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Growth of the bryozoan *Pentapora fascialis* (Cheilostomata, Ascophora) around submarine freshwater springs in the Adriatic Sea

S. COCITO, M. NOVOSEL, Z. PASARIĆ & M.M. KEY, Jr.

A b s t r a c t : Colony growth, size and mortality of the bryozoan *Pentapora fascialis* (Cheilostomata, Ascophora) growing in the vicinity of submarine freshwater springs at Grmac (north-eastern Adriatic Sea) have been analysed. Throughout a one year period (June 2002 - June 2003), repeated measurements of length and width of the living and necrotic parts of six colonies tagged with a steel stick were made. Notwithstanding the sharp variability of colony sizes recorded, *P. fascialis* mainly grew during the colder months (October to March) which coincide with the springs' highest discharge. A mean growth rate of 9.8 cm per year (± 4.0) was estimated. Numerous events of colony necrosis and fragmentation, maybe due to fragility of the carbonate colony, occurred throughout the one year period.

K e y w o r d s : Bryozoa, *Pentapora fascialis*, growth rates, submarine freshwater spring, vrulja, Adriatic Sea

Introduction

It has been reported that high concentrations of CO_2, bicarbonate, and nutrients around submarine freshwater springs in the north-eastern Adriatic Sea may provide optimal growth conditions for the carbonate producing bryozoan *Pentapora fascialis* (PALLAS 1776) (NOVOSEL et al. 2004). It is the dominant component of the benthos around the springs. CO_2 and bicarbonate are the building material for the carbonate skeleton of the bryozoan, whereas nutrients are a food source for the plankton which the bryozoan actively filters. Furthermore, these submarine freshwater springs, called 'vruljas', provide a low and constant seawater temperature as well as a strong and steady current throughout the year which enhances feeding and minimizes sediment accumulation on the colony.

While non-colonial organisms often have an upper size limit depending on their age, colonies, which add more and more genetically identical individuals to a single structure, may theoretically live and grow forever and in some cases reach large size (PALUMBI & JACKSON 1983). HAYWARD & MCKINNEY (2002) described *P. fascialis* as the largest and most conspicuous calcified bryozoan in the northern Adriatic, with mound-like colonies up to 30 cm in diameter. It grows in exposed positions, on cobbles and boulders, and attached to gorgonian stalks or flexible bryozoans. In the close vicinity of the vruljas, under the influence of their outflow, the bryozoan develops unusually large colonies (mean diameter 65.8 ± 21 cm) (COCITO et al. 2004). There, the largest bryozoan colony size ever registered was found (diameter 100 cm). A recent record by NOVOSEL (2005) reported the presence of large colonies (diameter 50 to 80 cm) of the same species in the southern Adriatic Sea, in a narrow passage between two small islands characterised by constant and strong currents, but in a locality without vruljas. To date, field-based studies on growth rates of *P. fascialis* have been performed only in the Ligurian Sea (northwestern Mediterranean) (COCITO et al. 1998).

One of the most direct ways to measure colony growth rates is under laboratory conditions, but bryozoans are generally difficult to culture, and large, long-lived species have never been maintained in the laboratory for more than a few weeks (SMITH et al. 2001). Moreover, for large, fragile erect growth forms breakage during handling is a problem.

Growth dynamics of benthic species, particularly of colonial species, have usually been studied in the field using non-destructive methods, such as underwater photography. For erect species photography provides quantitative information on 2-dimensional variation of surface area covering the substrate, but measurements, such as extension rates of branched species, are more difficult (SGORBINI et al. 1996). As alternative solutions to the problem, other non-destructive methods have been used in the field: staining with Alizarin (SCHILLER 1993; BARNES 1995; COCITO & FERDEGHINI 1998) or Calcein (SMITH et al. 2001), and tagging with nylon tags (COCITO & FERDEGHINI 1998) or steel needle (CRUZ-PIÑON et al. 2003).

