Marine Biology (1999) 135: 473–481

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The gorgonian coral *Acabaria biserialis*: life history of a successful colonizer of artificial substrata

Received: 30 December 1998 / Accepted: 19 August 1999

Abstract The azooxanthellate coral *Acabaria biserialis* Kükenthal, 1908 (Octocorallia: Alcyonacea) is highly abundant on the vertical underwater structures of the oil jetties at Eilat (Red Sea), but it is rare on the adjacent natural reefs. To understand its success on such artificial substrata we examined various aspects of its life history and population dynamics. *A. biserialis* is a gonochoric brooder. The percentage of colonies on the artificial substrata bearing gonads ranged from none (September 1994 and 1995) to 100% (January 1994, 1995 and April 1994). Mature oocytes and sperm sacs reached rather small maximum diameters of 240 and 160 μm, respectively, probably dictated by the small gastrovascular cavities. A continuous release of planulae was observed in the laboratory from March to July 1995. Planulation occurred during various lunar phases, and both by day and night. Recruitment of *A. biserialis* on PVC plates attached to the jetties coincided with the breeding period inferred from the laboratory findings. Recruits reached a maximum height of 3 cm within 3 months, thus exhibiting a remarkably rapid growth rate compared with other gorgonians. This high colony growth rate may compensate for the lack of clonal propagation in the studied *A. biserialis* population. The complex substrata of the jetties provide the conditions required for successful colonization, which include upside-down orientation, an adequate light regime and exposure to flow. The findings of our study may provide a useful contribution to the design of artificial reefs aimed at attracting rapid colonization by *A. biserialis* colonies.

Communicated by O. Kinne, Oldendorf/Luhe

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Introduction

Gorgonians are an important group of octocorals inhabiting coral reefs world wide, particularly in the Caribbean, where they form a major benthic component (Bayer 1973; Brazaeu and Lasker 1989). The majority of gorgonian families comprise fan-shaped or whip-like colonies, with a narrow base attached to the substrate and mostly widely spread branches extending into the water column. This morphology provides the colony with a large surface area that exposes the polyps to water flow (e.g. Barnes 1987; Gili and Ballesteros 1991; Coma et al. 1994). Most ecological studies on gorgonians have been conducted in the Caribbean, on the species *Muriceopsis flavida*, *Pseudoptergorgia bipinnata*, *Pseudoptergorgia elizabethae* and *Eunicea clavigera* (see Kinzie 1970), *Plexaura homomalla* (see Goldberg and Hamilton 1974), *Briareum asbestinum* (see Brazaeu and Lasker 1990) and *Plexaura kuna* (see Brazaeu and Lasker 1989; Lasker et al. 1996). In the Mediterranean, where the marine fauna is mostly temperate, studies have been done on *Eunicella singularis* (see Weinberg 1979), *Corallium rubrum* (see Vighi 1970, in Coma et al. 1995) and *Paramuricea clavata* (see Coma et al. 1995). To date, little is known about the biology and ecology of Indo-Pacific gorgonians (Table 1), despite their high abundance in the region.

Distribution ranges and abundance of gorgonians depend upon environmental factors such as type of substrate (Kinzie 1970; Weinberg 1979), light, temperature, current regime and flow rates (Reidel 1966; Weinberg 1979; Russo 1985; Weinbauer and Velimirov 1996). Substrate is a major limiting factor for gorgonians, which typically grow on rocky sites, where algal cover is minimal (Bayer 1961; Kinzie 1970; Weinbauer and Velimirov 1996). Flow and water movement (Kinzie 1970) also play an important role in determining their distribution and growth rate (Dai and Lin 1993; Kim and Lasker 1997). Species found in strong flows show several morphological adaptations, such as longer and

Table 1 Reproductive patterns in gorgonian species studied so far

Species	Reproductive pattern	Locality	Reference
Suborder Scleraxonia			
Family Briareidae			
Briareum asbestinum	Gonochoric external surface brooding	Panama	Brazaeu and Lasker (1990)
Briareum stechei	Gonochoric external surface brooding	Australia	Alino and Coll (1989)
Family Coralliidae			
Corallium rubrum	Gonochoric brooding	Mediterranean	Allemand (1992)
Suborder Holaxonia			
Family Gorgoniidae			
Pseudoptergorgia bipinnata	Gonochoric brooding	Jamaica	Kinzie (1970)
Pseudoptergorgia elizabethae	Gonochoric brooding	Jamaica	Kinzie (1970)
Family Plexauridae			
Muricea californica	Gonochoric brooding	California	Grigg (1977)
Muricea furticosa	Gonochoric brooding	California	Grigg (1977)
Muriceopsis flavida	Gonochoric brooding	Jamaica	Kinzie (1970)
Eunicella stricta	Gonochoric brooding	Mediterranean	Theodor (1967)
Paramuricea clavata	Gonochoric external surface brooding	Mediterranean	Coma et al. (1995)
Eunicea clavigera	Gonochoric broadcasting	Jamaica	Kinzie (1970)
Plexaura kuna	Gonochoric boradcasting	Panama	Brazaeu and Lasker (1989); Lasker et al. (1996)
Plexaura homomalla	Gonochoric broadcasting	Florida	Goldberg and Hamilton (1974)

