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Sexual reproductive effort in the Mediterranean gorgonian *Paramuricea clavata*

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ABSTRACT: Sexual reproductive effort in the Mediterranean gorgonian *Paramuricea clavata* was studied from 1990 to 1993 in a population dwelling at a depth of between 17 and 19 m off the Medes Islands (northwestern Mediterranean). Variations in polyp fecundity with sex, polyp position within the colony, and colony size were studied, as was interannual variability. Onset of sexual maturity was on average delayed until colonies had attained a size of 20 (11 to 30) cm, i.e. an age of 13 (6 to 19) yr according to our estimates. Male and female colonies of *P. clavata* ripened synchronously and bore fertile polyps on nearly all branch orders. However, the percentage of fertile polyps and the number of gonads per fertile polyp decreased as branch order increased. Accordingly, reproductive effort was highest for polyps on first-order branches, which contributed 85 % of the entire production of gametes. Reproductive effort increased exponentially with colony size due to increases in the percentages of fertile colonies and polyps and in the number of gonads per polyp, at least to a size of 35 cm in height. No significant interannual variation was detected over the 3 yr study period. The gorgonians present on a representative plot with a surface area of 1 m^2 produced, on average, 2×10^6 sperm sacs (9 g dry wt of male sex products) and 7×10^5 eggs (7 g dry wt of female sex products). Total reproductive effort was on the order of 9 g C m^{-2} yr^{-1}.

KEY WORDS: Gorgonians · Reproductive effort · Gonadal biomass · Intra-colonial variation · Mediterranean

INTRODUCTION

Recent interest in the ecology of clonal organisms has pointed out the need to develop new models departing from the conventional concepts of population biology, which have traditionally focused on the biology of aclonal organisms (Jackson et al. 1985). Among clonal organisms (1) many demographic parameters such as mortality or reproductive capacity seem to depend less upon age than upon size (Hughes & Connell 1987, McKinney & Jackson 1991) and physical condition of the clone (Rinkevich & Loya 1987) and (2) growth of clones through the addition of modules is potentially unlimited (Strehler 1961), thus explanations of the reproductive strategies of a clonal organisms (Todd 1985) may be inadequate to explain the biology of clonal animals. Specifically, it has been predicted that in clonal organisms: (1) sexual processes can be expected to be deferred while modular growth is unlimited (Connell 1973); (2) perennial, iteroparous forms should prevail over semelparous, ephemeral forms; and (3) reproductive effort, the proportion of metabolic resources devoted to sexual reproduction, should be a graded genetic or phenotypic response to environmental conditions (Hughes & Cancino 1985). Clonal species dwelling in unstable habitats and hence with short life expectancies might be expected to mature faster and invest a larger share of assimilated energy in sexual reproduction than do species inhabiting more stable habitats. However, reliable data with which to substantiate these hypotheses are lacking. For instance, we have been unable to find any adequate measurements of reproductive effort in corals in the literature (Hughes & Cancino 1985). It also has been argued that the inability to establish the real size of clones surviving in a number of units (other than by means of costly genetic techniques) makes it impossible to estimate the total fecundity of clones (Hughes

& Jackson 1980, Jackson & Winston 1981). Nevertheless, it is still possible to estimate the reproductive effort in clonal species in which the units have little propensity to fragment or produce stolons. This would appear to be the case for the Mediterranean gorgonian *Paramuricea clavata*, whose reproductive biology has been described earlier (Coma et al. 1995, this issue). Among gorgonians, quantification of reproductive effort has not gone beyond estimates for modules (polyps) (Theodor 1967, Kinzie 1970, Vighi 1970, Grigg 1977, Martin 1982, Brazeau & Lasker 1989, 1990), with no integrated results for whole colonies or populations available. The present paper endeavours to quantify reproductive effort in a population of *P. clavata*, a common species in the northwestern Mediterranean, in the framework of a study designed to establish an overall metabolic budget for the species. To assess the reproductive effort, variations in polyp fecundity with sex, polyp position within the colony, and colony size have been studied, together with interannual variations.