The aim of this study is to determine growth rates of the large carbonate producing bryozoan *P. fascialis* in its natural setting with a non-destructive method. Analysing the occurrence of unusually large colonies and the almost exclusive presence of the species around submarine freshwater springs in the karstic area of the northeastern Adriatic Sea is of great ecological relevance, both because it allows new insights on the biology of a large carbonate producing bryozoan and because quantification of these bioconstructions help in contributing to the carbonate budget evaluation for the Adriatic Sea. We here analyse growth, size and mortality, which are critical for understanding the biology of clonal organisms.

Materials and methods

Velebit Channel, in the northeastern part of the Adriatic Sea, is a heavily karstified area where numerous submarine freshwater springs (or vruljas) are present (COCITO et al. 2004; NOVOSEL et al. 2004). Due to large quantities of freshwater inflow, the water in the Velebit Channel is characterized by 3 psu lower salinity and 1.5 to 3.0°C lower surface temperatures than outside the channel (SUPIĆ & ORLIĆ 1992; ORLIĆ et al. 2000). The temperature of the vruljas' outflow is low (10.5°C ± 0.3) and varies minimally throughout the year between about 10 and 14°C, while the temperature of ambient sea water varies throughout the year between about 8 and 24°C (15.1°C ± 3.7) (NOVOSEL et al. 2004).

Pentapora fascialis colonies were surveyed in the field by SCUBA diving at the locality of Grmac (44°52'41''N, 14°53'33''E), 5 km south of Sv. Juraj town (Fig. 1). At Grmac the coast is rocky and steep, and the cliff comprises a more or less vertical wall from 25 m below sea level to 20 m above.

In May 2002, on the rocky bottom from 20 to 23 m depth, six colonies of *P. fascialis* growing in the vicinity of vruljas outflow were selected. A stainless steel rod (0.3 cm in diameter and 50 cm long) was inserted along the main growth axis of each colony. Throughout a one year period, until June 2003, eight repeated measurements of the distance from the tip of each stick to the distal growing tip of the colony were made using a calliper (1 mm precision). Length and width of the living and necrotic parts of each colony were measured. Since *P. fascialis* is a colonial filter feeding animal, it has been considered that the 'area' (cm^2), i.e. length (both of living and necrotic parts of which each colony is composed) times width, is a better indicator of colony size. Net change in living colony area was calculated as the change of the living part of colonies. Three arbitrarily chosen periods of growth were analysed: the three month summer period (June 2002 to September 2002), the six month fall-winter period (September 2002 to March 2003) and 12 month period (June 2002 to June 2003).

Results

The general appearance of the living parts of the colonies was bright orange with extruded lophophores during winter and spring. In contrast, during the summer and autumn, the colonies were pale orange with retracted lophophores, and partially covered by sediment and epibionts. Epibionts included algae, mainly Dictyotales, the serpulid *Salmacina dysteri*, and bryozoans (*Aetea truncata*, *Beania magellanica*, *B. mirabilis*, *Bugula fulva*, *Diplosolen obelia* and *Patinella radiata*). Epibionts mainly affected the side of the colony away from the vruljas outflow. Furthermore, living parts of the colonies always faced toward the vruljas. Another feature of *Pentapora fascialis* found near the vruljas was breakage of the colonies, probably due to their fragility and probably caused by strong currents. Colony fragments were seen lying at the base of the cliff on the sandy bottom.

Of the six colonies tagged, only five were included in this study as colony one was never found. Tables 1, 2 and 3 report length (cm) of the living and necrotic parts, and width (cm) of the entire colonies (living and necrotic combined) of *P. fascialis* measured in the field from May 2002 to June 2003. By measuring increment of colonies' length and width, a mean growth rate of approximately 9.8 (± 4.0) cm per year was determined for *P. fascialis* in vruljas habitats. Interestingly, our measurements showed that *P. fascialis* growth rate was identical both into the length and the width of the colonies, since both measurements showed it grew about 9.8 cm per year.

The area of living and necrotic parts of the colonies did not show any clear temporal patterns (Fig. 2). However, during spring (March to May 2003) all colonies showed the largest area, while in summer (June to September 2002) both living and necrotic area of the colonies declined. Colonies 3 and 4 between June and September 2002 displayed a much smaller area than the other colonies. By March 2003, all the colonies were bigger than they were six months earlier. During the remainder of the year, particularly from March 2003 to May 2003, colonies 1 and 3 were reduced in area. Colonies 2, 4 and 5, during the rest of 2003 retained their same approximate area of both living and necrotic parts.

