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REPORT

Effects of a mass mortality event on gorgonian reproduction

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Abstract The impact of a disturbance is normally measured in terms of its effects on adult mortality, whilst the less obvious impact on reproductive biology is generally ignored. Although previous studies have contributed to understanding the effects of a mass mortality of gorgonians in 1999 at NW Mediterranean Sea, none of them have considered its impact on reproduction. The goal of this study was to determine the impact of mass mortality events on the reproduction of the gorgonian *Paramuricea clavata*, and examine the effect of the damage 1 year (June 2000) and 2 years (June 2001) after the event. The reproductive parameters of female colonies were more affected than those of males. In female colonies that were moderately or severely damaged, the proportion of fertile polyps decreased by about 22–35%, whilst in the worst affected males there was only a 12% decrease. Female colonies showed a progressive decrease in gonadal biomass with increasing damage to a maximum reduction of 73–75% of oocyte production observed in colonies with >33% injury. In contrast, in males, the gonadal biomass decreased rapidly for colonies with 5% of injured surface, with a reduction in spermary production of 49–64%. The same pattern of decrease in gonadal output compared to the extent of the injury was observed in 2001, two years after the mass mortality event. This indicated that the observed pattern was a response to the extent of the injury rather than a direct effect of the event. These severe effects on the reproduction of the red gorgonian species have implications for the recovery of affected populations in the long-term. This study demonstrated that an evaluation of the impact over different demographic parameters is needed to understand all the consequences of these disturbances.

Keywords Octocoral · Injury · Partial mortality · Sexual reproduction · Fecundity · NW Mediterranean

Introduction

There is general agreement that coastal marine ecosystems are being threatened by mass mortality events and diseases linked to climate warming (Harvell et al. 1999, 2002; Romano et al. 2000). These events provoke ecological responses related to the performance of individuals, population dynamics and processes determining the structure of the communities (Harley et al. 2006).

The impact of a disturbance is usually measured in terms of its effects on adult mortality, while the less obvious effects on reproductive biology are often ignored (Hughes and Connell 1999; Coma et al. 2004). However, it is well documented that damage to coral tissue and skeleton caused by different agents (storms, sedimentation or predation) affects important biological processes such as reproduction (Kojis and Quinn 1981; Van Veghel and Bak 1994;

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Kramarsky-Winter and Loya 2000; Oren et al. 2001). Although there are numerous studies about the effects of coral bleaching (Glynn 1993; Brown 1997), only a few have quantitatively examined its impact on coral reproduction. Such studies have shown the negative effects of these events on different reproductive parameters (Szmant and Gassman 1990; Michalek-Wagner and Willis 2001; Baird and Marshall 2002; Mendes and Woodley 2002).

Mediterranean hard-bottom communities dominated by long-lived species have recently been affected by mass-mortality events associated with unusual climatic anomalies (Cerrano et al. 2000; Perez et al. 2000; Garrabou et al. 2001; Linares et al. 2005; Coma et al. 2006). In 1999 and 2003, two mass mortality events affected hard-bottom communities on a regional scale in the NW Mediterranean. These events were the most damaging ever recorded in the area and affected a wide variety of species and taxa along hundreds of kilometres. Several studies examined the impact of these mortalities on different gorgonian species shortly after the occurrence of the event (Cerrano et al. 2000; Perez et al. 2000; Garrabou et al. 2001). Other studies assessed the effects of the mortalities in the medium term and revealed that delayed effects were much greater than evaluations conducted shortly after the event suggested (Linares et al. 2005; Coma et al. 2006).

These previous studies contributed to our understanding of the impact of the 1999 mass mortality on sessile stages of populations of different benthic invertebrates (but see Cerrano et al. 2005 for the examination of the population sex ratio). The present study examined the impact of the 1999 mass mortality event on reproduction of the gorgonian *Paramuricea clavata*. The impact was related to an increase in the partial mortality of the colonies (the extent of injuries to a colony's surface) during the event. Studies of the effects of mass mortality on sexual reproduction are necessary because of the importance of sexual reproduction for the replenishment of Mediterranean gorgonian populations (Coma et al. 1995a; Ribes et al. 2007). The impact of the mass mortality on the reproductive effort of the gorgonian *P. clavata* was assessed by measuring gonadal production one year after the event (June 2000) and by evaluating the persistence of this effect over time (June 2001).

