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Reproduction and developmental pathways of Red Sea Xeniidae (Octocorallia, Alcyonacea)

Y. Benayahu
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel

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Abstract

This work on Red Sea alcyonaceans describes the reproductive patterns of 21 xeniid species. Gonochorism is the commonest sexual mode but simultaneous hermaphroditism was recorded in 4 species and brooding of planulae was observed in 15 species. The reproductive patterns of *Xenia umbellata* and *Heteroxenia fuscescens* were examined. *X. umbellata* exhibits seasonal spermatogenesis, continuous oogenesis and a 7 month period of planulation each year. *H. fuscescens* has continuous gametogenesis, and planulation occurs throughout the year, lacking any lunar pattern. The prolonged breeding season of *H. fuscescens* reflects intrapopulation asynchrony in larval development and subsequent maturation. Xeniids possess structurally similar gonads, but adopt diverse reproductive and developmental pathways.

Introduction

The Red Sea xeniids (Alcyonacea) comprise 5 genera (*Anthelia*, *Cespitularia*, *Heteroxenia*, *Sympodium* and *Xenia*) and 30 species which provide dense cover over large reef areas below the surf zone and form monospecific patches (Benayahu, 1985).

Gohar (1940) discovered that xeniids brood their planulae and presented evidence for planulation among some Red Sea Xeniidae. Larval expulsion of *X. macrospiculata* lasts for several months every year in biweekly cycles during interlunar phases (Benayahu & Loya, 1984a; 1984b). Embryogenesis of *X. umbellata* occurs in brooding pouches (Benayahu *et al.*, 1988). *H. fuscescens* exhibits brood care involving initial embryo development within the gastrovascular cavity. Subsequently, the immature planulae are extruded into intersiphonozooid compartments where they complete their development (Benayahu *et al.*, 1989). Comparative data are provided here on the reproductive features of 21 Red Sea xeniids. Results are compared with data available for other xeniids and used to examine major variations in their reproductive patterns. In addition, data on annual patterns of gonad development, gonad size, and timing of planulation are given for *X. umbellata* and *H. fuscescens.*

Material and methods

Material representing 21 xeniids (Table 1) was collected during 1972–1989 around the Sinai Peninsula. A variety of habitats was surveyed by SCUBA diving over the reefs of the Gulf of Eilat, the Gulf of Suez and the southern tip of Sinai. About 250 samples were collected, each containing at least 10 colonies of the same species. Material was fixed in formalin, rinsed in fresh water, then transferred to 70% v/v ethanol. Colonies from each sample were dissected and examined under a binocular dissecting microscope. Polyps with gonads or gravid colonies with planulae were sectioned by the method of Benayahu & Loya (1983). *H. fuscescens* and *X. umbellata* were sampled from August 1985 to August 1987. Every month, 6–8 dimorphic colonies of *H. fuscescens* and 20 large colonies of *X. umbellata* were collected randomly from Eilat reefs. Wet preparations of the gonads from 5 polyps of each colony were studied under a microscope and the diameters of the oocytes and spermaries were measured. Once monthly, 15–25 large colonies of *H. fuscescens* and 40–50 colonies of *X. umbellata* were transferred into aerated aquaria, and they were observed for planulation for 5–14 days each month.

Table 1. Summary of sexual reproduction of 21 Red Sea Xeniidae.

Species	Sexual mode	Brooding of planulae
Xenia biseriata Verseveldt & Cohen	Gonochoric	Yes
Xenia blumi Schenk	Gonochoric	Yes[1]
Xenia farauensis Verseveldt & Cohen	Gonochoric	Yes
Xenia garciae Bourne	Gonochoric	Yes
Xenia grasshoffi Verseveldt	Hermaphrodite	–
Xenia hicksoni Ashworth	Gonochoric	Yes[1]
Xenia impulsatilla Verseveldt & Cohen	Gonochoric	Yes
Xenia kukenthali Roxas	Gonochoric	–
Xenia lillieae Roxas	Gonochoric	–
Xenia macrospiculata Gohar	Gonochoric	Yes[2]
Xenia membranacea Schenk	Gonochoric	Yes
Xenia novaebritanniae Ashworth	Hermaphrodite	–
Xenia obscuronata Verseveldt & Cohen	Gonochoric	Yes
Xenia umbellata Savigny	Gonochoric	Yes[3]
Heteroxenia coheni Verseveldt	Hermaphrodite	Yes
Heteroxenia fuscescens (Ehrenberg)	Hermaphrodite	Yes[4]
Heteroxenia ghardaqensis Gohar	Gonochoric	Yes[1]
Anthelia fishelsoni Verseveldt	Gonochoric	–
Anthelia glauca Lamarck	Gonochoric	Yes[1]
Cespitularia exigua Verseveldt	Gonochoric	–
Sympodium caeruleum Ehrenberg	Gonochoric	Yes

