of various gorgonians, as does the "Flamingo Tongue" snail *Cyphoma gibbosum* (Linnaeus, 1758) [4]) and the polychaete *Hermodice carunculata* (Pallas, 1766).

Whereas the wounds inflicted by these predators are certainly not lethal, the denuded portions of the skeleton may become the site of settlement of other organisms. Two Octocorallia are specialized in the colonization of gorgonians: *Parerythropodium coralloides* (Pallas, 1766) and *Rolandia rosea* (Philippi, 1842) (see also Weinberg, 1975, 1977, 1978). Once settled, these animals grow very fast, gradually pushing back the living gorgonian tissue and investing the entire colony. This behaviour is apparent in the photograph of pl. III B. It is not rare to find gorgonian axes completely overgrown by either of these Octocorallia (pl. III C) [5]).

Many other invertebrates or algae may settle on denuded portions of gorgonian axes. Frequently encountered are the lamellibranch *Pteria hirundo* (Meuschen, 1787) and several large bryozoans, such as *Hippodiplosia fascialis* (Pallas, 1766), *Porella cervicornis* (Fleming, 1828) and *Schismopora avicularis* (Lamouroux, 1812). Whereas these animals have only a fairly small adherence zone on the gorgonian itself, therefore not directly killing the colony in the way both previously mentioned octocorals do, their fast growth will ultimately cause the gorgonian to topple over, either by the sheer weight of these calcareous colonies, or by the increased resulting drag in water currents (pl. III D).

The observation of toppled colonies, many of them entirely devoid of epibionts (pl. II F) eventually led us to the hypothesis that the natural death of gorgonians is also dictated by the forces exercised on the fan. Up to a certain size, the holdfast will be able to resist; whenever this size is exceeded, on a day of strong current or heavy swell, these colonies will be torn off their substratum. Similar observations have been made by Grigg (1977) for colonies of *Muricea* in California, and for Caribbean shallow-water gorgonians, especially after a hurricane (Cary, 1914). Once the gorgonians are toppled over, they will die by necrosis of the living tissues in contact with the bottom, or they will simply be buried under sediment.

In an attempt to verify this hypothesis, we measured the largest colonies in a population at different depths. First of all it was seen that the tallest colonies in the population were always less ramified than others. Broader, more ramified colonies never attained the maximum height for a given depth. The maximum fan surface remained rather constant however (2145 cm^2 for a 55 cm high poorly ramified specimen, 2257 cm^2 for a 37 cm high colony with many ramifications, both at 25 m at Cap l'Abeille), making our mechanistic explanation for gorgonian death rather plausible. It was further observed that with increasing depth (and decreasing water movement) the maximal height in each population of *E. singularis* increases. At one station near Cap Rédéris we measured a maximal height of 33 cm at 12 m depth, 64 cm at 25 m depth and 81 cm at 40 m depth. These findings tend to confirm that destructive water movement is the main limiting factor for gorgonian growth.

These data, combined with those on growth

[4]) Many species of the gastropod family Ovulidae are associated with gorgonians all over the world (Cate, 1973).

[5]) In the Caribbean, hydrocorals of the genus *Millepora* are able to invest gorgonians in much the same way (personal observations).

rates, lead to the conclusion that colonies of *Eunicella singularis* may live as long as 25-30 years, whereas *Lophogorgia ceratophyta* may grow over 35, and *Paramuricea clavata* over 50 years. A similar age was estimated for colonies of *Muricea californica* (see Grigg, 1974). The fast growing Caribbean gorgonian *Gorgonia flabellum* (see Cary, 1914) may attain 150 cm (personal observations), also indicating a life span of 20-30 years.

