

## Fragment growth-rates of six cultivated coral species: a reference framework for coral transplantation

Virginie VAN DONGEN-VOGELS and Jérôme MALLEFET

**Abstract:** Coral fragmentation is a natural process of asexual reproduction in many coral species. Fragment size is believed to be an important factor of fragment survival at least in some species. The degradation of coral reefs and its poor recovery in some localities had brought different management plans in coral transplantation. In this study we examined in controlled conditions the variation in fragment growth rates of six different scleractinian species belonging to two different growth forms. We showed that fragment growth rates increased over our 6 month survey and that *Pocillopora damicornis* exhibited the highest growth rate followed in decreasing order by *S. pistillata*, *Montipora* sp., *S. caliendrum*, *Echinopora* sp., and *T. reniformis* which may reflect their life history strategy, but also a difference in their surface-to-volume ratio as well as a difference in their skeletal density. Then, for each species, we determined whether growth rates might be affected by fragment size. We showed that there was a positive significant relationship between growth rate and fragment size, depending, however, on the interval time and the species considered. Difference in physiological resources allocation through a colony lifetime and genetic limitations in colony size may be related to our results. However, as in the wild many other parameters such as predation, can also play a role in fragment survivorship, we suggested that fragment size is an important parameter to take into account to successfully recover local coral population.

**Keywords:** *Coral Growth, Coral Fragmentation, Controlled Cultures, Hermatypic Corals*

### 1. Introduction

Many studies have investigated coral fragmentation (LOYA, 1976b : HIGHSMITH, 1982 : WALLACE, 1985 : SEEBAUER, 2001), a natural process used by many coral species to increase their local population density, and thus increase their probability of survival after e.g. physical disturbances (HIGHSMITH, 1982). Previous studies have reported a correlation between fragment size and survivorship in corals (LOYA, 1976b : HIGHSMITH *et al.* 1980 : HUGHES and JACKSON, 1985 : CHADWICK-FURMAN *et al.*, 2000 : ANTHONY *et al.*, 2002 : SOONG and CHEN, 2003 : GOFFREDO *et al.*, 2004 : ORTIZ PROSPER, 2005), whereas others have not (KINZIE and SARMIENTO, 1986 : BRUNO, 1998 : LIRMAN,

2000). Fragment size is one of the main characteristic of life history in many clonal organisms such as corals (KARLSON, 1988), which are known to have an indeterminate growth and hence unlimited colonial size (HUGHES and JACKSON, 1985 : SEBENS, 1987). While fragment survival may be species-dependent (HALL, 1997), it is still difficult to assess as many coral species have yet to be investigated.

Over the past few decades, increased awareness of the stresses occurring on coral reefs (HUGHES and CONNELL, 1999 : McCLANAHAN *et al.*, 2002 : HUGHES *et al.*, 2003 : FABRICIUS, 2005) has resulted in the development of coral recovery management plans of damaged areas using fragmentation as a tool for coral transplantation (OREN and BENAYAHU, 1997 : EDWARDS and CLARK, 1998 : SOONG and CHEN, 2003 : LINDHAL, 2003). The transplantation of coral fragments in artificial reefs has helped to

regenerate local coral communities (BOWDEN-KERBY, 2003). Many studies have focused on in situ fragment survival (e.g. YAP and GOMEZ, 1985 : SOONG and CHEN, 2003 : LINDHAL, 2003). The study of fragment growth in controlled conditions (stable physical parameters, no predation) would, however, facilitate the assessment of species-specific fragment growth rate, and hence survival rates. A fragment with higher growth rate would then sustain higher survival rates in the wild as it can extend faster. In particular, the comparison of growth and survival rates in the field and in controlled conditions allow for a direct assessment of species-specific response to predation, macroalgae over growth and flow field (YAP and MOLINA, 2003). Monitoring coral growth under controlled conditions may then be considered as an absolute prerequisite to provide baseline information for future studies involving coral growth in the field, including bleaching or recovery studies. A better knowledge in the potential relationship between growth rate and size might also provide further insights into the understanding of population dynamics in species of scleractinian corals.

In this context, the objectives of this work were to investigate the growth rate of fragments from six different cultivated species to provide baseline information on the growth of coral fragments after fragmentation under cultivated conditions. More specifically, a specific attention is given to (i) the inter-species variation of growth rate, (ii) the variation in growth rate between two growth forms (foliaceous vs branches), and (iii) the inter-fragments variability in growth rate for a given species.