thicker branches, fewer ramifications and narrower fans (Velimirov 1976; Michele and Ceccherelli 1993). Such conditions also affect the density and form of the sclerites, both of which contribute to tissue stiffness (Velimirov 1976; West et al. 1993). The impact of flow on both distribution and morphology of gorgonians is probably a consequence of their being passive suspension particle feeders (Kinzie 1970; Lasker 1981; Coma et al. 1994), or phytoplankton feeders (Fabricius et al. 1995). The ability to trap zooplankton has been reported for only a few species (Leversee 1976; Lasker 1981), and was attributed to the small number of nematocysts in their tentacles (Mariscal and Bigger 1977; Lasker 1981; Coffroth 1984). However, sweeper tentacles, densely packed with nematocytes and used for intraspecific competition, were described for *Erythropodium caribaeorum* (Sebens and Miles 1988).

Fleshy alcyonacean octocorals reproduce in several ways, including gonochoric spawning, gonochoric brooding, gonochoric external surface brooding and hermaphroditic brooding (Benayahu 1997). Most gorgonians studied so far appear to be either gonochoric brooders or external surface brooders (Table 1). Indo-Pacific soft corals were found to have short, seasonal and synchronized gamete release (Alino and Coll 1989; Benayahu et al. 1990), similar to the well-documented short, discrete annual spawning of stony corals (Harrison and Wallace 1990). Among octocorals spermatogenesis is shorter than oogenesis and many species demonstrate a prolonged oogenesis, lasting more than a year, ranging between 14 and 24 months (Benayahu 1997). Although broadcasters generally have a short spawning period, which is mostly synchronized with lunar phases, the soft coral *Dendronephtya hemprichi* displays year-round spawning (Dahan and Benayahu 1997). Brooders demonstrate year-round multiple gametogenic cycles, and a prolonged and continuous breeding activity, mostly synchronized with lunar cycles (Benayahu 1997).

In the Red Sea, the gorgonian *Acabaria biserialis* Kükenthal, 1908 (family Melithaeidae) is found mostly in shaded habitats and on vertical reef walls, where light does not exceed >0.5 to 2% of the surface intensity (Schuhmacher 1973; Grasshoff 1976). It is an azooxanthellate species with mostly fan-shaped, branched colonies, appearing in three distinct color morphs: orange, yellow and red, derived from pigmentation of their sclerites. In Eilat (Israel), *A. biserialis* is highly abundant on the vertical underwater structures of the oil jetties despite being rare on the adjacent natural reef. Its abundance on this artificial habitat stimulated our interest in various aspects of its life history and population dynamics, including gonadal cycle, mode of reproduction and the ecological parameters determining its occurrence, in order to understand its success as a colonizer of artificial structures.

Methods

Monthly sampling and gonadal development

The study was conducted at the oil jetties in Eilat, Israel, where a rich population of *Acabaria biserialis* is located at depths of 6 to 18 m, inhabiting the vertical metal support pillars of the jetties and the surrounding coiled barbed wire. Samples were collected monthly by SCUBA diving from January 1994 to October 1995.

Branches 10 to 15 cm long were removed once a month from 10 to 15 haphazardly selected colonies > 15 cm in height. The samples were placed in plastic bags and transferred to the Marine Biology Laboratory at Eilat (MBL) where they were fixed in 4% formalin in sea water for 24 h, rinsed in fresh water and then transferred into 70% ethanol. These samples were decalcified overnight with a solution of formic acid and tri-sodium citrate (Benayahu and Loya 1983). From each sample 10 to 15 polyps were then dissected under a binocular microscope using fine-pointed forceps. The sex of each colony was determined, and the diameter of ~100 oocytes or spermaries (> 40 μm) from these polyps were measured using a calibrated ocular microscope, and divided into three size classes representing their developmental phases (primordia < 40, intermediate 41 to 200 and mature > 201 μm). In addition, oocytes from individual polyps (~30 polyps from each female colony sampled) were counted, and the fecundity as mean number per polyp (± SD) for each month was calculated for the size classes mentioned above. A sample of three to five polyps containing gonads from each branch was embedded in paraffin, and longitudinal serial sections, 10 μm thick, stained with Dealafield hematoxilin + eosin were made (Benayahu and Loya 1983).

Mode of reproduction

To determine the mode of reproduction, 10 to 5 cm long branches were removed once a month from 10 to 15 randomly selected colonies >15 cm in height; they were transferred alive and kept in tanks with running sea water at the MBL for 1 to 2 h. The branches were then placed in aerated aquaria containing 5 liters of Millipore-filtered (0.45 μm) sea water for 3 to 4 d. Water samples were taken daily and checked under a microscope for reproductive products (planulae or eggs). The water was changed daily and maintained at ambient sea water temperature. Released planulae were removed and counted, and the color morph of the parent colony was recorded. Colonies that did not planulate were fixed in 4% formalin in sea water, and their sex and fecundity were determined later.

Settlement and growth rate in the laboratory and field

In the laboratory, planulae were placed in PVC containers (ca. 500 ml), and the time to settlement on the container walls and bottom and to metamorphosis was recorded.