Analysis of change in colony area over time is illustrated in Tables 4 and 5. From June 2002 to September 2002, colony area, both of the whole colony (i.e. living plus necrotic parts) (Tab. 4) and of the living part (Tab. 5) decreased for three of the five colonies. When examining longer time frames, i.e., six months (from September 2002 to March

2003) and twelve months (July 2002 to July 2003), colony area, both of the whole colony and living part, increased for all five colonies (Tab. 4-5).

Discussion

Results showed that *Pentapora fascialis* colonies in the Velebit Channel grew very fast, despite frequent breakages. It could be hypothesised that this marked growth is due to the large quantities of carbonates and nutrients provided by the vruljas' outflows (NOVOSEL et al. 2004). Large carbonate colonies, such as *P. fascialis*, benefit from the rich source of building materials from the vruljas. Furthermore, low salinities and dissolved oxygen could result in fewer predators near the vruljas which may add to the fast growth rates, and the high current flows allow for less energetically costly feeding. These may be partially offset by the fragility of the colonies since numerous breakages were observed. Colony fragmentation could also be a method of asexual dispersal for *P. fascialis* (sensu MCKINNEY 1983) dispersal since broken parts of the colonies often continue to grow (Novosel, pers. obs.).

Our data suggest one of the fastest bryozoan growth rates ever recorded (9.8 cm/yr). By comparison, growth rate measurements performed in other localities showed about 3 cm/yr growth rate for *P. fascialis* from the Ligurian Sea, Italy (COCITO & FERDEGHINI 1998) and approximately 2 cm/yr for *P. foliacea* from the Bristol Channel, UK (PÄTZOLD et al. 1987), later classified by HAYWARD & RYLAND (1999) as the same species of *P. fascialis*. Published growth rate data for *P. fascialis* and other bryozoans are shown in Tab. 6.

The highly variable colony sizes observed during the one year of measurements made data interpretation difficult. The change in size of the living part of a colony resulted from two opposing processes: growth of newer parts of the colony and destruction of older ones. The increase in the size of the necrotic parts resulted from transformation of living parts to necrotic parts, whereas the decrease in the size of the necrotic parts resulted from breakage of the pre-existing necrotic parts. Such events are difficult to systematically observe, unless, for example, a permanent underwater still camera or video camera is used.

Pentapora fascialis colonies mainly grew during the colder months of the year, namely from September to March, which coincides with the vruljas' highest discharges (NOVOSEL et al. 2004). Together with the increase of the ambient seawater temperature and decrease of vruljas activity, namely from May to September, colonies showed the slowest growth and greatest breakage.

A number of factors are known to influence growth rates in sessile suspension-feeders. Quantity and quality of suspended food particles, degree of seasonal thermal variation and, specifically for carbonate bryozoans, the concentration of CO_2 and bicarbonate affect the development of colony size (MCKINNEY & JACKSON 1989). Field experiments should be addressed to better understand the prevailing influence of single environmental factors and to explain interactions among them in relation to the observed growth pattern within a peculiar environment such as that represented by submarine freshwater springs in the north-eastern Adriatic Sea.

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Resumé

Croissance du carbonate bryozoaire *Pentapora fascialis* (Cheilostomata, Ascophora) près des émissions sous-marines d'eau douce dans la mer Adriatique. La croissance, la taille et la mortalité du carbonate bryozoaire *Pentapora fascialis* qui se développe près des émissions sous-marines d'eau douce à Grmac au nord-est de la mer Adriatique, ont été analysées. Pendant une année (Juin 2002 – Juin 2003), plusieurs mesures de la longueur et de la largeur des zones vivantes et nécrotiques des six colonies marquées avec une baguette d'acier ont été relevées. Malgré la grande variabilité de la taille des colonies, la croissance de *P. fascialis* s'est effectuée principalement la période la plus froide qui coïncide avec la plus forte activité des émissions sous-marines d'eau douce. Il a été estimé une croissance moyenne de 9.8 cm (± 3.96) par an. De nombreux évènements de nécrose et de fragmentation des colonies, qui sont probablement dus à la fragilité du squelette de carbonate, ont été enregistrés pendant cette année d'observations.