Materials and methods

Reproductive biology of *Paramuricea clavata*

The red gorgonian *P. clavata* is a surface brooder species which invests heavily in sexual reproduction each year (Coma et al. 1998). *P. clavata* is a dioecious species with a sex ratio that generally does not significantly vary from 1:1. Spawning is synchronous and occurs every June in two separate episodes. Oocyte development lasts between 13 and 18 months, while sperm development lasts between 6 and 7 months. Whereas all male gonads spawn each year, only female gonads larger than 200 µm spawn in a given year (Coma et al. 1995a, b). After the mass mortality occurred in late summer 1999, the best time to examine its effects on sexual reproduction was at the end of the next reproductive cycle (June 2000).

Gonadal production

The effect of the damage to a colony's surface on gonadal production was examined by sampling 120 different colonies divided into 4 categories according to the extent of the injury to the colony's surface (<5, 5–33, 33–66, >66%). The extent of the injury was estimated as the proportion of each colony's total surface that showed no tissue (i.e., denuded axis) or was overgrown by other organisms (as in Harmelin et al. 1999). During June 2000, samples at a depth of between 20 and 25 m were collected by scuba divers from two populations affected by the 1999 mass mortality (Gabiniere and Montremian) located in Port-Cros National Park in France (see Linares et al. 2005). Samples were immediately fixed in 10% formalin in seawater. For each category, an apical fragment from 30 colonies ranging in height from 30 to 40 cm was randomly collected. In the laboratory, the sex of the colonies was determined in order to examine ten male and ten female colonies. Ten polyps from each colony were dissected under a binocular dissecting microscope. Therefore, 100 polyps in each damage category and of each sex were examined at each location. We recorded the number and diameter of all spermaries in each male polyp and of all oocytes larger than 200 µm in the female colonies (Coma et al. 1995a).

The proportion of fertile polyps, the number and diameter of oocytes and spermaries per polyp, and gonadal biomass per polyp were estimated to compare the effects of the extent of injury with gonadal production. For both sexes, gonad diameter was used to estimate gonad biomass using the relationship reported in a previous study (Coma et al. 1995b). The sex ratio was taken as the proportion of the sexes of the 120 colonies (30 for each damage category) sampled at both sites studied in 2000. Deviation of the sex ratio from parity was tested using a Chi-square test.

In June 2001, apical fragments from colonies with <5% damage to the colony surface and from colonies with >66% damage were collected at one of the two locations sampled in June 2000 (Montremian). To evaluate the effect of the event two years after it occurred, gonadal production was estimated using the same number of colonies and method as previously described.

Three-way ANOVA was used to examine the effects of location, extent of the injury to a colony's surface and colonies (nested in location and injury) on gonadal biomass of male and female colonies. Three-way ANOVA was also used to examine the effect of time, extent of the injury and colonies (nested in time and injury) on gonadal biomass for both sexes.

Results

Sex ratio

The samples collected in June 2000 revealed similar proportions of sexes in all damage categories and locations (Table 1). Overall, the species sex ratio was not significantly different from unity (female to male: 1.02, 115/113). The number of indeterminate colonies corresponds to colonies with high levels of damage (>33% surface affected, Table 1) and ranged from 3 to 9 colonies, depending on the location.

Table 1 Sex ratio of *Paramuricea clavata* colonies in relation to their injury degree at both studied localities of the Port-Cros National Park

Injury degree (%)	Montremian				Gabiniere			
	Female	Male	Indet.	*N*	Female	Male	Indet.	*N*
<5	14	16	0	30	18	12	0	30
>5 to <33	16	14	0	30	16	14	0	30
>33 to <66	13	16	1	30	15	12	3	30
>66	13	15	2	30	10	14	6	30
Total	56	61	3	120	59	52	9	120

Indet. colonies where sex was not possible to determine

Effects of injuries on gonadal production one year after the 1999 mass mortality

The extent of the injury to a colony's surface negatively affected the proportion of fertile polyps of both sexes. However, this effect was more marked for female colonies than for male colonies. Uninjured colonies, as well as those exhibiting low levels of injury (<33%), exhibited nearly 100% of fertile polyps (i.e., those containing oocytes or spermaries). Female colonies moderately damaged (33–66 %) exhibited a 17 or 28% decrease (Gabiniere and Montremian, respectively) and severely affected colonies (>66%) showed approximately a 35% decrease at both locations. In contrast, a significant decrease in the proportion of fertile polyps in male colonies was only observed in the severely affected colonies (>66%), which exhibited a 12% decrease in the proportion of fertile polyps at both locations (Table 2).

