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Recruitment, growth, mortality and orientation patterns of *Balanus trigonus* (Crustacea: Cirripedia) during succession on fouling plates*

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SUMMARY: Succession studies on artificial substrates in the Bay of Santa Marta, Colombian Caribbean showed *Balanus trigonus* (Darwin) as one of the more prominent members of the fouling community. This fact prompted the interest for a closer examination of its biology. Four aspects were touched upon: recruitment, growth and mortality rates, and orientation with respect to the horizon line. Two hypotheses were tested. First, that orientation of individuals was random within the orientation range observed during succession, and second, that there was no relationship between orientation and age of the individuals. Larvae settling was found to occur throughout the year but with a well delimited peak in the dry season (January to April). The availability of competent larvae is reflected in the abundance of the species during succession. Growth and mortality proceed rapidly. Maximal growth (6.2 mm average carino-rostral distance) is reached in 20 weeks after settlement. Mortality is substantial: 50% of recruits, on average, died after 3-4 weeks from settlement. Orientation at settlement was found to be not random: for instance, 64% of individuals orientated between 0º-60º from the horizon. With age the orientation patterns at settlement changed statistically. Biological and ecological implications of these findings are discussed and comparisons made with other studies. It is concluded that *Balanus trigonus* could act as a model species for latitudinal comparisons in view of its wide distribution, adaptability and sessile habit.

Key words: Cirripedia, *Balanus trigonus,* population dynamics, orientation

RESUMEN: PATRONES DE RECLUTAMIENTO, CRECIMIENTO, MORTALIDAD Y ORIENTACIÓN DE *BALANUS TRIGONUS* (CRUSTACEA: CIRRIPEDIA) DURANTE SUCESIÓN EN PLACAS DE 'FOULING'. – En el curso de un estudio sobre sucesión en sustratos artificiales en la Bahía de Santa Marta, Caribe colombiano, se encontró que *Balanus trigonus* (Darwin) era uno de los miembros más prominentes de la comunidad de 'fouling' que se desarrolló sobre los sustratos. La oportunidad se aprovechó para tocar cuatro aspectos de la biología de *B. trigonus* según se manifestaron en la población de los sustratos: reclutamiento, tasas de crecimiento y mortalidad, y orientación respecto a la línea del horizonte. Se probaron dos hipótesis: primero, que la orientación de los individuos dentro del rango de orientaciones encontrado es al azar; segundo, que la orientación es independiente de la edad de los individuos. El asentamiento de larvas cubre todo el año, si bien con un pico bien marcado en la estación seca (enero a abril). Esta disponibilidad se refleja en la abundancia de la especie durante la sucesión. Crecimiento y mortalidad son rápidos. El crecimiento máximo (6.2 mm en promedio, distancia carino-rostral) se alcanza en aproximadamente 20 semanas desde el asentamiento. La mortalidad es sustancial. En promedio 50 % de los reclutas han perecido después de 3-4 semanas del asentamiento. La orientación en el asentamiento se encontró que sigue un patrón no azaroso: por ejemplo, 64 % de los individuos se orientaron entre los 0º y los 60º del horizonte. Con la edad los patrones de orientación cambiaron estadísticamente. Se discuten las implicaciones biológicas y ecológicas de estos resultados y se compara con estudios hechos sobre la misma especie en otras latitudes. Se concluye que *Balanus trigonus* en razón a su hábito sesil, amplia distribución y capacidad de adaptación podría servir de modelo para estudios latitudinales comparativos.

Palabras claves: Cirripedia, *Balanus trigonus,* dinámica poblacional, orientación

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INTRODUCTION

During the course of an investigation on succession patterns on fouling plates, it was found that the barnacle *Balanus trigonus* was a prominent member of the sublittoral benthic community (García and Salzwedel, 1995). This finding stimulated a closer look at its population dynamics and its orientation patterns as an important aspect for sessile filter feeders.