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Author's addresses:

S. COCITO
ENEA Marine Environment Research Centre
P.O. Box 224, I-19100 La Spezia, Italy
E-mail: silvia.cocito@santateresa.enea.it

Dr. Maja NOVOSEL
Faculty of Science, Dept. of Biology
Rooseveltov trg 6, HR-10000 Zagreb, Croatia
& Ecological Research Society Paks
Vojnovićeva 19, HR-10362 Kašina, Croatia

Z. PASARIĆ
Faculty of Science, Dept. of Geophysics
Horvatovac bb, HR-10000 Zagreb, Croatia

M.M. KEY Jr.
Dept. of Geology, Dickinson College
P.O. Box 1773
Carlisle, PA 17013-2896, USA

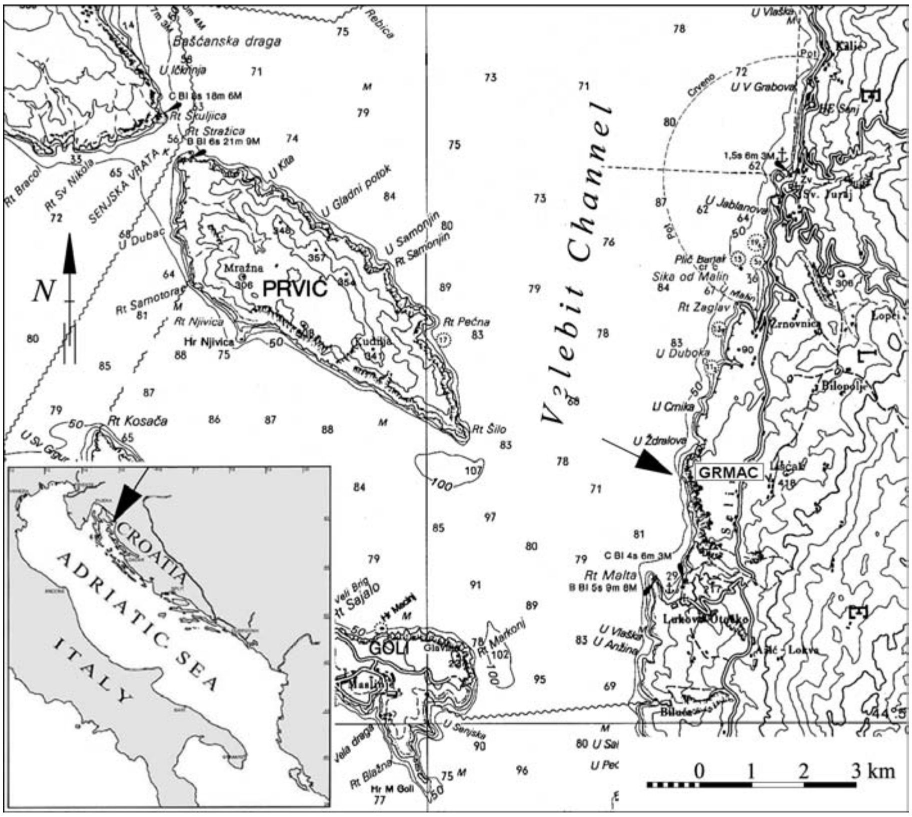

Fig. 1: The eastern Adriatic Sea with a detailed map of the study location.