The gonadal biomass of female colonies was significantly different at the two locations and depended on the extent of injury (Table 3, Fig. 1a). Despite the differences between the locations, colonies at both displayed a similar pattern of decrease in gonadal biomass with the increase in damage up to 33%. In the two highest damage categories, the biomass of oocytes did not vary between the two locations (Fig. 1a). On average, badly damaged female colonies (>33%) exhibited a 73–75% reduction in oocyte production.

The mean diameter of oocytes was not affected by the extent of the damage to the colonies (Fig. 1b): it was the number of oocytes per polyp that accounted for the pattern of decrease in female gonadal biomass with increasing damage (Fig. 1c).

Table 2 Proportion of polyps with oocytes or spermaries observed in colonies pooled in four injury categories in June 2000 at two studied sites

Sex	Year	Location	Injury (%)	N colonies	N polyps examined	Fertile polyps (%)
Female	2000	Gabiniere	<5	10	100	99
			>5 to <33	10	100	100
			>33 to <66	10	100	83
			>66	10	100	66
	2000	Montremian	<5	10	100	100
			>5 to <33	10	100	100
			>33 to <66	10	100	72
			>66	10	100	64
Male	2000	Gabiniere	<5	10	100	100
			>5 to <33	10	100	100
			>33 to <66	10	100	100
			>66	10	100	88
	2000	Montremian	<5	10	100	99
			>5 to <33	10	100	99
			>33 to <66	10	100	98
			>66	10	100	88

Table 3 3-way-ANOVA comparing gonadal biomass for female colonies of *Paramuricea clavata* among locations (i.e., La Gabinière and Montremian), injury (four categories of extent of injury: <5, >5–33, >33–55 and >66% of the colony surface) and colonies

Source	*df*	SS	MS	*F*	*P*
Location	1	0.036	0.036	6.923	0.011
Injury	3	0.439	0.146	27.919	<0.001
Colony	56	0.294	0.005	7.578	<0.001
Location × injury	3	0.020	0.007	1.302	0.283
Error	576	0.399	0.0007		

Colony nested in location and injury

df degrees of freedom, *MS* mean square, *SS* sum of squares, *F* F ratio, *P* probability

Probability values <0.05 have been considered significant

In male colonies, gonadal biomass also varied significantly between locations and according to the extent of the injury (Table 4, Fig. 2a). Despite the differences observed between locations, gonadal biomass followed the same pattern at both locations, decreasing rapidly even at low levels of damage (>5%). On average, male colonies showed a reduction of between 49 and 64% in spermary production (Fig. 2a).

As for female colonies, the mean diameter of spermaries did not vary with level of damage (Fig. 2b). Again, the lower number of spermaries per polyp was responsible for the reduction in the biomass of male gonads, with increasing damage (Fig. 2c).

Comparison of 2000 and 2001

In 2001, the pattern of decreased gonadal biomass with the increase in the damage to the colonies was similar to that observed in 2000 (Fig. 3, Table 5). The gonadal biomass of uninjured colonies was about twice as much as for badly damaged colonies for both sexes.

As observed in 2000, the differences in gonadal biomass documented in 2001 were not due to differences in the mean diameter of gonads, but to differences in the number of oocytes or spermaries per polyp (Table 6).

Discussion

The consequences of the 1999 gorgonian mass mortality event in the NW Mediterranean on gorgonian reproductive and population biology is a crucial step in understanding the capability of gorgonian populations to recover from major disturbances. This study showed the severe effects of the event on reproduction of the species, complementing the previous observations on population structure and dynamics of *P. clavata* populations at Port-Cros National Park (Linares et al. 2005). The reproductive damage has further implications for the recovery of affected populations in the long term.