## 2. Material and methods

### 2.1. Coral species

Six different coral species were considered here : three branched species (*Stylophora pistillata*, *Seriatopora caliendrum*, and *Pocillopora damicornis*) and three foliaceous colonial species (*Echinopora* sp., *Montipora* sp., and *Turbinaria reniformis*). All species are hermatypic corals harbouring the symbiotic algae zooxanthellae, which greatly accelerate the process of calcification, thus enabling their

host corals to rapidly establish fragments in coral reefs (SOROKIN, 1995 : SPRUNG, 2000 : VERON, 2000).

### 2.2. Fragmentation and coral cultures

Cuttings were performed with a pair of pliers on a few mother heads colonies of each coral species, providing a large number of fragments. During the growing period, fragments were placed on plastic plates in 800 l aquaria equipped with a circulating pump (*Eheim* 1060, 1200 l h<sup>-1</sup>), allowing sufficient water flow to support coral growth. Illumination was provided with two m *et al* halide lamps (HQI) located one meter above each aquarium, allowing 100  $\mu\text{E cm}^{-2} \text{s}^{-1}$  to 500  $\mu\text{E cm}^{-2} \text{s}^{-1}$ , from the surface of fragments growing near the glass of the aquarium to the surface of those growing in the centre of the aquarium respectively. Fragments of the same species were clustered to avoid any influence from other coral species and were reorganised every month in the aquaria to minimize the possible effects of water flow and light irradiance. The aquaria seawater temperature was maintained at 26.5–27.5 °C during the whole study. Two aquaria were used in this study. In addition to the studied species, the aquaria contained herbivorous organisms (e.g. fish or invertebrates). The presence of those organisms as well as a weekly cleaning were necessary to prevent excessive algal growth in the aquaria.

In order to measure the growth of fragments, they were taken out of the aquariums and put on a tray for five minutes before weighing them to allow excess water drain away (DELAHAYE, 2003). Fragments were then weighed one by one. All fragments of the six species were weighed within a day. The weight of each fragment was measured at the beginning of the study in November 2004 (just after fragmentation) and after 8 weeks of recovery, one weight measurement was performed each month from January to May 2005 ( $n=6$  species  $\times 30$  to 46 fragments).

### 2.3. Statistical analysis

A two way analyse of variance was used to test the variation in growth rate with time and between species (factors : species, time, and the

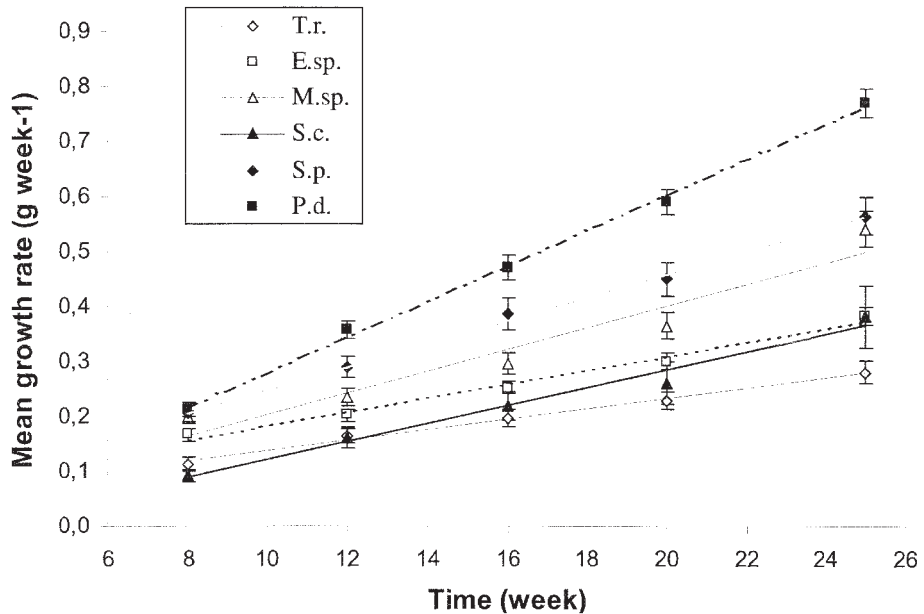


Fig. 1 Time course of fragment growth rates ( $\text{g week}^{-1}$ ) of the six different coral species. The error bars are the standard error.

interaction species  $\times$  time). Parametric test (Levene's test,  $>0.05$ ) of a one-way analysis of variance was then used in order to compare the increase in growth-rates between coral species with a Scheffe's multiple comparison test, and a  $t$ -test was done to compare those of the two growth forms (branches vs. foliaceous). Linear regressions were performed in order to test the relationship between the initial weight of the fragments of a given species and their growth rate.