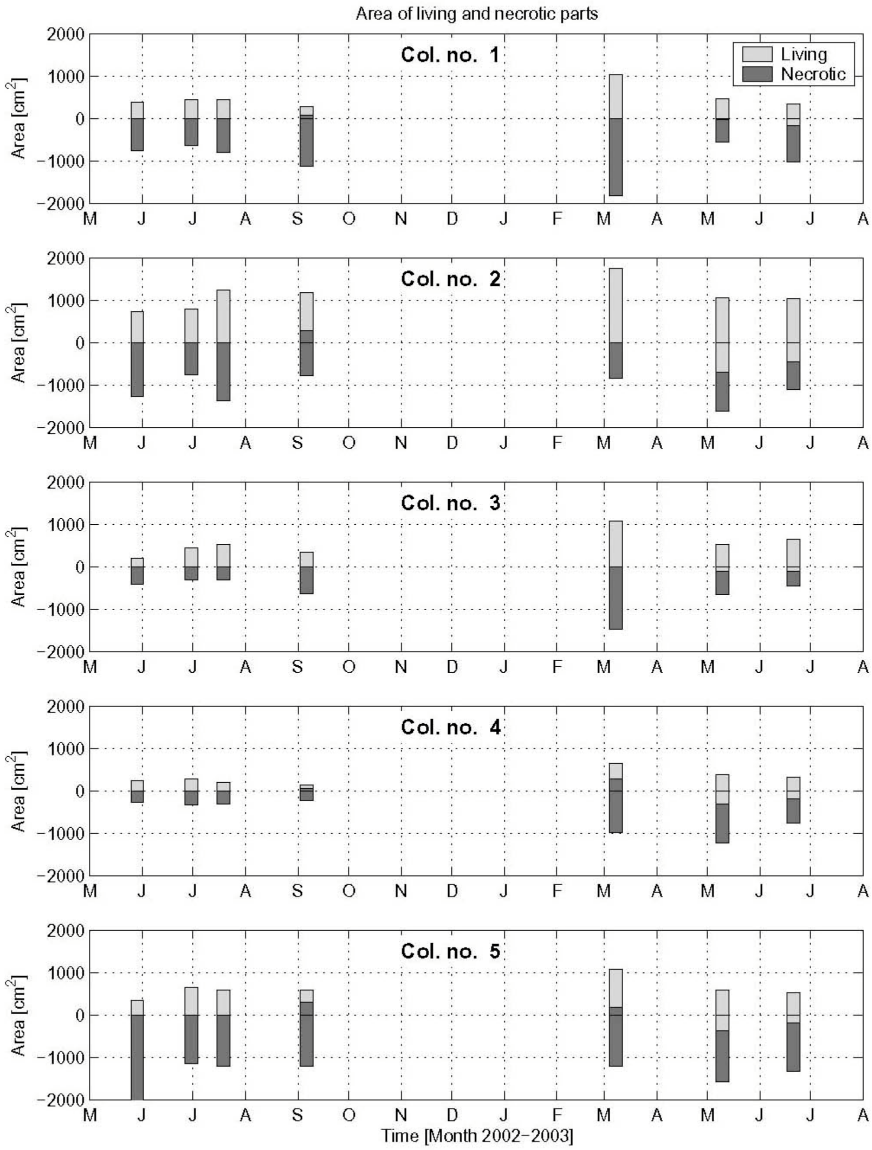

Fig. 2: Area variations (cm^2) of living and necrotic parts of the five colonies of *Pentapora fascialis* monitored from June 2002 to June 2003.

Table 1: Summary statistics for the length (cm) of the living part of the colonies of *P. fascialis* measured in the field from May 2002 to June 2003. SD = standard deviation of the arithmetic mean.

Colony number	May 02	June 02	July 02	Sept 02	March 03	May 03	June 03	Min	Mean	Max	SD
1	10.0	10.0	10.0	5.0	16.0	14.0	15.0	5.0	11.4	16.0	3.8
2	14.0	16.0	19.0	13.0	25.0	25.0	23.0	13.0	19.3	25.0	5.1
3	9.0	15.0	35.0	10.0	27.0	24.0	27.0	9.0	21.0	35.0	9.8
4	8.0	9.0	10.0	5.0	10.0	18.0	17.0	5.0	11.0	18.0	4.8
5	7.0	11.0	10.0	5.0	15.0	16.0	12.0	5.0	11.0	16.0	4.0
Min	7.0	9.0	10.0	5.0	10.0	14.0	12.0				
Mean	9.6	12.2	16.8	7.6	18.6	19.4	18.8				
Max	14.0	16.0	35.0	13.0	27.0	25.0	27.0				
SD	2.7	3.1	10.9	3.7	7.2	4.9	6.1				

Table 2: Summary statistics for the length (cm) of the necrotic part of the colonies of *P. fascialis* measured in the field from May 2002 to June 2003. SD = standard deviation of the arithmetic mean.