MATERIAL AND METHODS

The population of *Paramuricea clavata* located near Carall Bernat (Medes Islands, northwestern Mediterranean) was studied from 1990 to 1993. The population is located at depths between 15 and 27 m and occupies a surface area of approximately 1000 m^2.

Sampling. Samples from the population were collected at depths of 17 to 19 m by a SCUBA diver. Maximum height (distance from the base to the farthest point) of all colonies sampled was measured to the nearest 0.5 cm. Samples consisted of either colonies or apical fragments and were immediately fixed in 10% formalin in sea water. At the laboratory, polyps were dissected under a binocular dissecting microscope, and the number of gonads and gonadal diameter were recorded for each polyp. Gonadal volume was estimated from the diameter based on the subspherical shape of the gonads. Total gonadal volume was estimated for each polyp for both sexes.

Reproductive effort. Sexual reproductive effort has been expressed as colony gonadal biomass as a proportion of the organic tissue of the colony, in units of organic carbon. To calculate reproductive effort, the following inputs are required: (1) number of polyps per colony; (2) percentage of fertile polyps and intracolonial variation; (3) total gonadal volume per polyp and intra-colonial variation; (4) gonadal density; and (5) gonadal carbon content.

Production of gametes by the colonies present in a representative 1 m^2 plot was also calculated. The inputs required, besides colony reproductive effort, are colony density and the size structure of the population (Coma 1994) along with variation in reproductive effort with colony size. This source of variation was quantified by taking into account: (1) variation in the percentage of fertile colonies; (2) variation in the percentage of fertile polyps; and (3) variation in total gonadal volume per polyp.

Intra-colonial variation. To examine the relationship between reproductive effort and polyp position within the colony, the different branches of the colony were classified following the system used to describe branching patterns in gorgonians (Brazeau & Lasker 1988, Mitchell et al. 1993). This system defines distal branches as first-order (1°) branches. Higher branch orders arise only when 2 branches of equal lower order join. At the beginning of June 1993, 3 colonies of each sex with heights between 35 and 45 cm were collected. For each colony 3 replicates consisting of 10 polyps each were collected, and the number of fertile polyps, number of gonads per fertile polyp, and gonadal diameter were recorded. The values were compared by analysis of variance (ANOVA) and Scheffé's contrast test (Zar 1984).

Variation with colony size. The relationship between reproductive effort and colony size was considered by classifying the colonies sampled into 10 cm size intervals based on maximum colony height, spanning the entire size range of the population (1 to 55 cm). Before onset of the spawning period in 1991 (beginning of June; Coma et al. 1995), apical fragments were collected from 10 male and 10 female colonies in each size class. Five polyps from each fragment were examined, and the number of gonads present and gonadal diameter were recorded.

Gonadal biomass. At the beginning of June 1993, during the period of gonadal ripening, 3 colonies of *Paramuricea clavata* were collected, and 5 replicates of 200 unfixed ovaries each and another 5 replicates of 200 unfixed sperm sacs (male gonads) each were collected. The diameter of each gonad was measured, gonadal volume estimated, and total gonadal volume calculated for each replicate. Mature *P. clavata* ovaries contain only a single oocyte within a thin layer of tissue (Coma 1994). Consequently, ovarial volume can be taken as representative of oocyte volume. After the measurements were taken, the replicates were dried in an oven at 70°C for 24 h and weighed using a microbalance (precision: 0.1 µg) to obtain the dry weight value of each replicate. Next, the replicates were heated in an oven at 550°C for 5 h. The ashes were weighed and the ash-free dry weight (AFDW) calculated for each. In no case did the ashes exceed 2% of replicate dry weight.