9. CONCLUSION

Populations of *E. singularis* are characterized by long-lived individuals (low turnover rate) with a rather short reproduction period. In the concept of the *r-K* continuum, as worked out by Pianka (1970) this corresponds to *K* selection, characteristic of populations living at their maximum size in a stable environment, to which the individuals are well adapted. However, another characteristic of *E. singularis* is its high rate of recruitment with high larval and juvenile mortality, typical of *r* selection. The same was found by Grigg (1977) for populations of *Muricea* in California. Most coral populations probably occupy such an intermediate position in the *r-K* continuum, one known exception being the opportunistic Red Sea species *Stylophora pistillata* (Esper, 1791) (see Loya, 1976).

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LEGENDS TO THE PLATES

PLATE I

A, Diver at a depth of 20 m in *Eunicella*-"meadow", collecting ripe female colonies (photograph by S. Weinberg). B, Ovocyte (o) of *Eunicella singularis* in septum; septal musculature (m) is clearly visible; 120 × (light micrograph by S. Weinberg). C, Ovocyte of *E. singularis* surrounded by a layer of entodermal cells (en); cytoplasm (c), nucleus (n) and nucleolus (nu) can be distinguished; 240 × (light micrograph by S. Weinberg). D, Detail of the peripheral cytoplasm of an ovocyte of a gorgonian (*Corallium rubrum*), containing electron-dense yolk granules (dg), electron-light yolk granules (lg) and lipid droplets (li); the ovocyte is surrounded by the mesogloea (mg) and entoderm (en) of the polypean septum; 4500 × (electron micrograph by W. Schäfer). E, Immature sperm cell of *E. cavolinii*; residual cytoplasm (rc) of spermatocyte surrounds the nucleus (n) and the flagellum (f) between which centrioles are visible; the flagellum is separated from the cytoplasm by a flagellar canal (fc); no acrosome or mitochondrial sheath are to be seen; 24000 × (electron micrograph by H. Schmidt). F, Longitudinal section of a planula larva of *E. singularis*; ectoderm (ec), mesogloea (mg) and entoderm (en) can be distinguished; the barely visible cilia (ci) are 20-30 μm long; 60 × (phase-contrast micrograph by E. Kniprath).

PLATE II

A, Detail of cross section of planula larva of *E. singularis*; ectoderm (ec) with cilia (ci), mesogloea (mg) and entoderm (en) are visible; 580 × (light micrograph by E. Kniprath). B, Detail of planula larva of *E. singularis*; the ectoderm consists of epithelial cells (ep) with microvilli (mv), cilia (ci) and osmiophilic vacuoles (arrows) and of glandular cells (gc); the entoderm contains vitelline material (vi) and symbiotic zooxanthellae (z); both layers are separated by the mesogloea (mg); 2000 × (electron micrograph by E. Kniprath). C, Cross section through a settled larva of *E. singularis* in the process of septation; ectoderm (ec), mesogloea (mg) and entoderm (en) surround the gastric cavity (gc) resulting from the digestion of the vitelline material from the planula larva; septae (s) originate from mesogloea and entoderm (see inset); 90 ×, inset 750 × (light micrograph by S. Weinberg). D, Cross section through primary polyp of *E. singularis*; holes resulting from the dissolution of sclerites (sc) can be seen in ectoderm (ec) and mesogloea (mg); mesogloea and entoderm (en) are continuous with the septae (s) in which the musculature (m) is visible; columnar epithelium of ectoderm surrounds the stomodaeum (st) with its ciliated siphonoglyph (si); 90 × (light micrograph by S. Weinberg). E, Four months old colonies of *E. singularis*; 6 × (photograph by J. Lecomte). F, One normally attached colony of *E. singularis* (upper left) and several torn-off colonies lying on the bottom, some of them (barely visible, arrows) are only skeletons, having lost their (white) living tissue (photograph by S. Weinberg).

PLATE III

A, The ovulid gastropod *Neosimnia spelta spelta* feeding on a branch of *E. singularis*; 8 ×. B, Colony of the alcyonacean *Parerythropodium coralloides* (dark coloured) spreading over the basal parts of a colony of *E. singularis*. C, Colony of *E. singularis*, completely overgrown by the stoloniferan *Rolandia rosea* next to healthy colonies (right). D, Colony of *E. singularis* with several epibionts, the octocoral *Parerythropodium coralloides* (pc) and the bryozoan *Hippodiplosia fascialis* (hf). (All photographs by S. Weinberg.)