Ten tagged PVC plates, measuring 14 × 20 cm and 3 mm in width, were attached horizontally to the barbed wire surrounding the jetty pillars at depths of 10 to 15 m. An additional ten plates were placed every 2 months from April 1994 to October 1994. They were monitored monthly from May 1994 to September 1995. Recruitment of *Acabaria biserialias* was recorded by visual counts, and the height of recruits was measured in situ with a ruler. In addition, the plates were photographed underwater, using a Nikonos V camera with a 28 mm lens attached to a close-up frame matching the plate dimensions. The slides were used for additional recruitment analysis in the laboratory.

Spatial distribution and ecological features of the habitat

The distributional patterns of *Acabaria biserialias* were studied in quadrates measuring 50 × 50 cm within the barbed wire surrounding three of the pillars at depths of 10 to 16 m. Three quadrates were randomly allocated in each direction (north, south, east and west) attached to the barbed wire around the pillars. Spatial distribution of the colonies was determined by the Morisita index (I_δ) (Morisita 1959; Sokal and Rohlf 1981) as follows:

$$I_\delta = \frac{q\Sigma n_i(n_i - 1)}{N(N-1)};\ \text{the } F \text{ was calculated as follows:}$$

$$F_0 = \frac{I_\delta(N-1) + q - N}{q-1}\ ,$$

where q is the number of quadrates, n_i the number of colonies in the i quadrate, N the total number of colonies in the sample and I_δ the Morisita index. Significance was determined by comparing F_0 to the critical value in the F-distribution $(F_\infty, q-1)$.

The direction of water flow adjacent to the colonies ($N = 39$) was determined by injecting fluorescein, and recording its direction (in degrees) with a compass (for details, see Abelson et al. 1991). The orientation of the broad side of the fan toward the flow was also recorded with a compass, and its correlation to the measured flow was calculated using a circular correlation test (Batschelet 1981).

Light intensity was measured in May 1995 at noon, using a Li-cor Li-185a photometer connected to a 20 m underwater cable lowered from a boat at the study site. Measurements ($\mu E\ m^{-1}\ s^{-1}$) were taken from the water surface and at 2-m intervals to a maximal depth of 16 m. At each depth two measurements were taken: within the barbed wire (where applicable), and 50 cm away from the pillar in areas with no wire. The measurements were later converted to relative percentages from the surface light intensity.

Results

Monthly sampling and gonadal development

Of the 309 colonies examined throughout the study, 209 possessed gonads and were found to be gonochoric colonies: 122 were females and 87 males, a sex ratio of 4:3 (females were significantly more abundant than males, χ^2-test, $p < 0.05$). The percentage of colonies bearing gonads ranged from 0 (September 1994 and 1995) to 100% (January 1994, 1995 and April 1994), showing a significant difference (ANOVA, $p < 0.001$, Fig. 1).

The gonads of both sexes developed along the mesenteries below the anthocodial level of the polyps. Histological sections revealed primordia of gonads with a diameter of < 40 μm. Preserved oocytes were round and bright white in color, turning orange-yellow when ripe. Spermaries were pear-shaped, opaque white and had a granulated texture. Ripe oocytes and sperm sacs reached maximum diameters of 240 and 160 μm, respectively. Oocytes were scored into three size classes: primordia < 40 μm, intermediate 41 to 200 μm and mature > 201 μm (Fig. 2). There were significant differences in percentage of oocytes in these three size

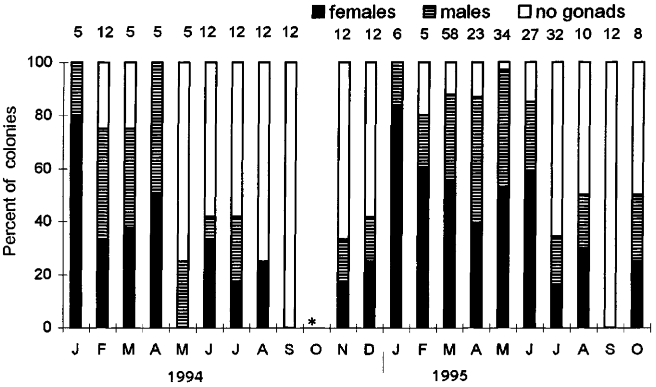

Fig. 1 *Acabaria biserialis*. Percentage of males, females and colonies with no gonads during the study period. Numbers of colonies are indicated on each column (* indicates no sampling)

classes within the same month and throughout the study period (two-way ANOVA, $p < 0.001$). Post hoc comparisons revealed that the difference was due to the intermediate size classes ($p < 0.001$), but comparisons among months showed no main effect. The same pattern was obtained for colony fecundity (Fig. 3). There were significant differences among the number of oocytes per polyp in the different size classes and among months throughout the course of the study (two-way ANOVA, $p < 0.001$). Post hoc comparisons showed that the intermediate size class was the main cause of the differences ($p < 0.001$), while no such effect was found for the differences among the months.

Mode of reproduction

Acabaria biserialis reproduces by release of planulae. During 1994, planulation was observed only once in August, when only three planulae were found. However, a continuous release of planulae was observed from March to July 1995, when 8 to 50% of the colonies kept in the laboratory released planulae (Table 2). Planulation occurred during various lunar phases. No significant differences were found in the number of planulae released during day (0600 to 1800 hrs) or night (1900 to 0500 hrs) (Fig. 4, ANOVA, $p > 0.05$). Maximum planula length was 300 μm. They were pear-shaped and generally rather active in the water column.