[1] From Gohar (1940)
[2] From Benayahu & Loya, 1984a, b
[3] From Benayahu *et al.*, 1988
[4] From Benayahu *et al.*, 1989
– Data unavailable

Results

Sexuality and gonads

Reproductive traits of the 21 species studied are summarized in Table 1. Gonads develop along ventral and lateral mesenteries except for the anthocodial section of the polyps. The majority of the species are gonochoric. Four of them (*X. grasshoffi*, *X. novaebritanniae*, *H. fuscescens* and *H. coheni*) are simultaneous hermaphrodites, containing male and female gonads within a single polyp.

The Xeniidae have remarkably uniform gonad development. Primordiae of the oocytes and spermaries were seen to have developed on the edges of the mesenteries. As the gonads grew, they gradually covered the surface of the mesenteries. In all species examined, male and female gonads were attached to the mesenteries by short pedicels, the mesoglea and endoderm of which were continuous with the polyp cavity tissues (*e.g.* in *X. obscuronata*, Fig. 1a). The oocytes were seen to contain a nucleus embedded in granular ooplasm and to be enveloped by a mesogleal layer and an outer follicular endoderm (Fig. 1b). During early spermatogenesis, the spermatogonia stained darkly (Fig. 1c). Spermatogenesis was shown to be typical of the Anthozoa (Fig. 1d, e).

Brooding of planulae

Xeniids brood their fertilized eggs to planulae (Table 1). Ripe eggs, heavily laden with yolk, and detached from the mesenteries, pass to the gastrovascular cavities and occasionally protrude into the anthocodiae or the tentacles. Subsequently, in *Xenia*, the eggs pass into brood chambers located in the coenenchyme between adjacent polyps (Fig. 2a). Brooding of planulae by *H. coheni* resembles the brooding mechanism of *H. fuscescens* (see Benayahu *et al.*, 1989). Planulae of *S. caeruleum* are brooded in the gastrovascular cavities of the parent colony (Fig. 2b) with no recognizable structural adaptation for the larval development.