### 3. Results

All fragments from each of the species investigated showed a similar exponential growth patterns over the 6-month survey. The related growth rates significantly ( $p < 0.0001$ ) increased linearly over time (Fig.1). The increasing gradients in growth rates over time were estimated as  $0.0095 \text{ g week}^{-2}$  ( $N=30$ ) for *Turbinaria reniformis*,  $0.0127 \text{ g week}^{-2}$  ( $N=43$ ) for *Echinopora* sp.,  $0.0197 \text{ g week}^{-2}$  ( $N=46$ ) for *Montipora* sp., and  $0.0164 \text{ g week}^{-2}$  ( $N=30$ ) for *Seriatopora caliendrum*,  $0.0210 \text{ g week}^{-2}$  ( $N=37$ ) for *Stylophora pistillata*,  $0.0322 \text{ g week}^{-2}$  ( $N=39$ ) for *Pocillopora damicornis*. This results in significantly higher gradients in

branched species than in foliaceous ones ( $t$ -test,  $p < 0.0001$ ). However, while *P. damicornis* increased its growth significantly faster than *S. pistillata* and *S. caliendrum* (Multiple comparison Scheffe's test,  $p < 0.05$ ), *Montipora* sp. was found to growth significantly faster than the two other foliaceous species ( $p < 0.05$ ).

The relationship between fragment weights (g) and their related growth rates ( $\text{g week}^{-1}$ ) has been investigated for five time intervals over the course of our survey. Our results indicate first that for most species, bigger fragments had significantly higher growth rates for the different time intervals considered. In other words, the length of time it took a fragment to double its weight decrease steadily with larger fragment size. Figure 2 shows for each studied species, the mean growth rates of the fragments as a function of their mean initial weight obtained at the beginning of each interval times. However, the strength of the correlation between initial weight and growth rate varied between species, and showed for most species a general increase of the significant effect of fragment sizes on growth rates through the different time intervals (Table 1). Fragments of *Echinopora* sp. did not show any