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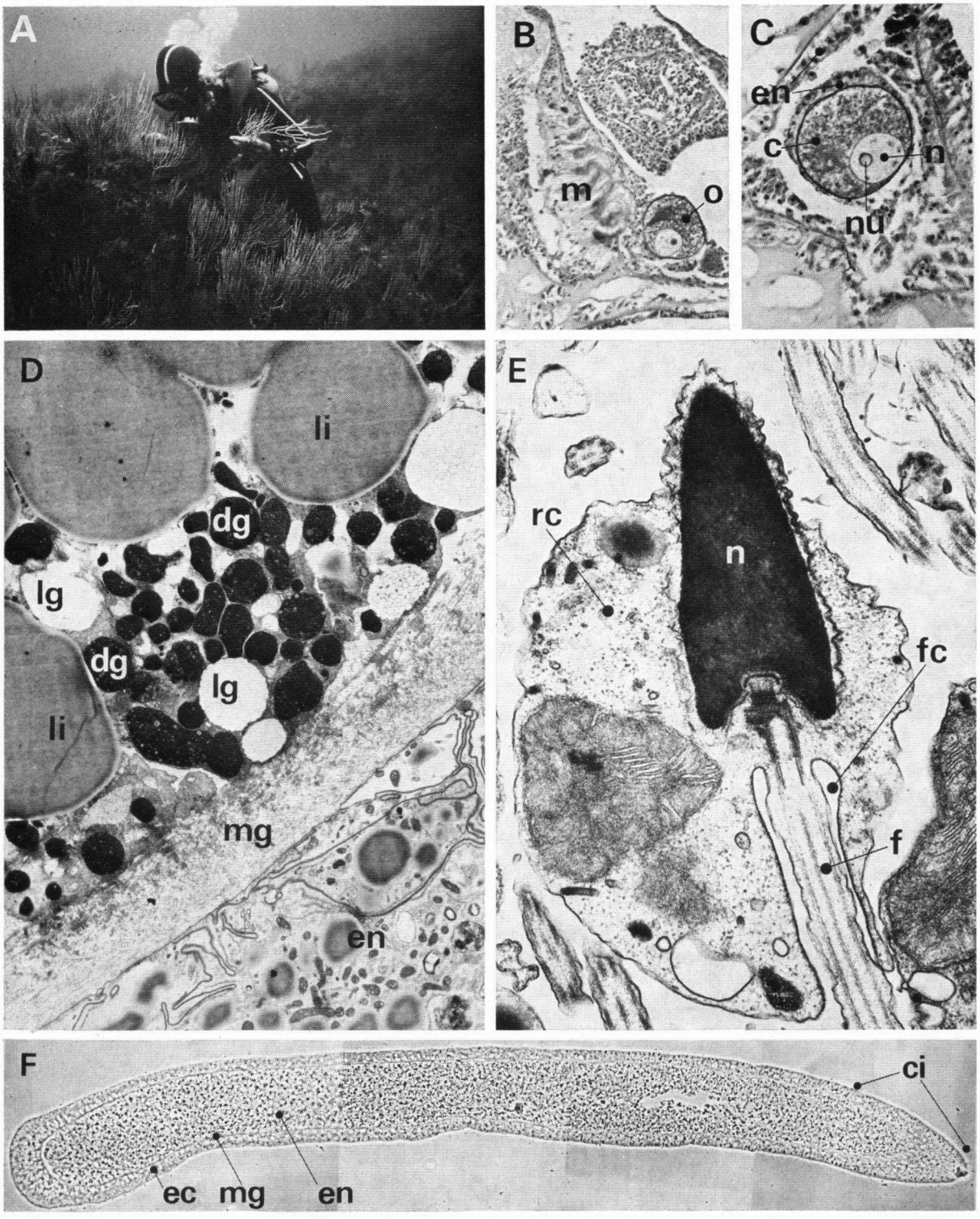