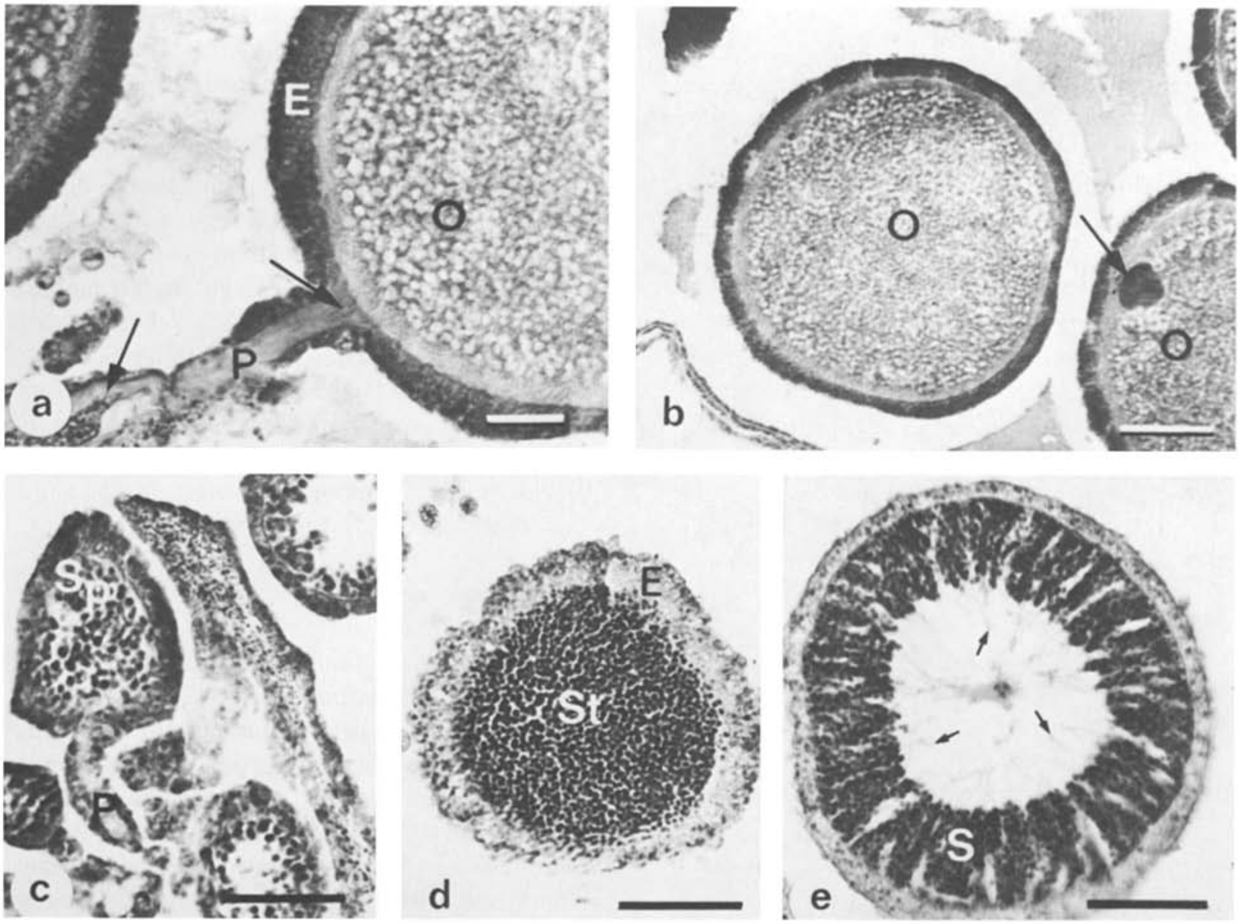

Fig. 1. Gonads of *X. obscuronata*. a: Bar = 20 μm: oocytes (O); follicular endoderm (E); pedicel (P); arrows indicate mesoglea. b: Bar = 100 μm: oocytes (O); arrow indicates nucleus. c: Bar = 25 μm: spermatogonia (Sp); pedicel (P). d: Bar = 50 μm: sperm sac surrounded by endoderm (E); spermatids (St). e: Bar = 50 μm: sperm sac with sperm (S), their tails (arrows) directed to the cavity.

Reproductive features of X. umbellata

The monthly size range of *X. umbellata* sperm sacs is shown in Fig. 3. Sperm sac primordiae appeared in male colonies during winter: February-March (1986); January-February (1987). Within a few weeks they increased in diameter and simultaneously additional spermaries develop along the mesenteries. Ripe spermaries, 180–290 μm in diameter, were continuously present in the population of *X. umbellata* during 8–9 months of the year. In June–July, the gastrovascular cavities of the males were filled by numerous sperm sacs but during the following months their abundance decreased due to successive spawning.

In female colonies, various developmental stages of oocytes were seen throughout the year. Oocyte sizes ranged from small, barely detectable primordiae up to 400 μm diam. (Fig. 3). Planulation of *X. umbellata* lasted for about 7 months each year (Fig. 3). There was no indication of lunar periodicity in planula shedding.

Reproductive features of H. fuscescens

There was no indication of seasonality in sperm or oocyte production of *H. fuscescens*. Auto-