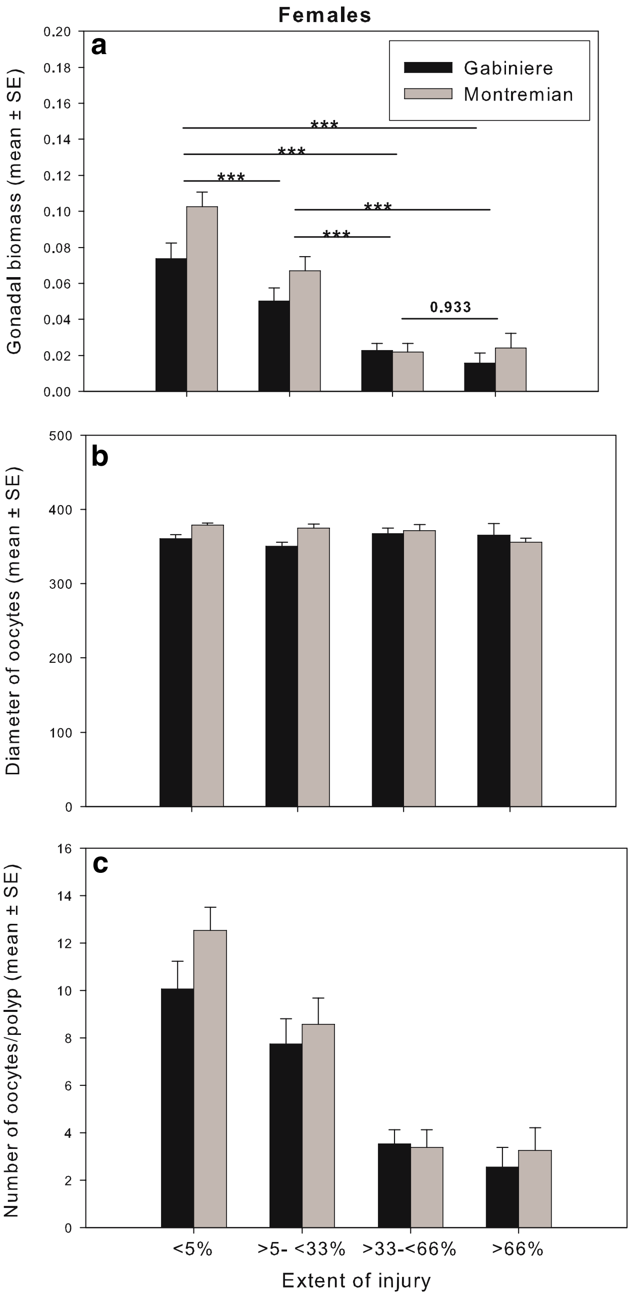

Fig. 1 Female colonies. Changes in reproductive parameters with the extent of the injury at both sites studied (Gabiniere and Montremian) in 2000. **a** Variation of gonadal biomass. Probability of post-hoc comparisons (Scheffé test) between two means is indicated above corresponding horizontal lines (*** $P < 0.001$). **b** Variation in the mean diameter of oocytes. **c** Variation in the mean number of oocytes/polyp

Previous studies of bleaching on coral reproduction suggested that the effects on reproductive output were dependent upon the severity of the impact and the species affected (Szmant and Gassman 1990; Michalek-Wagner and Willis 2001; Baird and Marshall 2002; Mendes and Woodley

Table 4 3-way-ANOVA comparing gonadal biomass for male colonies of *Paramuricea clavata* among locations (i.e., La Gabinière and Montremian), injury (four categories of extent of injury: <5, >5–33, >33–55 and >66% of the colony surface) and colonies

Source	*df*	SS	MS	*F*	*P*
Location	1	0.590	0.590	21.818	<0.001
Injury	3	1.181	0.394	14.564	<0.001
Colony	72	1.946	0.027	6.575	<0.001
Location × injury	3	0.296	0.099	3.654	0.016
Error	720	2.960	0.004		