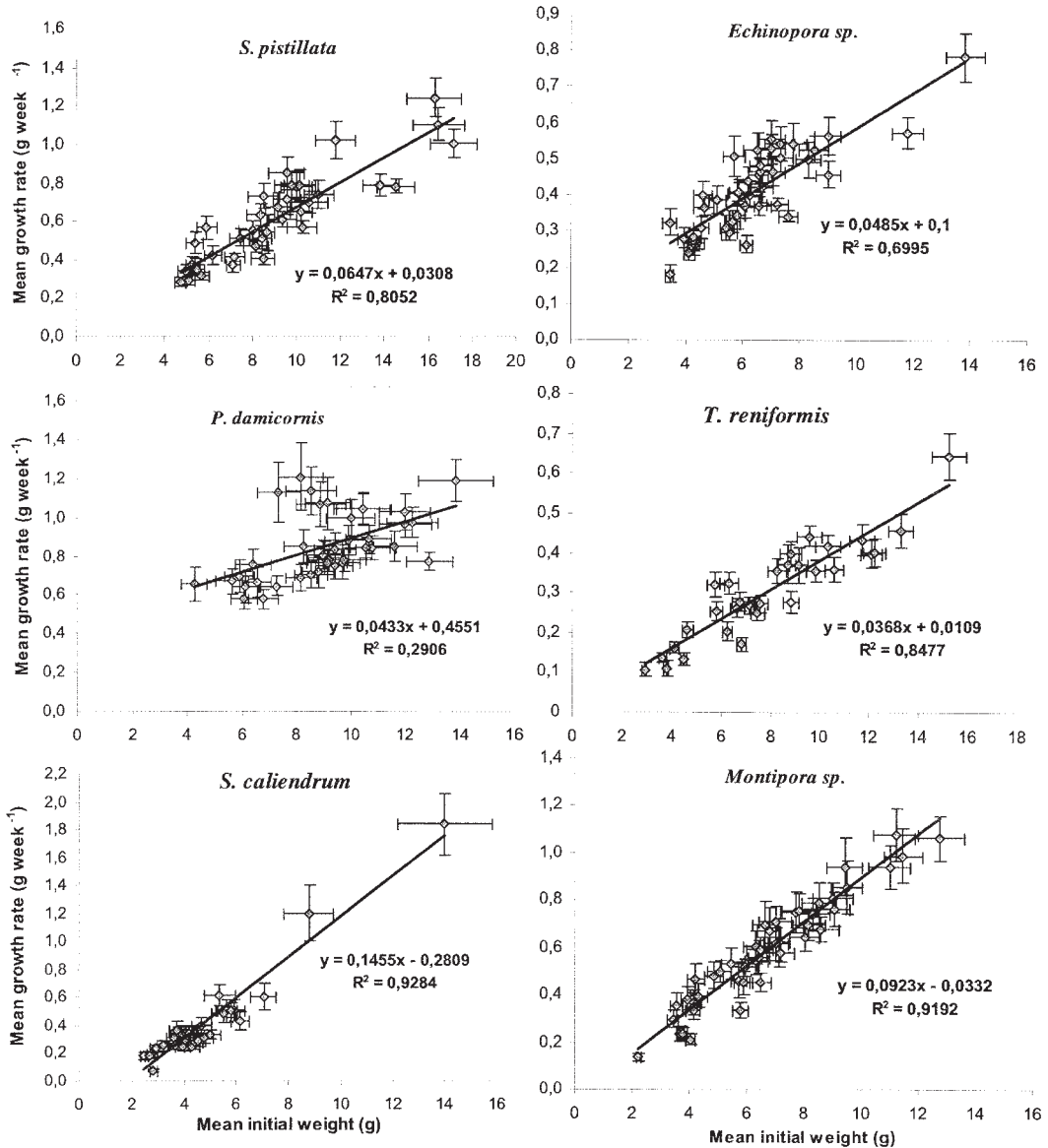


Fig. 2 Relationship between initial weight (g) and growth rate (g week<sup>-1</sup>) for each species. The error bars are the standard error.

size-dependent growth during the first 8 weeks of this study, but well for the following months. In contrast, the decrease of the significant correlation from the  $t_{12}$ - $t_{16}$  interval time obtained for *P. damicornis* results in that, 20 weeks after fragmentation, the smallest fragment growth as fast as the largest one, and coral growth did not slow down or stop as fragments grew bigger ( $p > 0.05$ ). Although

fragments of *S. caliendrum* had the smallest range of initial weight at the beginning of this study, the significant correlation between fragment sizes and growth rates was observed to be stronger than that of the other species (higher correlation coefficient).

Table 1. Growth rate and correlation between initial weight and growth rate for different time intervals over our 6-month survey. Pearson correlation coefficient ; \* : 5% significance levels, \*\* : 1% significance levels, and ns : non-significant relationship

Species	N	Time interval					
		$t_0-t_8$	$t_8-t_{12}$	$t_{12}-t_{16}$	$t_{16}-t_{20}$	$t_{20}-t_{25}$	
T. reniformis	30	Initial weigh (g)	2.5 to 10.9	2.6 to 12.2	2.7 to 15.3	3.1 to 17.7	3.8 to 20.2
		Growth rate (g/wk)	0.013 to 0.263	0.00 to 0.775	0.05 to 0.625	0.013 to 0.675	0.20 to 1.06
		Pearson corr. coeff. (r)	0.60**	0.71**	0.69**	0.83**	0.89**
Echinopora sp.	43	Initial weigh (g)	1.7 to 8.6	2.3 to 11.0	3.2 to 13.3	4.1 to 16.7	4.5 to 19.6
		Growth rate (g/wk)	0.05 to 0.325	0.05 to 0.675	0.1 to 0.85	0.10 to 0.875	0.24 to 1.46
		Pearson corr. coeff. (r)	0.25ns	0.40**	0.55**	0.72**	0.59**
Montipora sp.	46	Initial weigh (g)	1.6 to 6.6	1.8 to 8.6	2.1 to 11.3	2.5 to 16.4	3.2 to 21.0
		Growth rate (g/wk)	0.025 to 0.363	0.025 to 0.875	0.075 to 1.275	0.175 to 1.15	0.3 to 2.32
		Pearson corr. coeff. (r)	0.50**	0.66**	0.77**	0.83**	0.82**
S. caliendrum	30	Initial weigh (g)	1.5 to 4.5	1.9 to 7.0	2.2 to 11.0	2.7 to 18.4	3.5 to 29.1
		Growth rate (g/wk)	0.00 to 0.313	0.075 to 1.00	0.125 to 1.850	0.00 to 2.675	0.04 to 3.36
		Pearson corr. coeff. (r)	0.80**	0.82**	0.84**	0.92**	0.92**
S. pistillata	37	Initial weigh (g)	2.7 to 10.0	3.6 to 12.9	4.6 to 15.6	5.5 to 21.5	7.0 to 27.1
		Growth rate (g/wk)	0.088 to 0.50	0.1 to 1.2	0.15 to 1.65	0.20 to 1.55	0.38 to 1.86
		Pearson corr. coeff. (r)	0.62**	0.61**	0.84**	0.71**	0.68**
P. damicornis	39	Initial weigh (g)	1.4 to 6.9	2.1 to 9.4	3.5 to 12.1	5.8 to 20.8	8.5 to 24.5
		Growth rate (g/wk)	0.05 to 0.45	0.35 to 1.25	0.35 to 2.175	0.625 to 1.725	0.86 to 2.98
		Pearson corr. coeff. (r)	0.34*	0.48**	0.52**	0.28ns	0.09ns

## 4. Discussion

### 4.1. Growth rate variation between species and growth forms

An early exponential growth in colonial organisms such as corals reflects the ability of each polyp (clone) to produce new polyps (SEBENS, 1987). The subsequent linear increases observed in growth rate over time (Fig. 1) may reflect the absence of predation or competition for space as the species considered in this study have grown under optimal conditions.