Settlement and growth rate

In laboratory experiments freshly released planulae settled on PVC substrate within 24 ± 13 h ($n = 28$); early settled polyps became shorter, and considerably flattened. By 25 to 30 h a pharynx and buds of eight tentacles appeared, and a primary polyp was recorded on Day 4 post-settlement. Planulae derived from parent colonies of all color morphs were pale pink, although primary polyps with sclerites always showed the same color as their mother colony.

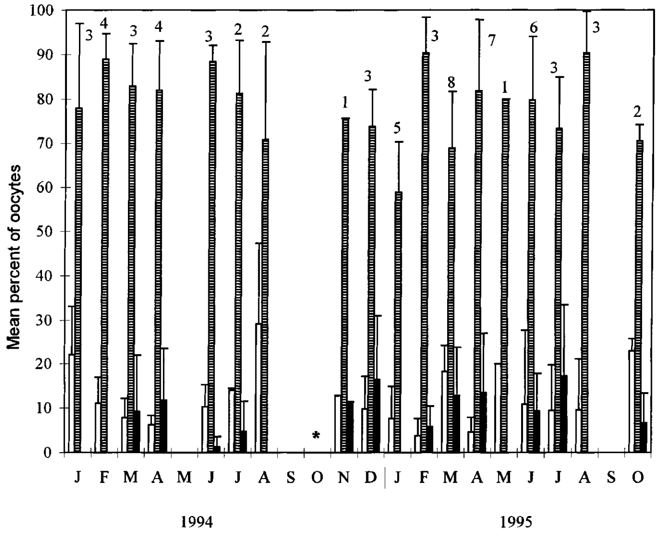

Fig. 2 *Acabaria biserialis*. Size distribution of mean percentage of oocytes in colonies during the study period. Numbers of colonies are indicated above each column (~100 oocytes per colony) (size classes are indicated as follows: □ < 40 μm; ▤ 41 to 200 μm; ■ > 201 μm; * indicates no sampling)

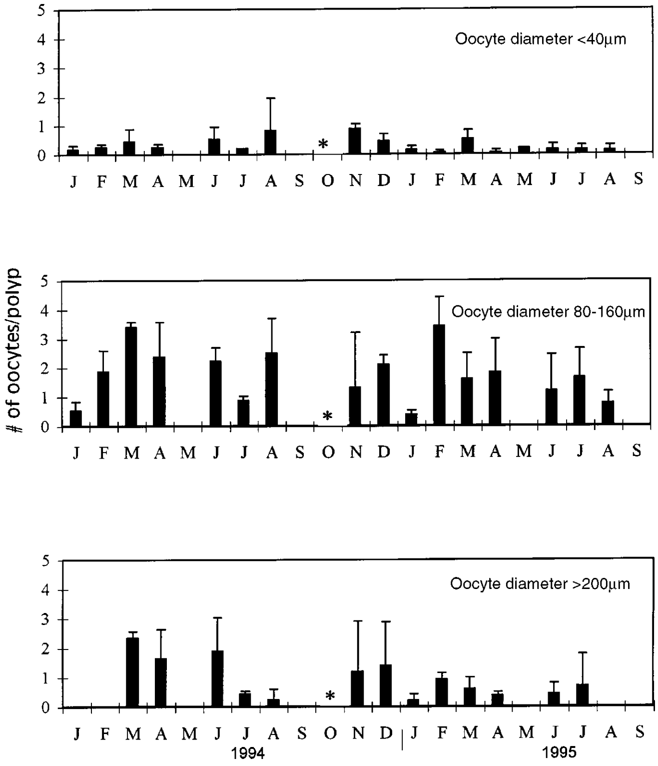

Fig. 3 *Acabaria biserialis*. Fecundity of female colonies in terms of mean number of oocytes per polyp ±SD (~30 polyps per colony) throughout the study period (* indicates no sampling)

The first recruits of *Acabaria biserialias* were observed in July 1994 on the first series of PVC plates placed in April 1994, and all 32 were attached on the underside of the plates. Additional recruits were observed in April 1995 and their number was monitored until September 1995 which was the last date that recruitment occurred (Fig. 5). Size-frequency distribution of the recruits found in all counts is presented in Fig. 6. Note that the highest number of new recruits (< 0.5 cm in height) was observed in June 1995. The juveniles reached a maximum height of 3 cm within 3 months (July 1995).