Mean ovarian and sperm sac densities were calculated based on the dry weight to total gonadal volume

Table 1. *Paramuricea clavata*. Mean (± SD) diameter (n = number of gonads; 5 samples of 200 gonads), dry weight, density, and carbon content (C) for mature oocytes and sperm sacs

	Diameter (µm)	n	Dry weight (mg)	n	Density (mg mm^{-3})	n	C/dry wt	n
Oocyte	342 ± 43	731	0.010 ± 0.0010	5	0.47 ± 0.03	5	0.59 ± 0.07	5
Sperm sacs	281 ± 129	1725	0.005 ± 0.0005	5	0.38 ± 0.04	5	0.53 ± 0.01	5

ratio for each sex in the 5 replicates. Both mean density values were later used to estimate ovarian and sperm sac biomass based on gonadal diameter.

At the same time a further 5 replicates of 200 ovaries each and 5 replicates of 200 sperm sacs each were collected. The carbon content of each replicate was determined using a Carlo-Erba model 1500 C:N elementary analyzer (Table 1).

Interannual variability. A total of 10 male colonies and 10 female colonies between 30 and 50 cm in height were tagged in the same study area. An apical fragment from each was collected at the beginning of June 1991, 1992 and 1993. Gonadal volume was measured for 5 polyps from each colony per sample. Interannual variability was considered for number of gonads produced (female gonads > 200 µm, male gonads > 150 µm), and the values for number of gonads converted to total volume and dry weight per polyp.

RESULTS

Intra-colonial variation

Male and female colonies of *Paramuricea clavata* ripen sexually synchronously and bear fertile polyps on all branches except 5° branches. However, the percentage of fertile polyps decreases with increasing branch order on colonies of both sexes (Table 2; ANOVA, $p < 0.005$). Also the number of gonads per fertile polyp fell off significantly with increasing branch order on colonies of both sexes (Table 2; ANOVA, $p < 0.001$):

Male colonies	1° 2° <u>3° 4°</u>
Female colonies	1° 2° <u>3° 4°</u>

The fecundity of 1° branches was higher in that they had a higher percentage of fertile polyps and more gonads per polyp. Furthermore, since they make up the largest share of colony biomass (Coma 1994), they contribute 85% of all gametes and were thus the main contributors to sexual reproduction by the colonies. Mean diameter of ripe male ($\bar{x}$ ± SD, 254.1 ± 46 µm) and female (235.1 ± 79 µm) gonads did not vary significantly with branch order (ANOVA, $p > 0.05$).

Variation with colony size

The percentage of gonad-bearing colonies increased with size (Fig. 1). Most colonies (around 70%) belonging to the first size class (between 0 and 10 cm tall) had no gonads (Fig. 1). In the following 2 size classes the percentage of colonies with gonads rose rapidly, reaching 100% at heights above 30 cm. The smallest fertile male colony (with sperm-containing sperm sacs) was 8 cm in size. No female colonies smaller than 11 cm with ripe gonads (ovaries with mature oocytes) were observed. From a height of 30 cm all colonies were fertile. On average, sexual maturity was delayed until colonies had reached a size of 20 (11 to 30) cm, i.e. an age of 13 (6 to 19) yr according to our estimates (Coma 1994). The number of gonads per polyp increased significantly (ANOVA, $p < 0.001$) with colony size (Table 3). In contrast, the diameter of ripe male and female gonads did not vary with colony size (ANOVA, $p > 0.05$). Fecundity increased in both sexes with colony size because of the higher percentages of fertile colonies and polyps and a larger number of gonads per polyp (Table 3). Gonadal biomass in colonies 39 cm tall was thus approximately double that of colonies 30 cm high and some 4 times that of colonies 25 cm in size (Fig. 2).

Table 2. *Paramuricea clavata*. Percentage of fertile polyps, number of gonads per fertile polyp, and gonadal volume per fertile polyp in male and female colonies according to branch order. Values are mean ± SE; n: number of colonies examined