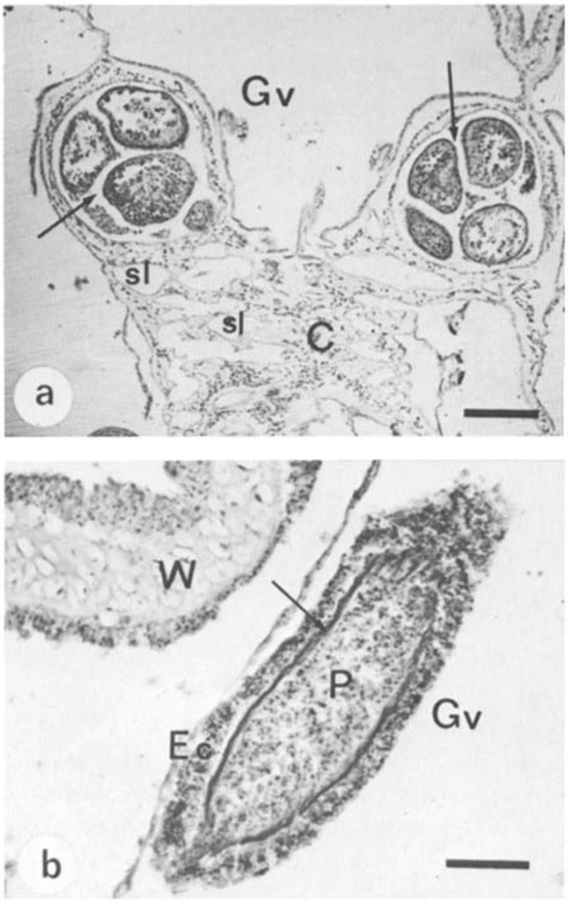

Fig. 2. Brooded planulae. a: Bar = 500 μm: embryos of *X. obscuronata* in brooding chambers (arrows); gastrovascular cavity (Gv); coenenchyme (C); solenia (Sl). b: Bar = 20 μm: young planula of *S. caeruleum* (P) within gastrovascular cavity (Gv); differentiated into ectoderm (Ec), mesoglea (arrow) and inner yolky endoderm; section through a polyp wall (W).

zooids of all examined colonies constantly bore gonads. Fig. 4 illustrates the monthly occurrence of brooding colonies with embryos inside the autozooids and externally among the siphonozooids. Colonies with embryos within the autozooids constitute *ca* 60% minimum of the monthly samples studied. Colonies with planulae among the siphonozooids, although less frequent, were, however, constantly found in the samples (apart from March 1987). Planulation of *H. fuscescens* occurred in almost every month throughout the study period (Fig. 4). Neither lunar seasonal cyclicity nor synchronized planulation among the colonies were observed. Thus, planulation of *H. fuscescens* is temporally random in nature.

Discussion

The 21 species of Xeniidae studied are similar in the structure and development of their gonads. The general mode of gonadal initiation and their appearance on the mesenteries resemble those previously described for other soft corals of the Alcyoniidae (Benayahu & Loya, 1983; 1986), Nephtheidae (Farrant, 1986) and Clavulariidae (Benayahu, 1989). Hence, it is highly probable that the major structural features of the gonads are common to a large variety of octocorals. In *X. macrospiculata*, prior to the breeding season, the gonads cover 70–80% of the surface area of the mesenteries (Benayahu & Loya, 1984a). Preliminary counts indicated that some *Xenia* species

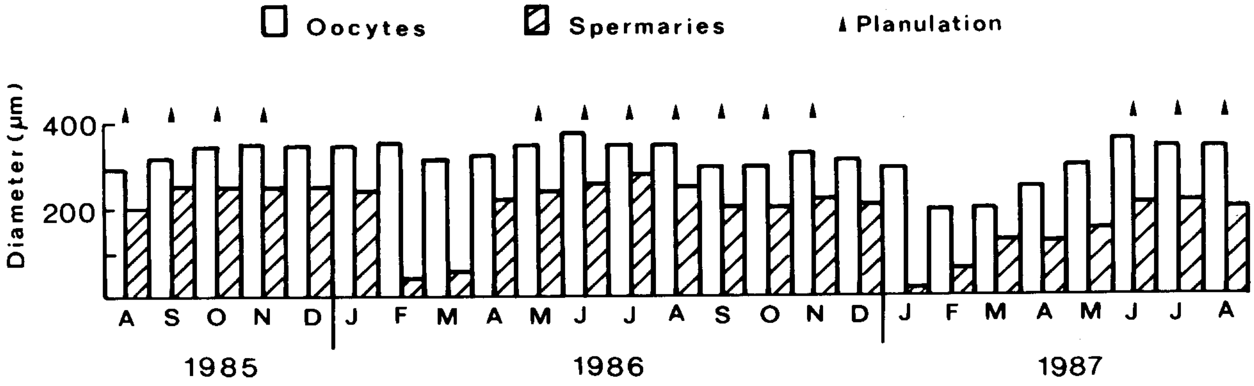

Fig. 3. Monthly changes in size range of oocytes of *X. umbellata* and timing of planulation.