The barnacle *Balanus trigonus* has been characterised as an opportunistic, widely distributed, sublittoral species (Ayling, 1976; Werner, 1967). According to Werner (1967) it is confined to subtropical and tropical regions. It exhibits an extended depth distribution with records as deep as 3000 m (Werner, 1967, and references therein). In the Colombian Caribbean it has been reported from depths up to 50 m (Young and Campos, 1988).

Balanus trigonus reproduces throughout the year. Recruitment, however, shows seasonal peaks (Werner, 1967; Williams *et al.*, 1984). Sexual maturity may be reached in less than three weeks from settlement (Ayling, 1976; Werner, 1967). Under rearing conditions, *B. trigonus* can produce 11 broods yr^{-1} with an average of 6000 embryos $brood^{-1}$, and was observed to be a self-fertilizing species (El-Komi and Kajihara, 1991).

Growth is rapid in this species. Werner (1967) found that in Florida (USA) maximal growth rates occurred until 10 weeks of life, after which growth slowed. In New Zealand, some individuals were able to reach maximal size in only 25 days (Ayling, 1976). Mortality, in turn, was found to be extremely high. Ayling (1976) reported that in her experiments 50% of the barnacles were dead after 7 to 17 days from settlement, while less than 15% remained alive after 30 days.

Ayling (1976) found that *B. trigonus* was able to orientate to water movement in order to allow for efficient food collection over a wide range of conditions. Moreover, she found that water movement was the primary orientation stimulus for this species, in contrast with the review of Crisp and Bougert (1985) who state that the effect of water currents on orientation of barnacles is negligible compared with the effect of grooves on the surface and the effect of the direction of light.

In this paper, we touch upon the referred topics of *Balanus trigonus* life history and compare our results with the results mentioned above. We also examine the relationship between orientation and mortality, assuming that suboptimal oriented individuals will have a higher probability of dying than optimally oriented individuals, as suggested by Ayling (1976).

MATERIAL AND METHODS

Fouling plates (10 x 10 cm) were fixed to a PVC frame anchored to the bottom under a pier in the Bay of Santa Marta, Colombian Caribbean (11º15'08''N; 74º13'13''W). The frame was maintained vertical by means of buoys so as to place the plates at approximately 9-m depth. Only the side of the plates facing north, i.e. into the current (Wedler, 1975), was studied. The plates were sampled biweekly in order to evaluate the biweekly potential of recruitment (plates placed at one date and retrieved two weeks latter, hereafter called recruitment plates, 26 for this study), and the colonization and succession patterns in this system (plates placed at the beginning of the experiment and retrieved every two weeks, hereafter called succession plates: 19 for this study). Sampling lasted from April 30, 1981 to April 29, 1982 (see García and Salzwedel, 1993, 1995).

Balanus trigonus was the only adult barnacle found on the plates. Therefore barnacles of all sizes were considered as belonging to this species (García and Salzwedel, 1993, 1995). Individuals were

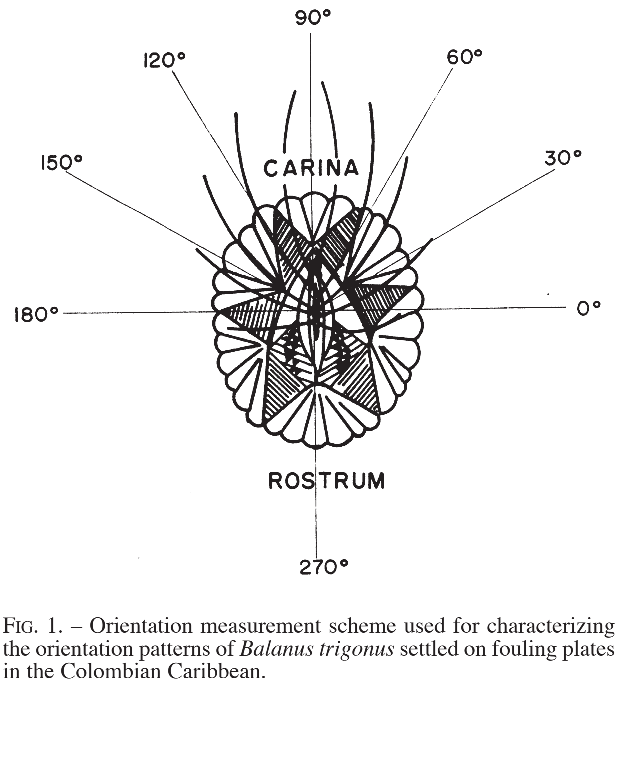

FIG. 1. – Orientation measurement scheme used for characterizing the orientation patterns of *Balanus trigonus* settled on fouling plates in the Colombian Caribbean.