Colony nested in location and injury

df degrees of freedom, *MS* mean square, *SS* sum of squares, *F* F ratio, *P* probability

Probability values <0.05 have been considered significant

2002). Stress, such as temperature increase or contamination, can produce alterations in the gametogenic cycle (by reducing gonad size, Guzman and Holst 1993), the production of gonads, or in both parameters (Szmant and Gassman 1990; Michalek-Wagner and Willis 2001; Mendes and Woodley 2002). In the present study the observation that oocyte and spermary diameters were not affected indicates that the mortality event did not alter the cycle of gonadal development, but only reduced the amount of gonads produced. The pattern of decrease in gonadal output at different levels of damage was repeated at both locations studied. Long-term monitoring of the reproductive output of the species indicated that the differences observed between the two locations were within the natural range of spatial variability observed for the species (Coma et al. 1995a, b). The fact that gonadal biomass in 2001 was higher than in 2000 could indicate that the event produced a sub-lethal effect on the reproductive output of colonies where damage was not evident. Nevertheless, these results demonstrate that the extent of damage to the colonies was the main factor causing reduced gonad production. The persistence of a decrease in gonadal output at different levels of injury (from 2000 to 2001) indicated that the pattern was not a direct effect of the mass mortality event but rather a consequence of the damage to the colonies. The persistence of the negative effects of stress factors (e.g., exposure to high temperatures and/or contamination) on reproductive output has been recorded in several coral species (Szmant and Gassman 1990; Guzman and Holst 1993; Mendes and Woodley 2002).

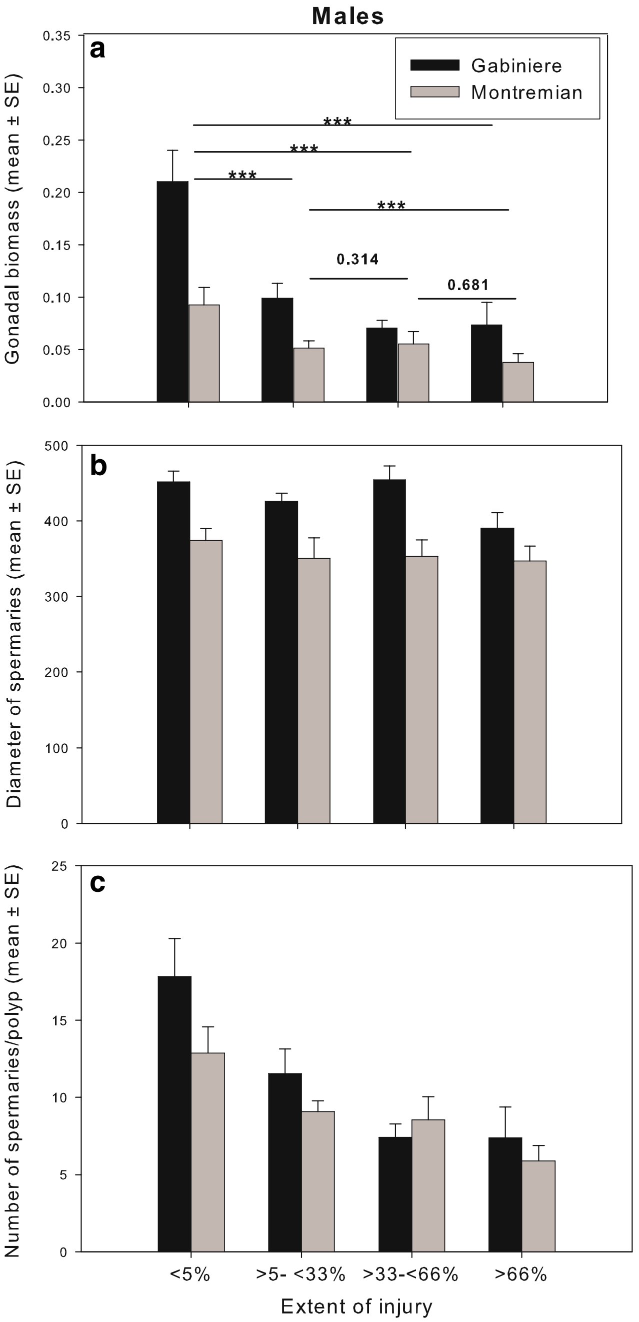

Fig. 2 Male colonies. Changes in the reproductive parameters with the extent of the injury at both sites studied (Gabiniere and Montremian) in 2000. **a** Variation of gonadal biomass. Probability of post-hoc comparisons (Scheffé test) between two means is indicated above corresponding horizontal lines (*** $P < 0.001$). **b** Variation in the mean diameter of spermaries. **c** Variation in the mean number of spermaries/polyp