The differences in the growth rate gradients observed between the studied species might reflect the difference in their life history traits. *P. damicornis*, *S. pistillata*, and *Montipora* sp. are opportunist species (strategy *r*) with rapid growth rates and a great capacity to colonise new environment (LOYA, 1976a, b : SOROKIN, 1995 : CONNELL *et al.* 1997 : SPRUNG, 2000 : VERON, 2000). In contrast, *S. caliendrum*, *Echinopora* sp., and *T. reniformis* use an intermediate strategy and can therefore show characteristics that are more related to a strategy

$\kappa$  (SOROKIN, 1995). Moreover, our results indicate that branched species have a higher ability in regeneration than foliaceous species. This is consistent with previous observations (LOYA, 1976b : HALL, 1997). This difference in growth rate gradients might also be explained by (i) the greater surface-to-volume ration of branched species, and (ii) the difference in skeleton density between species in the fact that it may incur a large drain of resources (HALL, 1997), hence slowing down the growth of dense skeleton fragments. For example, while the branched coral *Acroporas* shows a much dense skeleton at the base than at the tip resulting in a fast addition of a fine porous layer of tissue and skeleton at the growing end of its branches, the massive coral *A. palifera*, which has a slower rate of regeneration compared to the branched species *Acroporas*, do not show such axial gradient in skeletal density and have a dense column from base to tip (HALL, 1997). However, this is still debated in the literature as BOSSCHER (1993) showed an inverse relationship in the extension rate and

the skeletal density of colonies of *Montastrea annularis*, while ANTHONY *et al.* (2002) suggest that skeletal density may have only a minor effect on energetic investment during the linear extension of a colony. In this study, the thickness of the skeleton was observed to vary as follow: *T. reniformis* > *Montipora* sp. > *Echinopora* sp. for the foliaceous species, and *S. pistillata* > *P. damicornis* > *S. caliendrum* for the branches species.

#### 4.2. Growth rate variation between fragment size

We identified a size-dependence in growth rates at different time intervals for most of the species investigated, i.e. larger fragments show higher growth rates. However, fragments of *Echinopora* sp. and especially *P. damicornis* did not show the same trends as the other species studied here. The non significant relationship between growth rates and initial weight of fragments of *Echinopora* sp. found at the interval t0-t8 may be due to the fact that all fragments were too small to show any differences in growth rates, or that they may need a longer time interval for recovering from fragmentation. In contrast, we showed that 16 weeks after fragmentation, and therefore after reaching a weight ranging from 5.8 to 20.8 g, all fragments of *P. damicornis* growth well and fast whatever their size. KINZIE and SARMIENTO (1986) found similar results in *P. damicornis* analysing the skeletal extension rate of branches of colonies from 1.9 to 19 cm in diameter. Moreover, RODGERS *et al.* (2003) found that after fragmentation, the survival rates of the fragments were size- and species-dependent. In their study, they found that, 11 months after fragmentation induced by experimental trampling *in situ*, only 5 % of the small fragments of *Montipora capitata* survived compared to 77 % of larger ones. However, the difference in survival rates for fragments of *Pocillopora meandrina* was not highly related to the size of the fragment since 70 to 78 % of fragment survivorship was found for the small size class (< 5 cm) to the larger one (> 5 cm), respectively. The fact that fragments of *S. pistillata*, *S. caliendrum*, *Montipora* sp., *Echinopora* sp. (after 8 weeks) and *T.*

*reniformis* showed growth rates dependent on their initial weight over time might reflect a variability in their growth rate throughout their lifetime, with growth accelerating with fragment size (LOYA, 1976b). Moreover, the fact that this relationship between growth rate and size was positive may also reflect a genetic limitation on maximum size which may allow to these species an adaptation to breakage (HUGHES and JACKSON, 1985). Although this is hard to tell yet here as this study cover only a 6 month period growth under cultivated conditions, *S. pistillata* is a well known studied species and was found to asexually reproduce by fragmentation in the Gulf of Eilat (Red Sea) (LOYA, 1976b).