Branch order	% Fertile polyps	No. of gonads	Volume (mm^3)	n
Male				
1°	100	25.7 ± 4.2	0.53 ± 0.16	3
2°	95.5 ± 10.1	14.3 ± 4.8	0.26 ± 0.16	3
3°	59 ± 39.2	5.2 ± 2.2	0.07 ± 0.04	3
4°	31.1 ± 37.9	2.8 ± 0.6	0.03 ± 0.01	3
5°	0	0	0	3
Female				
1°	93.3 ± 14.1	12.8 ± 6.4	0.27 ± 0.14	3
2°	82.2 ± 21.6	7.4 ± 4.2	0.15 ± 0.09	3
3°	67.7 ± 30.7	4.2 ± 2.3	0.09 ± 0.06	3
4°	23.3 ± 39.4	6.3 ± 3.1	0.14 ± 0.09	3

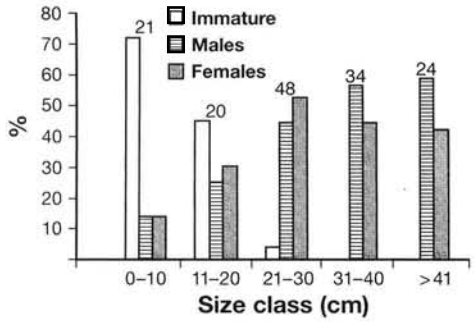

Fig. 1. *Paramuricea clavata.* Sex ratio and proportion of immature colonies on colony size (10 cm size classes); number of colonies examined in each size class written above the bars

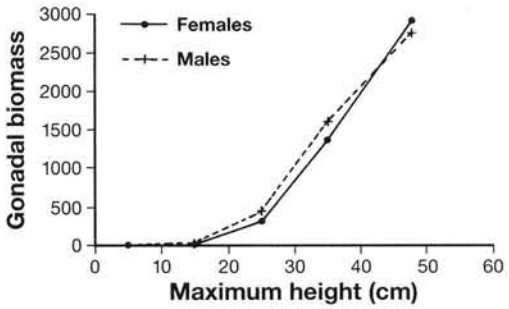

Fig. 2. *Paramuricea clavata.* Gonadal biomass (mg dry weight) for male and female colonies with respect to colony height

We considered 2 different manifestations of sexual senescence in this species; (1) a decline in fecundity and (2) cessation of sexual reproduction. It was possible to determine the sex of all colonies larger than 30 cm in height, and no decline in fecundity was observed with size, assuming that size equals age (see specific data in Coma 1994). Rather, colony fecundity was higher in the larger specimens in the study population (maximum colony height: 57 cm).

Interannual variability

There were no significant differences in the number of ripe gonads per polyp or in gonadal volume in either sex over the 3 yr considered (Table 4).

Reproductive effort

Reproductive effort of colonies increased with colony size (Fig. 3). Colonies smaller than 10 cm invested between 0.2 and 2% of their biomass, expressed as organic carbon weight of tissue, in reproductive effort, whereas colonies larger than 40 cm invested between 84 and 98% of the carbon weight of tissue. The increasing trend in reproductive effort levelled off somewhat at a height of approximately 35 cm, when reproductive effort had reached levels of around 80%.

The number of sperm sacs produced by the male colonies in a representative 1 m^2 plot (56 colonies m^{-2}) was 2 053 940, substantially higher than the 729 516 oocytes produced by the female colonies (Table 5). However, in terms of biomass, the contribution to the community was very similar in the 2 sexes, 9 g dry wt m^{-2} yr^{-1} for males, 7 g dry wt m^{-2} yr^{-1} for females. When expressed in terms of carbon, the contribution to the plankton of reproduction in this species was on the order of 9 g C m^{-2} yr^{-1} (Table 5).

DISCUSSION

The development and release of mature gametes was observed in the same colonies of *Paramuricea*

Table 3. *Paramuricea clavata.* Mean (± SE) reproductive effort values according to colony size: percentage of fertile colonies and of fertile polyps, number of gonads per fertile polyp, gonadal volume per fertile polyp, and total gonadal volume per fertile polyp. n: number of colonies examined. Maturity of gonads not determined in females