Spatial distribution and ecological features of the habitat

The average number of colonies (±SD) per quadrate, along each depth and for each side of the pillars is presented in Table 3. Two-way ANOVA showed significant differences only among depths but not among the sides (Table 4, $p < 0.05$). The Morisita index calculated from 38 quadrates was $I_\delta = 2.72$, thus indicating a

Table 2 *Acabaria biserialis*. Percentage of colonies that released planulae when kept in the laboratory for successive days in 1995 (● new moon; ◐ first quarter; ○ full moon; ◑ last quarter)

Date	Number of examined colonies	% of planulating colonies
20 Mar ◑	10	30.0
21 Mar	13	30.8
22 Mar	13	23.1
23 Mar	12	16.7
24 Mar	12	33.3
25 Mar	12	16.7
31 Mar	11	27.3
1 Apr ●	12	16.7
2 Apr	12	33.3
3 Apr	12	25.0
4 Apr	12	16.7
5 Apr	12	8.3
25 Apr ◐	23	33.3
26 Apr	23	17.4
27 Apr	23	26.1
28 Apr	23	17.4
29 Apr	23	17.4
1 May ●	23	17.4
15 May ○	10	50.0
16 May	20	35.0
17 May	20	35.0
18 May	20	10.0
27 Jun ◑	11	9.1
28 Jun	11	45.5
29 Jun	17	29.4
30 Jun	17	29.4
1 Jul	17	35.3
2 Jul	17	35.3

clumped spatial distribution ($F_0 = 6.31$, greater than the critical value of $\alpha = 0.01$).

Colonies of *Acabaria biserialis* appeared at the study site in all three color morphs (orange, yellow and red) known for this species. The colonies were mostly fan-shaped with a maximal height of 25 cm measured from base to top (Zeevi 1996). We found a positive correlation between orientation of the fan-shaped colonies and the ambient flow (Table 5, $p < 0.001$).

Light intensity declined exponentially from the sea surface to 6 m depth, and then moderately from 10 to 16 m (Fig. 7a). There was a difference of ~100 μE m^{-1} s^{-1} units between measurements carried out at 10, 12, 14 and 16 m among the barbed wire and at 50 cm from it. Light intensity by depth adjacent to the wires expressed as a percentage of surface intensity is given in Fig. 7b.

Discussion

Acabaria biserialis, like most gorgonians studied so far, is a gonochoric brooder producing a small number of eggs per polyp (Table II in Brazaeu and Lasker 1989). The remarkably low fecundity values of this species and other gorgonians, in contrast with most fleshy alcyonaceans (Benayahu 1997), is possibly due to the thin coenenchyme and the short gastrovascular cavities that leave only limited space for the development of gonads (Coma et al. 1995). Dominance of the intermediate oocyte size class, over the small number of other size classes, may imply a rapid development of the primordial oocytes, followed by a continuous and slow maturation together with possible resorption of some ripe oocytes (see also Brazaeu and Lasker 1989). In most studied fleshy alcyonaceans, the spermatogenic cycle is much shorter than the oogenic cycle (Benayahu 1997), as demonstrated for the gorgonians *Plexaura homomalla* and *Briareum asbestinum* (Goldberg and Hamilton 1974; Brazaeu and Lasker 1990).

The high variation in number of planulae released by different colonies of *Acabaria biserialis* during the breeding season may reflect a lack of synchronization in egg development and maturation within the population. Such a pattern has also been revealed in soft corals, such as the broadcaster *Dendronephtya hemprichi* (Dahan and Benayahu 1997) and the brooder *Heteroxenia fuscescens* (Ben-David-Zaslow et al. 1999).

Reproductive success in gonochoric species is related to the spatial distribution and sex ratio. Brooding by females in a gonochoric species should result in a sex ratio skewed towards a higher proportion of females (Szmant 1986). Brazaeu and Lasker (1992) showed a positive relationship between embryo production and nearby male densities in the soft coral *Briareum asbestinum*. In *Acabaria biserialis*, females were significantly more abundant than males. Shinkarenko (1981) suggested that such a sex ratio may occur along with a clumped spatial distribution, which is also the case in *A. biserialis* (see "Results").

Broadcast spawners usually have a short and synchronized annual reproductive period that lasts a few nights, while brooders maintain a continuous release of planulae (Babcock et al. 1986; Alino and Coll 1989; Brazaeu and Lasker 1989; Harrison and Wallace 1990; Benayahu 1997). The azooxanthellates *Dendronephtya hemprichi*, *D. sinaiensis* (Benayahu 1997) and *Telesto riisei* (see Bardalesul> 1981) are exceptions, maintaining a continuous gamete release. *Acabaria biserialis* similarly lacks symbiotic algae, and is the first brooding gorgonian to be observed to maintain a long planulation period.

Year-to-year variations in reproductive success are known for several alcyonacean and scleractinian species (Rinkevich and Loya 1982; Sadot 1988; Brazaeu and Lasker 1989; Weil 1990; Ben-David-Zaslow et al. 1999), and were in part related to environmental fluctuations. No significant difference in water temperature in Eilat was found between the two study years, 1994 and 1995 (Genin et al. 1995), indicating that this parameter most probably could not have caused the observed differences in the reproductive output of *Acabaria biserialis* noted between the two years. *A. biserialis* is a phytoplankton feeder (Fabricius et al. 1995), so it was interesting to find that its planulation occurred after the major seasonal algal bloom at Eilat (see Lindell and Post 1995). While this may indicate that phytoplankton availability