For some species, the weak correlations observed between growth rates and fragment size at some interval times suggests that factors other than initial size might have influenced the growth rates of the fragments. As this study was performed under fully controlled conditions, these factors might then include differences in e.g. shape and/or genetic composition. Colony or fragment size, as well as the shape of a colony, are critical parameters likely to impact the physiology and ecology of a coral species (SEBENS, 1987 : KIM and LASKER, 1998). The energetic investment between tissue and skeletal vary according to the colony size, with for example, colonies with small radius branches showing a greater allocation to tissue formation than to skeletal formation, and inversely for colonies with thicker branches (ANTHONY *et al.*, 2002). The allocation of resource to skeleton extension may not be the same in every parts of the colony at the same time (MARTIN and LE TISSIER, 1988). A modelling approach of a branching colony showed that small-scale resource translocation in a coral colony has potential effects on the morphology of the colony and this may be regulated by the so-called 'polyp competition hypothesis' (MERKS *et al.*, 2004). This phenomenon might also be related to species-specific architectural constraints and be genetically regulated. Finally, as abiotic mechanisms is important in the explanation of the morphological patterns in corals (MERKS *et al.*, 2003, 2004), small colonies may be more



affected by disturbances than larger colonies. For instance, a massive coral species will be less affected by strong wave action than a thin branched coral species (RIEGL and RIEGL, 1996 : RODGERS *et al.*, 2003 : CROS and McCLANAHAN, 2003).

#### 4.3. Fragment size and coral transplantation

Colony size in corals has been often associated with survivorship, growth, and reproduction (e.g. HIGHSMITH, 1982 : LOYA, 1976b : BABCOCK, 1991) and many scleractinian corals with size-dependent growth/or survivorship/or mortality has been already investigated (e.g. *Acropora pulchra* (SOONG and CHEN, 2003), *S. pistillata* (LOYA, 1976b : VAGO *et al.*, 1997), *Fungia granulose* (CHADWICK-FURMAN *et al.*, 2000), *Balanophyllia europaea* (GOFFREDO *et al.*, 2004), *Agaricia agaricite*, *A. lamarcki*, *Leptoseris cucullata*, *Montastrea annularis*, *Porites astreoides* (HUGHES and JACKSON, 1985)). In the wild, larger colonies have showed a better capacity to resist invasion and damage (LOYA, 1976b), as well as to have higher fecundity and lower mortality than smaller colonies (BABCOCK, 1991), i.e. the probability for a small colony to be completely kill is greater than that for a larger one (HUGHES and JACKSON, 1985 : BABCOCK, 1991). SOONG and CHEN (2003) showed that very small fragment (e.g. 1 cm) of *Acropora* were too small to use for coral transplantation, but that fragment of intermediate size (e.g. 4 cm) was bigger enough to generate high growth rates and therefore had better potential of survivorship. In EDWARDS & CLARK (1998), by comparing many studies involving size-dependent survivorship, they argue that it is hard and dangerous to make a general frame for coral transplantation. Moreover, it was showed that growth rates of fragments highly vary from site and species (CRUZ-PINON *et al.*, 2003 : DIZON and YAP, 2006). Moreover, transplanted colonies was found to show lower growth rate than undisturbed colonies (YAP and GOMEZ, 1985) at least in the short term (0.5 to 1 year after fragmentation) (EDWARDS & CLARK, 1998) and therefore it may suggest considering a longer time of recover, such as in tanks or in shallow water (mariculture), before

transplantation. It is clear from our results that, in general, bigger colonies should be used in coral transplantation. However, although the success of transplanted fragments in the wild are depending on many other factors (e.g. type of substrate, wave action (RIEGL and RIEGL, 1996), predation (CROS and McCLANAHAN, 2003)), we believe, as suggested by LIRMAN (2000), that size may still affect the long term survivorship of fragments.

#### 5. Conclusions

Although growth rates was showed to vary between the six studied species with general lower growth rates obtained for foliaceous species, the optimal conditions investigated in this study results in that for all species growth rates increased through time. Branched species such as *S. pistillata* and *P. damicornis*, or those belonging to the genera *Acropora* showing high growth rates and recruiting well, have therefore often been used in many transplantation studies (see EDWARDS and CLARK, 1998). This is, in our knowledge, not the case for foliaceous species such as *Montipora* sp., *Echinopora* sp., and *T. reniformis*. However, if we want to enhance coral biodiversity in areas where transplantation is justify, all species have to be considered. This may need previous knowledge on the abiotic and biotic parameters of the transplantation area, as well as the life history traits (SEEBAUER, 2001) of potential species justified to be transplanted. Only one recent study on transplantation did involve different species of various growth form (DIZON and YAP, 2006). However, in the case where donor colonies may be hard to be supply culturing fragments in optimal conditions may be an option to supply transplants (EDWARDS and CLARK, 1998) of size big enough to minimize the risk of mortality after transplantation. Many (ornamental) coral species have seen to grow well in some Aquarium (pers. observations). Those Aquarium Centres have often yet well established materials for growing fragments, so a solution may be to find a certain agreement (or trade-off) between a short term lucrative coral trade and a long term sustainable coral management.