Size (cm)	% Fertile colonies	% Fertile polyps	No. of gonads Immature	No. of gonads Mature	Volume (mm^3) Immature	Volume (mm^3) Mature	Total volume (mm^3)	n
Male								
0–10	29	60 (40)	7.3 (5.4)	–	0.001	0	0.0002	10
11–20	55	43.3 (32)	6.9 (6.9)	1.5 (0.8)	0.001	0.031	0.0077	10
21–30	95	64.3 (28.5)	10.1 (4.5)	7.7 (5.2)	0.001	0.161	0.0990	10
31–40	100	80 (31.6)	26.3 (8.5)	14 (6.1)	0.004	0.293	0.2377	10
>40	100	82 (29)	28.7 (5.9)	18 (7.5)	0.004	0.377	0.3127	10
Female								
0–10	29	80 (20)	3.7 (3.5)		0.09		0.02	10
11–20	55	64 (22)	13.1 (4.5)		0.15		0.054	10
21–30	95	92 (10.9)	20.5 (20)		0.24		0.208	10
31–40	100	92.7 (13.5)	30.2 (8.2)		0.35		0.325	10
>40	100	98 (6.3)	36.1 (9.7)		0.42		0.411	10

Table 4. *Paramuricea clavata*. Interannual variation in the number and volume (mm^3) of mature oocytes and sperm sacs per polyp in the period 1991–1993 and analysis of variance (ANOVA) of the level of significance (*F*: Fisher's *F*-statistic; SE: standard error, n: number of polyps examined)

Measure		1991	1992	1993	df	*F*	p
Oocyte per polyp	$\bar{x}$	12.9	14.7	12.3	2.187	1.02	0.362
	SE	1.05	1.85	0.82			
Volume per polyp	$\bar{x}$	0.27	0.31	0.26	2.187	1.11	0.332
	SE	0.02	0.04	0.02			
	n	50	50	90			
Sperm sacs per polyp	$\bar{x}$	26.6	–	25.7	1.138	0.09	0.756
	SE	3.55	–	0.91			
Volume per polyp	$\bar{x}$	0.62	–	0.53	1.138	1.81	0.180
	SE	0.08	–	0.03			
	n	50	–	90			

clavata over a 4 yr period (1990 to 1993) and confirmed the iteroparous nature of the species, whose individuals partition their reproductive effort over successive annual periods over their lifetimes. This pattern has also been reported for different tropical species, such as *Briareum asbestinum* (Brazeau & Lasker 1990) and *Plexaura* A (H. R. Lasker pers. comm.).

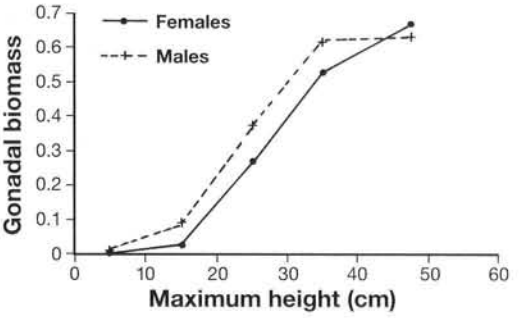

Fig. 3. *Paramuricea clavata*. Reproductive effort in terms of gonadal biomass (µg C μg^{-1} organic C in colony tissue) with respect to colony height

Intra-colonial variation

Consideration of reproductive effort on the basis of the branching pattern classification system postulates similar functional characteristics for all segments on a given branch order (Brazeau & Lasker 1988). Observations in *Paramuricea clavata* bore out such functional similarity, in that spatial variability in the polyp fecundity within a colony was much lower within each order than between orders. The high fecundities recorded for the apical segments of *P. clavata* contrasts with the findings reported for *Briareum asbestinum* (Brazeau & Lasker 1990), the only other gorgonian species in which intra-colonial variability in fecundity has been studied. In this latter species, fecundity was highest among polyps on the central portions of branches. The morphology, stolonal strategy, and high growth rate, and the importance of vegetative reproduction in this tropical species (Lasker 1983) may be some of the main factors responsible for this difference. The pattern followed by *B. asbestinum* is similar to that observed in corals with localized growth zones and, additionally, high growth rates (Rinkevich & Loya 1979, Oliver 1984, Wallace 1985, Kojis 1986a, Soong &