The sex ratio in the population studied was 1:1. This is similar to ratios reported for a red gorgonian population on the Spanish coast (Coma et al. 1995a) and for the Italian population two years before the event (Cerrano et al. 2005). The greater reduction of gonadal biomass observed in female colonies, compared to male colonies (73–75% vs. 49–64%) and the greater decrease in fertile polyps (35% vs. 12%) suggest that female colonies were more affected. This may, in part, explain previous results obtained for another *P. clavata* population located at the Portofino promontory (Italy), where a sex ratio bias towards male colonies was documented as one of the effects of the 1999 mass mortality (Cerrano et al. 2005).

Fig. 3 Female and male colonies. Comparison of the variation in gonadal biomass with the extent of the injury at Montremian between 2000 and 2001

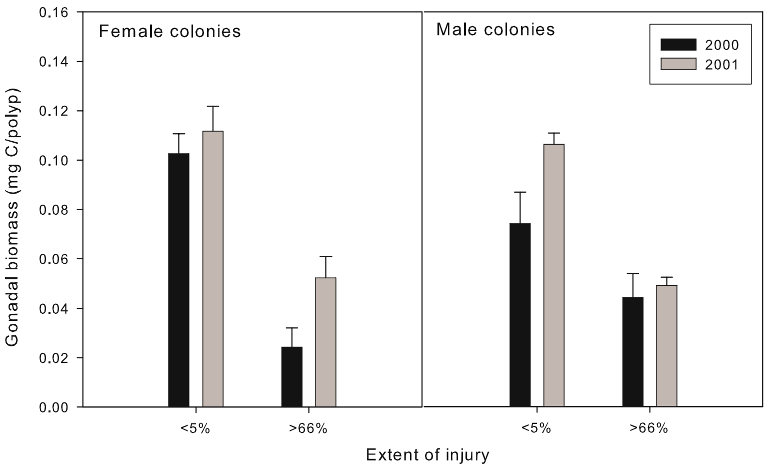

Table 5 3-way-ANOVA comparing gonadal biomass for male (a) and female (b) colonies of *Paramuricea clavata* among time (i.e., 2000 and 2001), injury (two categories of extent of injury: <5 and >66% of the colony surface) and colonies at the Montremian location

Source	*df*	SS	MS	*F*	*P*
a) Male colonies					
Time	1	0.103	0.103	9.467	0.004
Injury	1	0.402	0.402	36.830	<0.001
Colony	36	0.393	0.011	5.126	<0.001
Time × injury	1	0.006	0.006	0.588	0.448
Error	360	0.767	0.002		
b) Female colonies					
Time	1	0.069	0.069	10.384	0.004
Injury	1	0.286	0.286	43.090	<0.001
Colony	20	0.133	0.007	1.755	0.027
Time × injury	1	0.0002	0.0002	0.283	0.868
Error	216	0.818	0.004		

Colony nested in location and injury

df degrees of freedom, *MS* mean square, *SS* sum of squares, *F* F ratio, *P* probability

Probability values <0.05 have been considered significant

In clonal organisms the loss of live tissue, such as defoliation in plants, can have a negative effect on survival, growth and reproduction. After defoliation, plants may compensate for lost tissue (Crawley 1983). Consequently, given that growth and reproduction often compete, there may be a trade-off between vegetative and reproductive growth. However, although some species reduce reproductive output and change resource allocation patterns (Chazdon 1991), others do not (Belski 1986). The compensatory reproductive response of defoliated plants is not therefore a general pattern (Obeso 1993). A similar compensatory response has been documented for several coral species and the effects on reproductive output were related to the severity of the stress (Szmant and Gassman 1990; Michalek-Wagner and Willis 2001; Baird and Marshall 2002; Mendes and Woodley 2002).