PLATE I

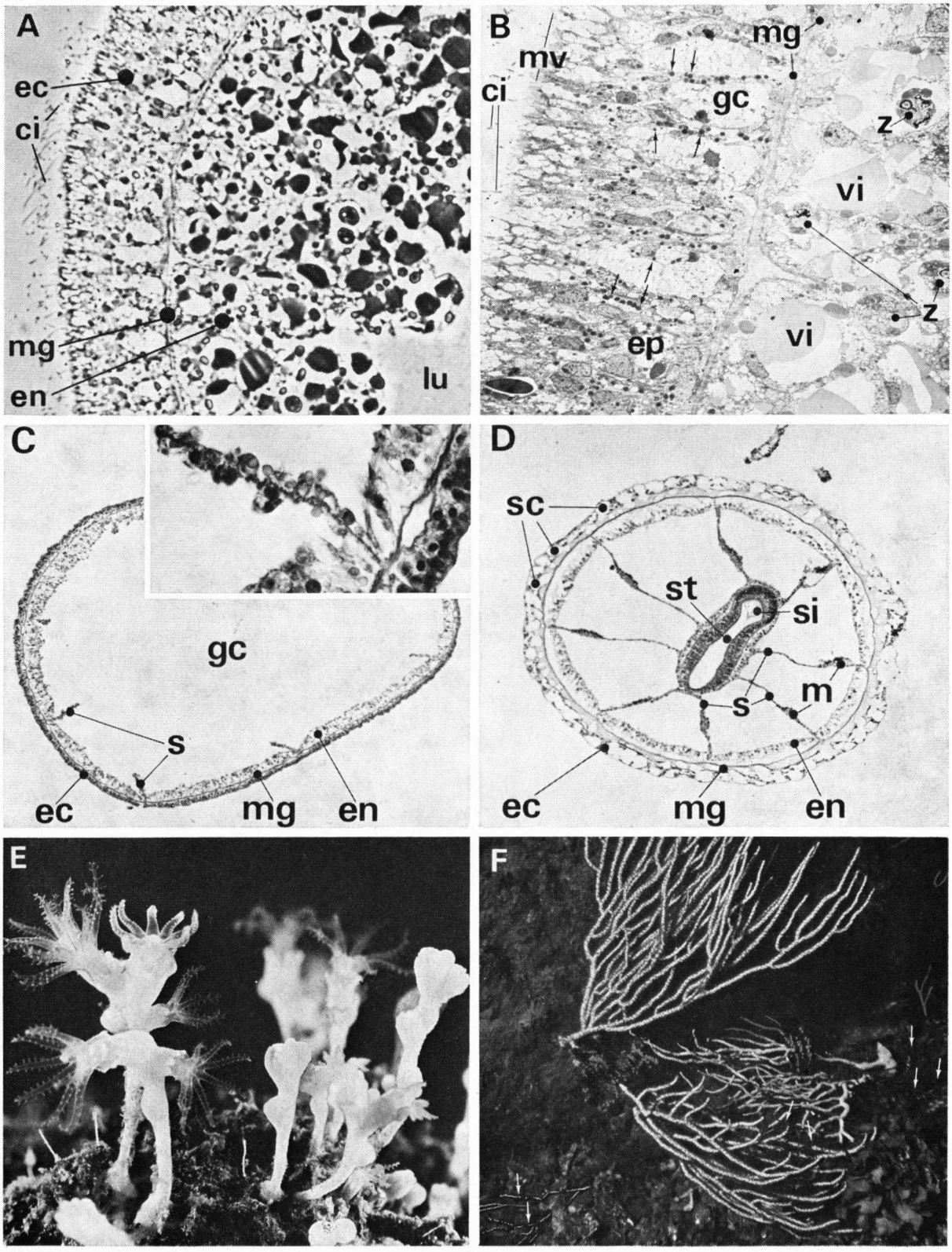
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PLATE II