## Acknowledgements

I gratefully thanks J. Mallefet who supervised this research and for all his support, advices and help all along this study. I thanks S. Hénard and N. Hirel for use of the facilities of Nausicaä and the discovering of the sphere of Aquariums. I thanks all the staff of Nausicaä for their help with the handling of corals. I especially thanks L. Seuront for his helpful advices and corrections of this manuscript, as well as J. Mitchell and L. Seuront for suggesting me to write this manuscript. This study was part of a Master research partially funded by the Catholic University of Louvain (UCL). JM is research associate F.N.R.S.

## References

- ANTHONY, K.R.N., S.R. CONNOLLY, and B.L. WILLIS (2002) : Comparative analysis of energy allocation to tissue and skeletal growth in corals. *Limnol. Oceanogr.*, **47**, 1417-1429.
- BABCOCK, R.C. (1991) : Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecological Monographs*, **61**, 225-244.
- BOSSCHER, H. (1993) : Computerized tomography and skeletal density of coral skeletons. *Coral Reefs*, **12**, 97-103.
- BOWDEN-KERBY, A. (2003) : Coral transplantation and restocking to accelerate the recovery of coral reef habitats and fisheries resources within no-take marine protected areas : hands-on approaches to support community-based coral reef management. *International Tropical Marine Ecosystems Management Symposium 2*, Manila, Philippines, pp 15.
- BRUNO, J.F. (1998) : Fragmentation in *Madracis mirabilis* (Duchassaing and Michelotti) : how common is size-specific fragment survivorship in corals? *J. Exp. Mar. Biol. Ecol.*, **230**, 169-181.
- CHADWICK-FURMAN, N.E., S. GOFFREDO, and Y. LOYA (2000) : Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. *J. Exp. Mar. Biol. Ecol.*, **249**, 199-218.
- CONNELL, J. H., T. P. HUGHES, and C. C. WALLACE (1997) : A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Mono.*, **67**, 461-488.
- CROS, A. and T. McCLANAHAN (2003) : Coral transplant damage under various management conditions in the Mombasa Marine National Park, Kenya. *Western Indian Ocean J. Mar. Sci.*, **2**, 127-136.
- CRUZ-PINON, G., J.P. CARRICART-GANIVET, and J. ESPINOZA-AVALOS (2003) : Monthly skeletal extension rates of the hermatypic corals *Montastraea annularis* and *Montastraea faveolata* : biological and environmental controls. *Marine Biology*, **143**, 491-500.
- DELAHAYE, B. (2003) : Croissance des coraux au Nausicaä. *Rapport du Nausicaä*, pp 39.
- DIZON, R.T. and H.T. YAP (2006) : Effects of coral transplantation in sites of varying distances and environmental conditions. *Marine Biology*, **148**, 933-943.
- EDWARDS, A.J. and S. CLARK (1998) : Coral transplantation : a useful management tool or misguided meddling? *Mar. Poll. Bull.*, **37**, 8-12.
- FABRICIUS, K.E. (2005) : Effects of terrestrial runoff on the ecology of corals and coral reefs : review and synthesis. *Mar. Poll. Bull.*, **50**, 125-146.
- GOFFREDO, S., G. MATTIOLI, and ZACCANTI F. (2004) : Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). *Coral Reefs*, **23**, 433-445.
- HALL, V.R. (1997) : Interspecies differences in the generation of artificial injuries on scleractinian corals. *J. Exp. Mar. Biol. Ecol.*, **212**, 9-23.
- HIGHSMITH, R.C., A.C. RIGGS, and C.M. D'ANTONIO (1980) : Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia*, **46**, 322-329.
- HIGHSMITH, R.C. (1982) : Reproduction by fragmentation in corals. *Mar. Ecol. Progr. Ser.*, **7**, 207-226.
- HUGHES, T.P. and J.B.C. JACKSON (1985) : Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.*, **55**, 141-166.
- HUGHES, T.P. and J.H. CONNELL (1999) : Multiple stressors on coral reefs : a long-term perspective. Part 2 : The effects of multiple stressors on freshwater and Marine Ecosystems. *Limnol. Oceanogr.*, **44**, 932-940.
- HUGHES, T.P., A.H. BAIRD, D.R. BELLWOOD, M., CARD, S.R. CONNOLLY, C., FOLKE, R., GROSBERG, O., HOEGH-GULDBERG, J.B.C., JACKSON, J., Kleypas, J.M. LOUGH, P. MARSHALL, M. NYSTROM, S.R. PALUMBI, J.M. PANDOLFI, B. ROSEN, and J. ROUGHGARDEN (2003) : Climate change, human impacts, and the resilience of coral reefs. *Review. Science*, **301**, 929-933.
- KARLSON, R.H. (1988) : Size-dependent growth in two zoanthid species : a contrast in clonal strategies. *Ecology*, **69**, 1219-1232.
- KIM K., and H.R. LASKER (1998) : Allometry of resource capture in colonial cnidarians and constraints on modular growth. *Funct. Ecol.*, **12**, 646-654.
- KINZIE, R.A. and T. SARMIENTO (1986) : Linear extension rate is independent of colony size in the coral