Table 5. *Paramuricea clavata*. Mean annual gonadal production in number, dry weight, and carbon in male and female colonies per m^2 of substratum occupied by the population studied

Size (cm)	Oocytes col.$^{-1}$ (n)	Sperm sacs col.$^{-1}$ (n)	Density (col. m^{-2})	Oocytes m^{-2} (n)	Sperm sacs m^{-2} (n)	Oocytes m^{-2} (mg dry wt)	Sperm sacs m^{-2} (mg dry wt)	Oocytes m^{-2} (mg C)	Sperm sacs m^{-2} (mg C)
0–10	0	474	20.7	0	4902	0	22	0	11
10–20	1100	14113	19.6	10778	138307	106	611	63	324
20–30	31734	118172	9.4	149148	555410	1468	2452	866	1300
30–40	135473	330164	4.1	277719	676836	2734	2988	1613	1584
>40	291871	678485	2.0	291871	678485	2873	2995	1695	1588
Total			55.8	729516	2053940	7181	9068	4237	4806

Lang 1992). The low growth rate in *P. clavata* (Coma 1994) is the reason fertility of apical polyps is possible. Decreasing fecundity with increasing branch order could be related to the different prey capture rates for polyps on the different branch orders, probably as a result of differences in access to water flow. Murdock (1978) estimated substantial potential flow rates for metabolites through the axial channels of colonies, which would in theory enable ingested matter to be transported throughout the entire colony; however, those same authors reported that in practice most such matter normally seems to be distributed within the region lying in the vicinity of the point of capture. Soong & Lang (1992) observed infertility in the basal portions of *Acropora cervicornis* and *Porites furcata* and they also suggest low food availability could be the cause.

Variation with colony size

The size at first reproduction is lower in other species studied (Grigg 1977, Martin 1982, Brazeau & Lasker 1989, 1990). However, bearing in mind the low rate of growth in this species (Coma 1994), the minimum age at first reproduction can be estimated at around 7 to 13 yr, placing *Paramuricea clavata* among the slowest species to reach sexual maturity. Size at first reproduction is highly variable, as has been reported for other gorgonians (Brazeau & Lasker 1989, Wahle 1983); this would appear to be attributable to the high plasticity of clonal organisms, in which there may be considerable divergence in growth, survival, and fecundity in individuals the same age (Caswell 1982, Hughes & Cancino 1985).

Colonies larger than 40 cm were very scarce in the population studied (less than 3%), yet their contribution to the production of gametes was on the order of 40% of female gametes and 33% of male gametes. Higher fecundity levels with size means that the likelihood of reproductive success increases with colony size. Also other factors such as fertilization success and spatial location may ultimately determine reproductive success. McKinney & Jackson (1991) discussed these aspects in relation to certain populations of bryozoans and suggested that in such cases the evolutionary advantage of attaining a large colony size must be extremely great, because in some species a few clones may dominate the population genetically (Coffroth et al. 1992). This is one hypothesis postulated to account for the considerable delay in the onset of sexual reproduction that is characteristic in many clonal organisms (Hughes & Cancino 1985). Other non-exclusive interpretations of such delays have, however, also been put forward. Investment of resources nearly exclusively in growth during the critical early years of life may also be evolutionarily advantageous (Connell 1973) by: (1) enhancing the likelihood of survival associated with larger size (Kojis & Quinn 1981, Martin 1982, Szmant-Froelich 1986); (2) increasing future reproductive success through the greater availability of resources provided by larger size (Szmant-Froelich 1985); and (3) avoiding the cost of sex by achieving high exponential growth rates during periods of unlimited growth through modular replication (Allan & Goulden 1980). All these interpretations agree on the importance of attaining a minimum size before investing in sexual reproduction. This pattern of higher fecundity with colony size appears to be generalized among gorgonians (Kinzie 1974, Grigg 1977, Wahle 1983). This pattern also seems to be widespread among corals (Kojis & Quinn 1981, Tranter et al. 1982, Babcock 1984, 1986, Wallace 1985), although exceptions have been described, as in *Porites astreoides*, in which fecundity is correlated with age rather than with colony size (Chornesky & Peters 1987), or in *Pocillopora damicornis*, in which fecundity was not significantly correlated with colony size (Richmond 1987).