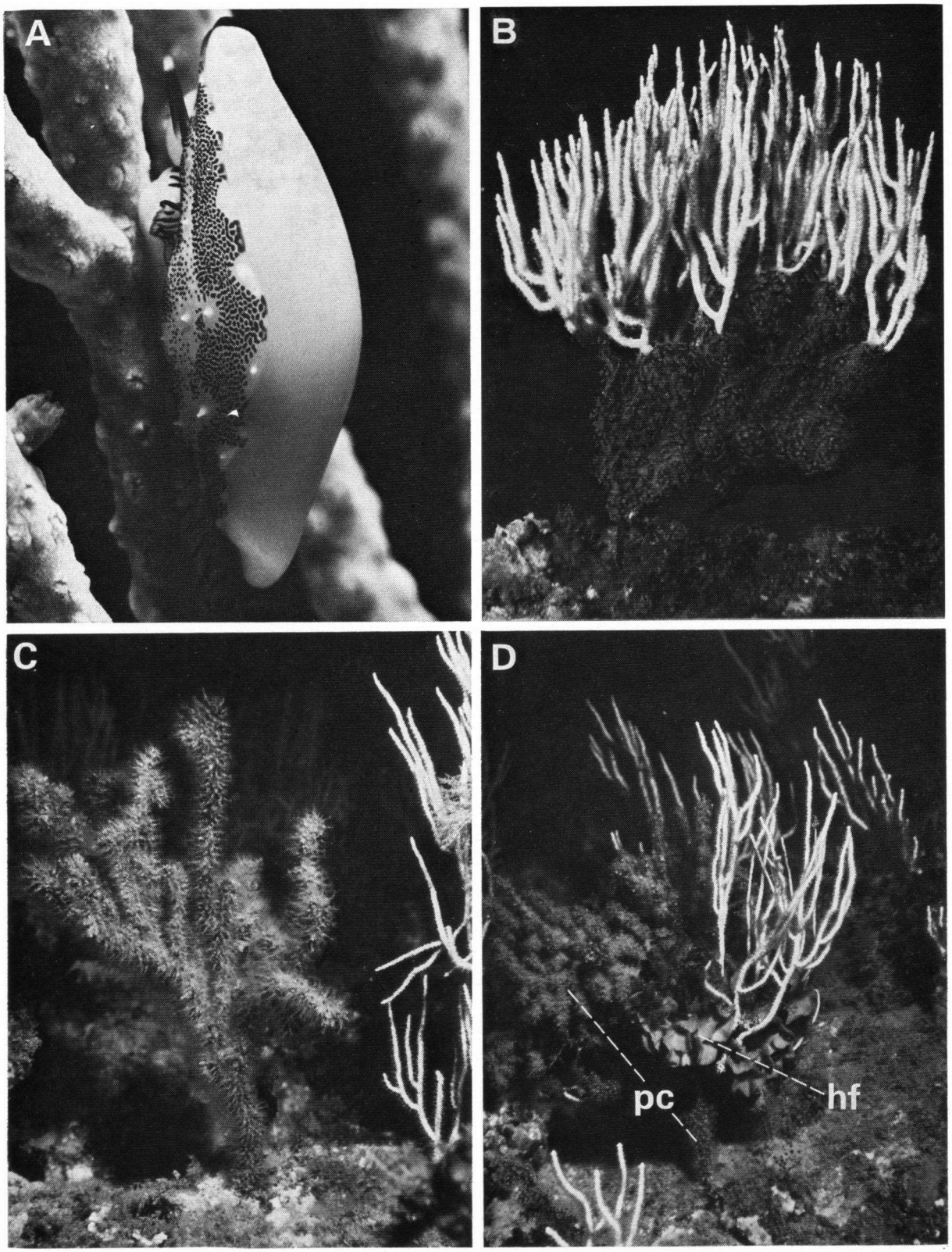

PLATE III