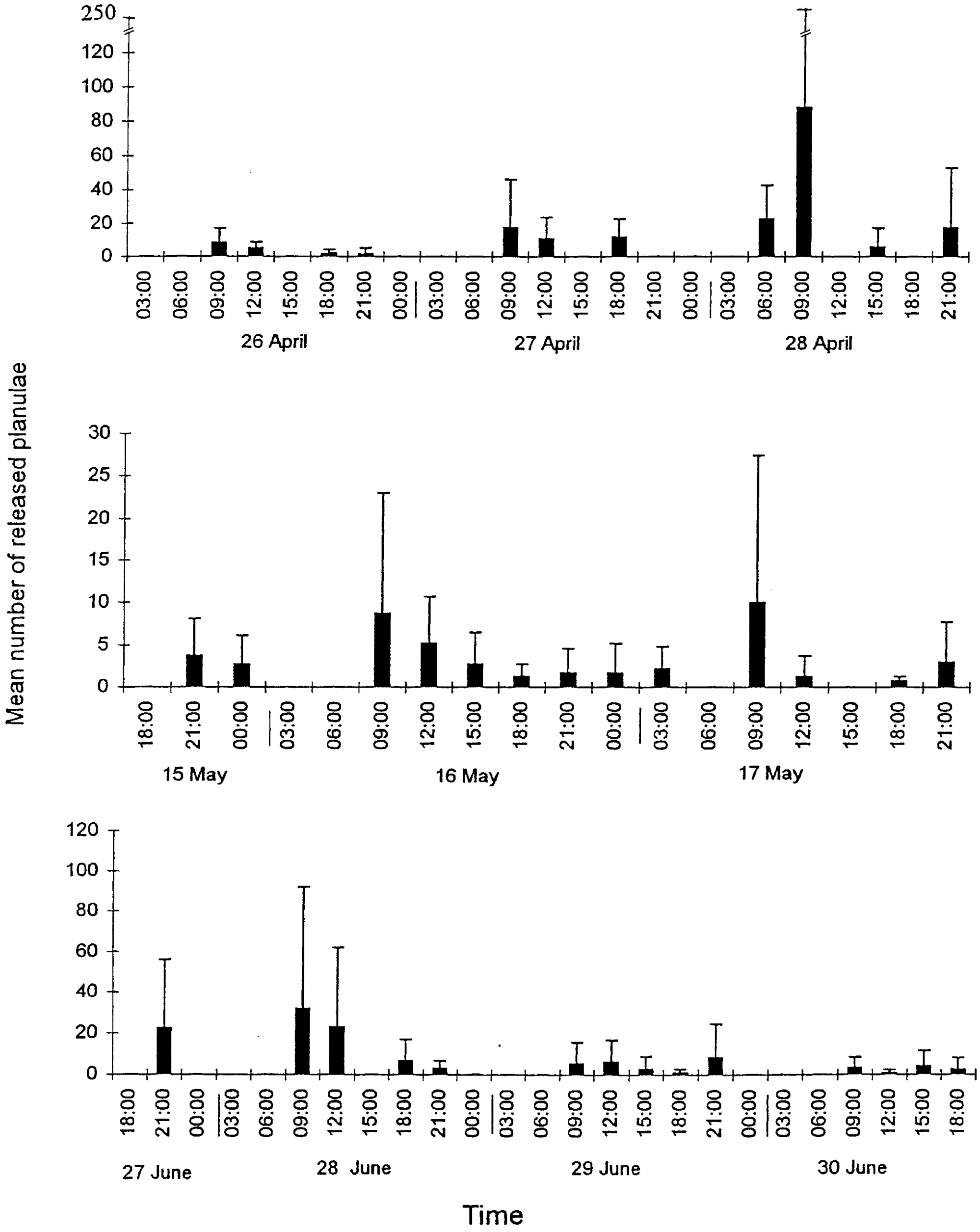

Fig. 4 *Acabaria biserialis*. Average number of released planulae (±SD) from colonies throughout successive monitoring days in 1995 (data for each observation is from four colonies)

determines reproductive output of this gorgonian in a given year, the precise nature of the causes for such annual variation still awaits further study.

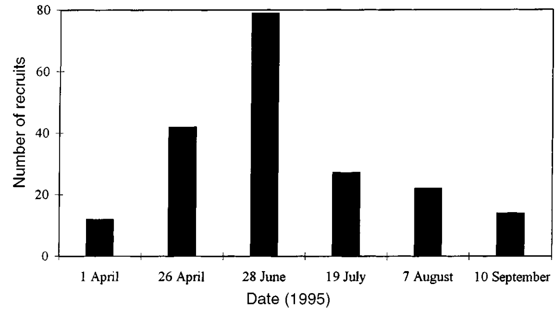

Fig. 5 *Acabaria biserialis*. Total number of recruits on 40 PVC plates from all counting dates

In the present study planulation of *Acabaria biserialis* in the laboratory did not follow lunar or diurnal cycles (Fig. 4). We assume that planulation was not a response to adverse laboratory conditions, because all planulae were alive upon release, and most of them settled and metamorphosed successfully. Furthermore, recruitment of *A. biserialis* on PVC plates in the sea coincided with the breeding period inferred from the laboratory observations.