Tissue damage in gorgonians takes the form of dead patches of tissue that expose the underlying skeletal axis (Perez et al. 2000). The colonies recover by regenerating the tissue and extending new tissue from the edges of the dead patches to cover the exposed skeleton. However, regeneration is essentially a growth process that can deplete energy and resources for other processes (Silveira and Van't Hoff 1977). The 1999 mass mortality event was extremely severe, leading to an average of 50% of the surface tissue of colonies being damaged (Linares et al. 2005). The decrease in gonadal production with the increasing damage suggests a resource limitation affecting the allocation of energy to reproduction. This would be consistent with the energy constraints observed in the energy budget of the species (Coma et al. 1998; Coma and Ribes 2003). The decrease in fecundity (considered as the number of gonads per polyp)

Table 6 Gonadal diameter, number of oocytes and spermaries/polyp, and proportion of fertile polyps at Montremian in 2001

Sex	Injury degree (%)	Gonadal diameter			Gonadal number/polyp		*N* polyps examined	Fertile polyps (%)
		Mean	SD	*N*	Mean	SD		
Female	<5	379.01	43.91	578	14.46	12.49	100	100
	>66	365.99	40.61	274	7.43	7.78	100	64
Male	<5	397.66	92.47	589	14.71	6.67	100	100
	>66	408.31	93.06	332	6.20	3.55	100	97

was probably related to a reallocation of energy to maintain fewer eggs and ensure that they reach maturity (Yamazato et al. 1981; Michalek-Wagner and Willis 2001). A trade-off between regeneration and reproduction has been reported for different coral species (Kojis and Quinn 1981; Van Veghel and Bak 1994; Kramarsky-Winter and Loya 2000). This trade-off being accomplished either by reducing coral fecundity in the affected area (Van Veghel and Bak 1994; Hall 1997), or by extending the effects far from the damaged area (Oren et al. 2001). As sampling of *P. clavata* colonies was not conducted in the damaged area, the results indicate that the different damage levels not only affect fecundity in the vicinity of the damaged area but over the whole of the colony affected. The pattern of decrease in fecundity with increasing damage to the colonies observed in *P. clavata* supports the hypothesis that in long-living organisms (such as gorgonians and corals) priority in energy allocation is given to recovery rather than to reproduction (Oren et al. 2001). Despite this, the survival of colonies affected by high levels of damage is much lower than uninjured colonies or colonies only slightly affected (Linares et al. 2005).

A previous study of the same populations showed that colonies >10 cm in maximum height were more affected by partial mortality (extent of the injury) than colonies <10 cm in maximum height (Linares et al. 2005). These results may reflect the importance of the loss of live tissue from reproductive colonies for their reproductive output. As in many clonal organisms (Hughes and Cancino 1985; Hall and Hughes 1996), the reproductive effort of the species increases with colony size and a few large colonies represent a considerable share of reproductive output (Coma et al. 1995b). *P. clavata* colonies larger than 40 cm in maximum height contribute about 40% of total gonadal production in female colonies and about 33% in male colonies (Coma et al. 1995b). Disturbances that have greater impacts on large colonies may therefore have dramatic consequences on reproductive output due to the partial loss of live tissue and reproductive colonies.

The large proportion of colonies exhibiting high levels of damage observed in Port-Cros National Park indicates that the fecundity of most of the colonies was severely affected by this event (Linares et al. 2005). The relationship between the extent of damage to the colonies and their reproductive output, together with the high degree of damage persisting four years after the 1999 mass mortality (on average about 35% of the whole surface; Linares et al. 2005) demonstrate the importance of delayed effects on the reproductive output of the species and, therefore, on long-term species recovery. The recovery of impacted populations may be strongly affected by the considerable reduction in reproductive output. Moreover, replenishment from other nearby non-affected populations is limited by the dispersal capability of red gorgonian larvae (Linares et al. 2007a) and the species' low recruitment rates (Coma et al. 2001, 2004; Linares et al. 2007b). Finally, this study demonstrates that an evaluation of the impact over different demographic parameters is needed to understand all the consequences of the disturbances.

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