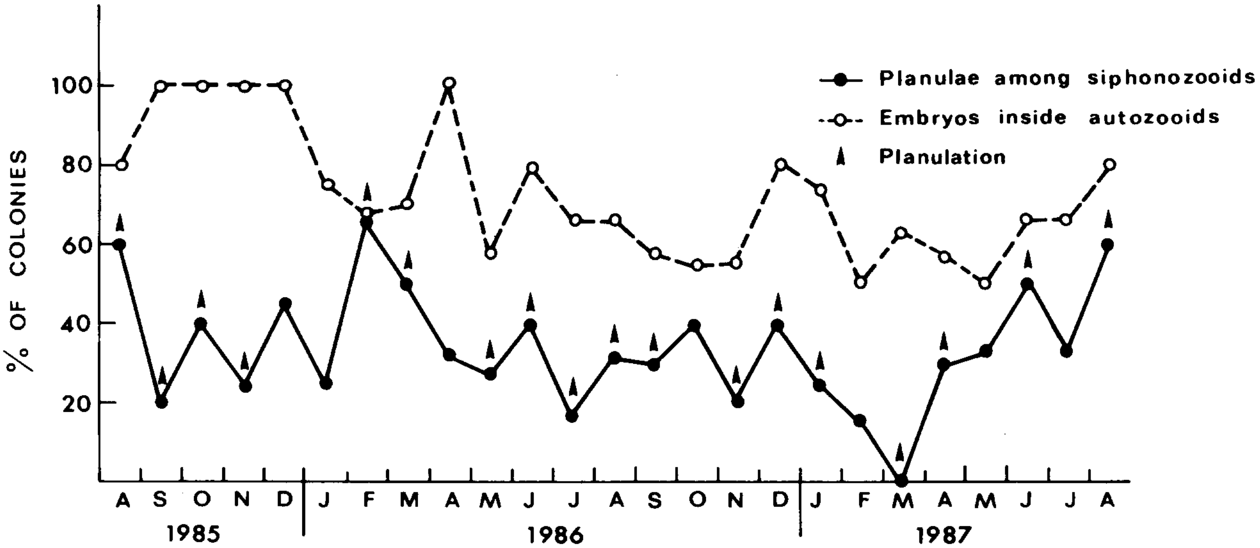

Fig. 4. Monthly occurrence of developed embryos and planulae of *H. fuscescens* and timing of planulation.

produce several hundred eggs per polyp. The encrusting structure of *Anthelia* and *Sympodium* (Gohar, 1940) results in a reduced volume, with only 8–12 eggs per polyp. A similar low egg production per polyp was found in other encrusting octocorals (Benayahu, 1989). Hence, it seems quite probable that coenenchyme thickness and gonad production in octocorals are related.

Among the species studied, gonochorism is widespread, while hermaphroditism is much less frequent (Table 1). The only previously reported hermaphroditic alcyonaceans appear to be the xeniids *H. fuscescens*, *H. ghardaqensis* and *X. viridis* Shenck (see Gohar, 1940). This study provides evidence for the hermaphroditism of 3 other species (viz. *X. grasshoffi*, *X. novaebritanniae* and *H. coheni*). Contrary to Gohar, I found *H. ghardaqensis* to be gonochoric. Perhaps this species has a mixed breeding system.

Brooding of planulae was the only reproductive mode observed among the Xeniidae studied. *Efflatounaria* sp., however, exhibits external brooding of the expelled eggs (Dinesen, 1985). The present study demonstrates for the first time internal brooding in gastrovascular cavities for *S. caeruleum* (Fig. 2b). *Xenia* and *Heteroxenia* species harbour young embryos in the gastrovascular cavities as well as within the anthocodiae and tentacles (Benayahu & Loya, 1984b; Benayahu *et al.*, 1989). Subsequently, planulae of *Xenia* species mature in temporary brooding chambers (Fig. 2a). Advanced stages of planula development of *H. coheni* and *H. fuscescens* occur among the siphonozooids. Brooding in extra-gastrovascular compartments may be advantageous in releasing gastrovascular space for gonad production, thereby increasing fecundity. The current results suggest genus-specific brooding mechanisms, although additional studies are required to verify this.

The absence of ripe sperm in *X. umbellata* during winter (Fig. 3) results in a 5 month pause in planulation. During this period, oogenesis continues and numerous cycles of oocytes are produced to be available for the following breeding season. *H. fuscescens* has several unusual reproductive features (Fig. 4). Spermatogenesis and oogenesis occur throughout the year and thus enable year round planulation. The yolky oocytes of *H. fuscescens* probably develop over a long period, resulting in overlapping oogenic growth cycles (Fadlallah & Pearse, 1982; Benayahu & Loya, 1986). The year round planulation of *H. fuscescens* reflects random, although successive, ripening of eggs and sperm. Such a pattern results in intrapopulation asynchrony in larval development, with subsequent maturation and release.

Additional information on the timing and mechanisms involved in various reproductive pathways of the Xeniidae is still required in order to determine the temporal processes regulating their reproductive features.

Acknowledgements

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