Colony number	May 02	June 02	July 02	Sept 02	March 03	May 03	June 03	Min	Mean	Max	SD
1	20.0	14.0	18.0	30.0	28.0	15.0	24.0	14.0	21.3	30.0	6.2
2	24.0	15.0	21.0	15.0	12.0	13.0	10.0	10.0	15.7	24.0	5.0
3	19.0	10.0	20.0	18.0	37.0	21.0	12.0	10.0	19.6	37.0	8.7
4	9.0	10.0	15.0	19.0	35.0	24.0	20.0	9.0	18.9	35.0	8.9
5	42.0	19.0	20.0	25.0	23.0	20.0	19.0	19.0	24.0	42.0	8.2
Min	9.0	10.0	15.0	15.0	12.0	13.0	13.0				
Mean	22.8	13.6	18.8	21.4	27.0	18.6	17.0				
Max	42.0	19.0	21.0	30.0	37.0	24.0	24.0				
SD	12.1	3.8	2.4	6.0	10.1	4.5	5.8				

Table 3: Summary statistics for the width (cm) of the living and necrotic parts colonies of *P. fascialis* measured in the field from May 2002 to June 2003. SD = standard deviation of the arithmetic mean.

Colony number	May 02	June 02	July 02	Sept 02	March 03	May 03	June 03	Min	Mean	Max	SD
1	38.0	45.0	45.0	40.0	65.0	35.0	35.0	35.0	43.3	65.0	10.4
2	53.0	50.0	65.0	70.0	70.0	70.0	65.0	50.0	63.3	70.0	8.4
3	22.0	30.0	15.0	35.0	40.0	26.0	28.0	15.0	28.0	40.0	8.2
4	30.0	32.0	20.0	15.0	36.0	38.0	29.0	15.0	28.6	38.0	8.3
5	50.0	60.0	60.0	60.0	60.0	60.0	60.0	50.0	58.6	60.0	3.8
Min	22.0	30.0	15.0	15.0	36.0	26.0	28.0				
Mean	38.6	43.4	41.0	44.0	54.2	45.8	43.4				
Max	53.0	60.0	65.0	70.0	70.0	70.0	65.0				
SD	13.1	12.6	22.7	21.6	15.3	18.4	17.7				

Table 4: Change in living and necrotic colony area (cm^2) as defined by length x width for three, six and twelve month periods for the five colonies of *Pentapora fascialis*. SD = standard deviation of the arithmetic mean.

Colony number	3 months June 2002 – Sept 2002	6 months Sept 2002 – March 2003	12 months July 2002 – July 2003
1	260	1460	285
2	- 54	630	595
3	364	1580	342
4	- 150	1260	465
5	- 650	480	60
Min	- 650	480	60
Mean	- 46	1082	349
Max	260	1580	595
SD	399	497	201

Table 5: Net change in living colony area (cm^2) as defined by length x width of living area for three, six and twelve month periods for the five colonies of *Pentapora fascialis*. SD = standard deviation of the arithmetic mean.

Colony number	3 months June 2002 – Sept 2002	6 months Sept 2002 – March 2003	12 months July 2002 – July 2003
1	- 180	840	75
2	168	840	695
3	152	730	306
4	- 165	285	205
5	- 50	600	205
Min	-180	285	75
Mean	- 15	659	297
Max	168	840	695
SD	168	231	237

Table 6: Published growth rate data for *Pentapora fascialis* and other bryozoans.

Species	Growth rate (cm/yr)	Source
Pentapora foliacea	2.0	Pätzold et al. (1987)
Pentapora fascialis	0.2-3.5	Cocito and Ferdeghini (1998)
Pentapora fascialis	9.8	This study
Adeonellopsis sp.	1.0	Smith et al. (2001)
Cellaria incula	0.8	Brey et al. (1999)
Cellaria sinuosa	3.2	Bader and Schäfer (2005)
Cellaria sinuosa	4.0	Bäder (2000)
Cellarinella watersi	0.5	Barnes (1995)
Flustra foliacea	1.2	Stebbing (1971)
Flustra foliacea	2.0	Eggleston (1972)
Melicerita obliqua	0.5	Brey et al. (1998)