Juveniles of *Acabaria biserialis* were observed only on the undersides of the settling plates, similar to the adult colonies, and could only have been a consequence of sexual reproduction. Such orientation of juveniles has also been reported for the zooxanthellate alcyonaceans *Parerythropodium fulvum fulvum* and *Xenia macrospiculata* and the azooxanthellate *Dendronephtya hemp-*

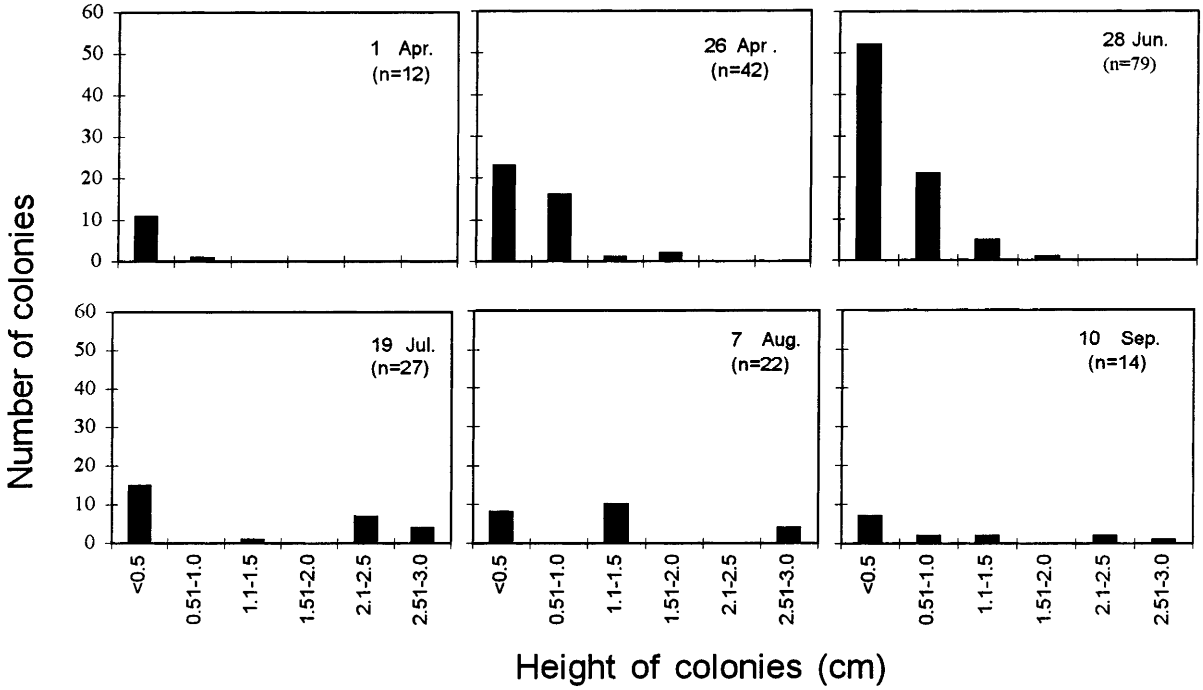

Fig. 6 *Acabaria biserialis*. Size distribution of recruits on 40 PVC plates at all monitoring dates (*n* number of recruits counted each date)

richi (Benayahu and Loya 1987; Dahan and Benayahu 1997). This pattern was explained as a response to high light intensity, grazing pressure and sedimentation (Benayahu and Loya 1987), which may also hold true for *A. biserialis*.

No clonal reproduction was observed in *Acabaria biserialis*. Insignificant clonal reproduction was found for the gorgonians *Leptogorgia virgulata* (Gotteli 1988) and *Paramuricea clavata* (Coma et al. 1995), while other species reproduce asexually, mainly by fragmentation, e.g. *Briareum asbestinum* and *Junceella fragilis* (Lasker 1983; Walker and Bull 1983). The onset of the reproductive season of *A. biserialis* (March, see Table 2) is earlier than that of most other Red Sea alcyonaceans (see Benayahu 1997), and its annual duration may contribute to the successful colonization of this species, despite the absence of clonal reproduction. Recruits of *A. biserialis* had a relatively rapid growth rate of ca. 1 cm per month, similar to *L. virgulata*, which does not reproduce asexually either (Gotteli 1988). Other

Table 3 *Acabaria biserialis*. Average number of colonies (±SD) in a quadrate (50 × 50 cm) at different depths and directions along the pillars of the oil jetty (n = 12, for each depth)

Direction	10 m	13 m	16 m	Average
North	0	9.0 ± 5.0	6.6 ± 4.5	6.0 ± 6.0
South	1.6 ± 1.2	3.0 ± 2.5	2.3 ± 0.4	2.0 ± 2.0
East	0.3 ± 0.4	2.0 ± 2.0	4.3 ± 6.0	2.0 ± 2.0
West	0.9 ± 0.6	0	5.0 ± 4.0	2.0 ± 3.0
Average	0.6 ± 1.0	5.2 ± 3.4	4.5 ± 4.5	3.2 ± 4.4

Table 4 *Acabaria biserialis*. Differences in the number of colonies according to different depths and directions (two-way ANOVA) (* significant at p < 0.05; *ns* not significant)

Source of variation	SS	*df*	*F*	*p*
Depth	10.38	2	4.23	0.0254*
Direction	6.42	3	1.77	0.1792 ns
Depth × Direction	12.13	6	1.675	0.1702 ns
Error	28.96	24		
Total	57.88	35		