No evidence of reproductive senescence has been observed in *Paramuricea clavata*, just as none was found in *Plexaura homomalla* (Martin 1982). A number of workers (Medawar 1957, Williams 1957, Hamilton 1966) have predicted that the onset of senescence should occur later in organisms with relatively low rates of adult mortality and constantly increasing fecundity levels than ... species with relatively high rates of adult mortality (by predators or pulling up by divers) and limited adult fecundity. Although fecundity levels have been reported to decrease in large colonies in certain species of corals (Holloran 1986), symptoms of senescence in clonal species like *Paramuricea clavata* could be expected to appear late, perhaps so late as to be virtually undetectable under natural conditions (Harper 1981, 1985, Palumbi & Jackson 1983, Silander 1985).

Interannual variability

Paramuricea clavata did not exhibit any interannual variation in fecundity over the 4 yr period considered. Similarly, Brazeau & Lasker (1990) did not record any significant differences in the fecundity of female colonies of *Briareum asbestinum* in the Caribbean. On the other hand, significant interannual differences have been observed in certain species of corals off eastern Australia (Wallace 1985) and in the Red Sea (Rinkevich & Loya 1987). Longer-term studies monitoring possible variability are called for, since to date no study has lasted for more than 4 yr.

Reproductive effort

Reproductive effort in gorgonians has been assessed by most researchers (Theodor 1967, Kinzie 1970, Vighi 1970, Grigg 1977, Martin 1982, Brazeau & Lasker 1989, 1990) as fecundity expressed as number of oocytes, number of eggs, or number of planulae per polyp. These estimates furnish useful indices of reproductive effort, provided that the size of oocytes and planulae and the number of annual reproductive cycles are reasonably constant (Kojis 1986b, Harrison & Wallace 1990). *Paramuricea clavata* appears to be the species that makes the highest investment in sexual reproduction in terms of number of mature oocytes produced per polyp (Theodor 1967, Kinzie 1970, Vighi 1970, Grigg 1977, Martin 1982, Brazeau & Lasker 1989, 1990). Validation of this supposition requires estimates of somatic biomass for the other species; in any event, the high fecundity of *P. clavata* ranks this species among the gorgonians with the highest investment in sexual reproduction of all those studied to date. This pattern of behaviour in *P. clavata* is in consonance with the general observation that the number of offspring is related to the broad characteristics of the habitat, with generally higher values in temperate regions with variable climates than in tropical regions (Margalef 1984).

The estimates of reproductive effort levels for *Paramuricea clavata* colonies, ranging up to 98% of their tissue biomass, cannot be contrasted with values for other species of gorgonians. At the beginning of its spawning period, the hydroid *Orthopyxis crenata* invests up to 10% of its biomass in reproduction daily (Coma 1994). Colonies of *Pocillopora damicornis* release between 25 and 50% of their total colony weight annually, and 1 colony released 4% of its tissue weight as planulae in just 48 h (Jokiel 1985). Richmond (1987) quantified spawning in *P. damicornis* at between 20 and 167% (mean: 62%, irrespective of colony size) of colony calorie content annually.

The estimated production of 730 000 eggs m^{-2} for the population is much higher than the level of larval production estimated by Theodor (1967) for *Eunicella singularis* in the Mediterranean (60 000 larvae m^{-2}). This discrepancy may be the result of differences in the densities of spawning colonies, though it may also be attributable to low fertilization rates. However, no percentage fertilization rates are available for *Paramuricea clavata*, although *in situ* fertilization has been reported to be low in other species of gorgonians (Brazeau & Lasker 1992). In conclusion, the results of this study have contributed to our knowledge of the biology of clonal organisms by verifying the iteroparuty of this species, the absence of senescence in natural populations, and the dependence between reproductive efficiency and colony size.

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