- Pocillopora damicornis*. Coral Reefs, **4**, 177–181.
- LINDAHL, U. (2003) : Coral reef rehabilitation through transplantation of staghorn corals : effects of artificial stabilization and mechanical damages. Coral Reefs, **22**, 217–223.
- LIRMAN, D. (2000) : Fragmentation in the branching coral *Acropora palmata* (Lamarck) : growth, survivorship, and reproduction of colonies and fragments. J. Exp. Mar. Biol. Ecol., **251**, 41–57.
- LOYA, Y. (1976a) : The Red Sea coral *Stylophora pistillata* is an r strategist. Nature, **259**, 478–480.
- LOYA, Y. (1976b) : Skel *et al* regeneration in a Red Sea scleractinian coral population. Nature, **261**, 490–491.
- MARTIN, D.A. and A. LE TISSIER (1988) : The growth and formation of branch tips of *Pocillopora damicornis* (Linnaeus). J. Exp. Mar. Biol. Ecol., **124**, 115–131.
- MCCLANAHAN, T., POLUNIN, N. and T. DONC (2002) : Ecological states and resilience of coral reefs. Conserv. Ecol., **6**, 1–18.
- MERKS, R.M.H., A.G., HOEKSTRA, J.A. KAANDORP, and SLOOT. (2003) : Models of coral growth : spontaneous branching, compactification and the Laplacian growth assumption. J. Theor. Biol., **224**, 153–166.
- MERKS R.M.H., A.G. HOEKSTRA, J.A. KAANDORP, and P. SLOOT. (2004) : Polyp oriented modelling of coral growth. J. Theor. Biol., **228**, 559–576.
- OREN, U. and Y. BENAHAJU (1997) : Transplantation of juvenile corals : a new approach for enhancing colonization of artificial reefs. Marine Biology, **127** : 499–505.
- ORTIZ PROSPER, A.L. (2005) : Population dynamics of hurricane-generated fragments of Elkhorn coral *Acropora palmata* (Lamarck, 1816). PhD thesis in Marine Sciences (Biological Oceanography). University of Puerto Rico Mayaguez Campus. pp 74.
- RIEGL, B. and A. RIEGL (1996) : How episodic coral breakage can determine community structure : a South African coral reef example. Marine Ecology, **17**, 399–410.
- RODGERS, K., E. COX, and C. NEWSTON (2003) : Effects of mechanical fracturing and experimental trampling on Hawaiian corals. Environmental Management, **31**, 377–384.
- SEBENS, K.P. (1987) : The ecology of indeterminate growth in animals. Ann. Rev. Ecol. Syst., **18**, 371–407.
- SEEBAUER, J. (2001) : Zoology of *Porites cylindrical* : potential for use in reef-rehabilitation transplantation efforts. SUNY Geneseo J. Sci. Math., **2**, 26–34.
- SOONG, K. and T. CHEN (2003) : Coral transplantation: regeneration and growth of *Acropora* fragments in a nursery. Rest. Ecol., **11**, 62–71.
- SOROKIN, Y.I. (1995) : Coral Reef Ecology. Springer-Verlag Heidelberg, Germany. Ecological Studies, **102**, pp 465.
- SPRUNG, J. (2000) : Coraux, guide pratique d'identification et de maintenance. Collection Océanographie. Ricordea Publishing Miami, Floride, USA. pp 244.
- VAGO, R., Z., DUBINSKY, A. GENIN, M. BEN-ZION, and Z. KIZNER (1997) : Growth rates of three symbiotic corals in the Red Sea. Limnol. Oceanogr., **42**, 1814–1819.
- VERON, J.E.N. (2000) : Corals of the world. Volume 1, 2, 3. Australian Institute of Marine Science.
- WALLACE, C.C. (1985) : Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Mar. Biol., **88**, 212–233.
- YAP, H.T. and E.D. GOMEZ (1985) : Growth of *Acropora pulchra*. III. Preliminary observations on the effects of transplantation and sediment on the growth and survival of transplants. Mar. Biol., **87**, 203–209.
- YAP, H.T. and R.A. MOLINA (2003) : Comparison of coral growth and survival under enclosed, semi-natural conditions and in the field. Mar. Poll. Bull., **46**, 858–864.

Received July 12, 2006  
Accepted October 17, 2006