Table 5 *Acabaria biserialis*. Position of colonies and the respective current direction measured near each colony

Colony no.	Position (degrees)	Current direction (degrees)	Colony no.	Position (degrees)	Current direction (degrees)
1	230	190	21	140	60
2	130	190	22	160	60
3	220	30	23	320	170
4	330	80	24	40	130
5	330	80	25	80	220
6	330	170	26	90	170
7	250	160	27	20	240
8	100	190	28	400	60
9	300	210	29	50	310
10	310	210	30	270	360
11	150	240	31	290	20
12	190	90	32	320	50
13	100	60	33	390	60
14	100	210	34	120	210
15	250	170	35	100	10
16	280	10	36	100	190
17	300	70	37	120	190
18	320	100	38	150	240
19	90	180	39	270	340
20	110	300			

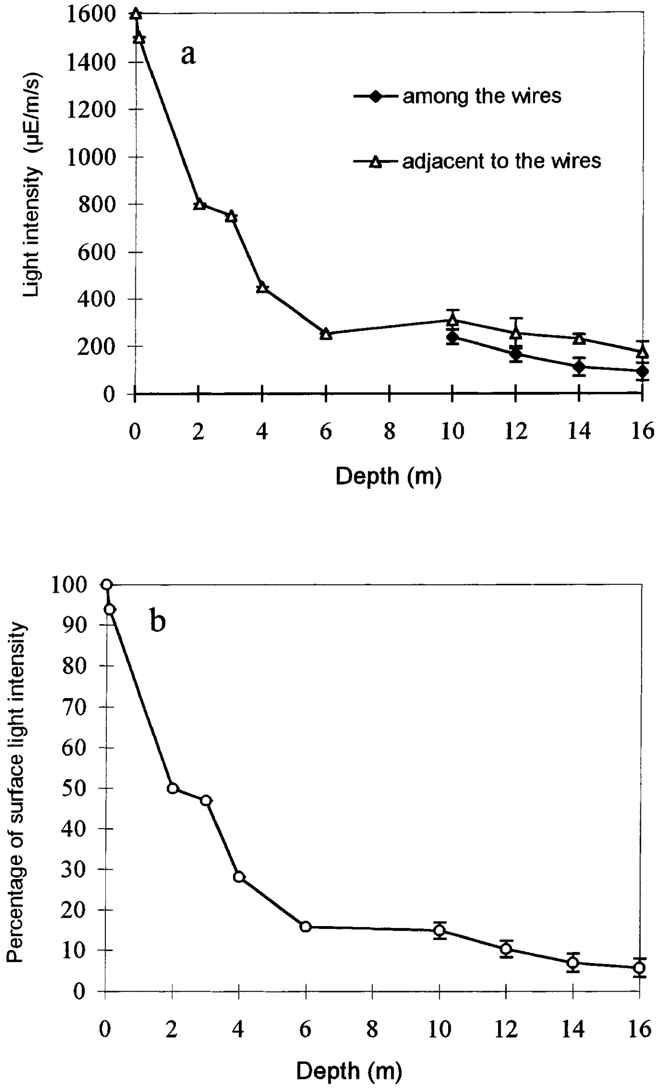

Fig. 7 Light measurements by depth at the oil jetty in Eilat ($n = 3$); **a** light intensity among and adjacent to the wires and **b** percentage of surface intensity

gorgonians have much lower growth rates, ranging between 0.08 and 0.33 cm per month, including *Plexaura homomalla*, which does reproduce asexually and has a growth rate of only 0.16 cm per month (Yoshioka and Yoshioka 1991). These findings suggest that in gorgonians there may be a trade-off between vegetative reproduction and growth rate.

The abundance of *Acabaria biserialis* was significantly higher at 13 and 16 m than at 10 m (Tables 3, 4). This may be due to the high quantity and complexity of the barbed wire at the former depths. Such a distribution may also be synergistically determined by diminished light intensity with depth (Fig. 7). Furthermore, the importance of currents to gorgonians is well known (Velimirov 1976; Weinbauer and Velimirov 1996). Branched, fan-shaped gorgonians have been shown to orient with their broad surface to the usual direction of water movement (Kinzie 1970). This was also found for *A. biserialis* colonies, and is probably adaptive for the passive phytoplankton feeding behavior of the species (Fabricius et al. 1995).

In conclusion, at Eilat the abundance of *Acabaria biserialis* on artificial substrata such as the oil jetties may be explained in part by the availability of the required conditions for successful recruitment. The vertical pillars and complex substrata provided by the barbed wire allow the colonies to achieve their preferred orientation in shaded microhabitats with exposure to flow. All these factors facilitate the development of dense populations of *A. biserialis* on this artificial structure. The results of the present study can thus contribute to the design of artificial reefs aimed at attracting rapid colonization by this gorgonian coral.

Acknowledgements We would like to thank B. Kinzie for his insightful comments on the manuscript. L.P. Van Ofurgen is greatly acknowledged for the taxonomic verification of the species examined in this study. We thank the staff of the Interuniversity Institute of Eilat for their kind hospitality and facilities and N. Paz for editorial assistance. The research was supported in part by a grant from the Israeli Diving Federation. This paper is a part of a M.Sc. thesis submitted by D. Z.

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