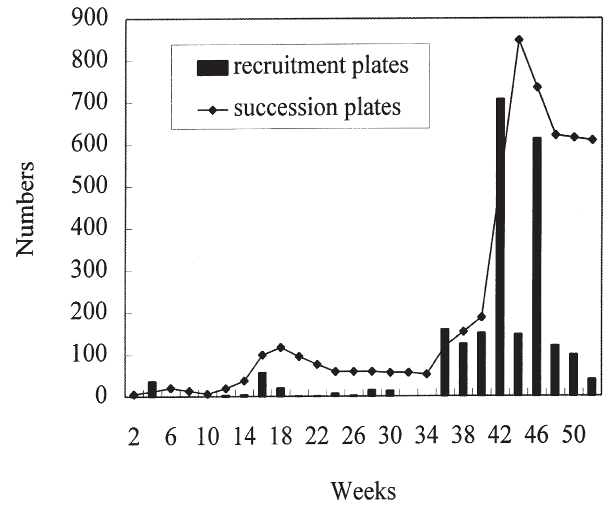

FIG. 2. – Biweekly settlement of *Balanus trigonus* on recruitment plates and relation to its abundance on succession plates.

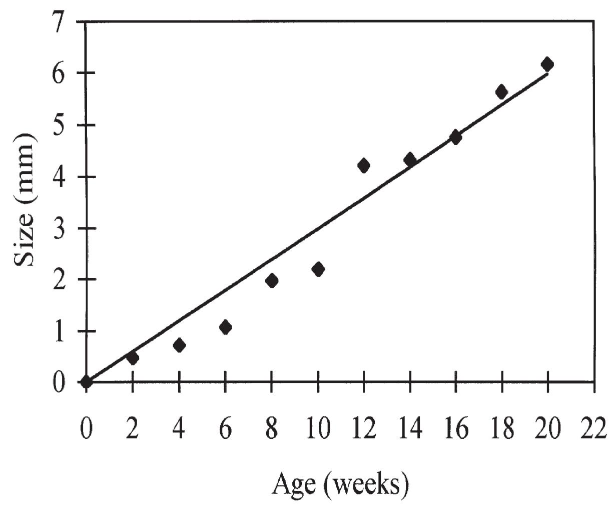

FIG. 3. – Growth curve of *Balanus trigonus*. $Y = 0.2988x$, $r^2 = 0.9579$

counted and the carino-rostral distance was measured (García and Salzwedel, 1995). The carino-rostral distance was selected as growth measurement because it better reflects growth than other distances under crowded conditions, which was the case in this particular succession (García and Salzwedel, 1995).

In order to estimate the age of individuals, we arbitrarily chose the mean carino-rostral distance of the five biggest individuals in a given succession plate as representing the size of an average individual of the age of the given plate. Thus, pairs of size-at-age data were constructed to which a linear regression model was fitted. The model was then used to estimate the age of all the individuals.

For the analysis of mortality, all the data (the population was made up of 3061 individuals) of the succession year were pooled under the assumption that reduction in numbers from one 2-week age class to the next represents mortality suffered by a cohort in the system.

Orientation is defined as the angle lying between the horizon, which represents 0°, and the carino-rostral axis. The horizon line was chosen as representing 0° (see Figure 1). Carino-rostral distance and angle measurements were done using a computerized image analysis system, not directly on the hard structures, but on the respective distances and angles translated to paper by means of a camera lucida. For this analysis 2966 individuals were considered. The difference with the population figure (3061 individuals) corresponds to detached individuals.

Two null hypothesis were tested. First, that orientation of individuals was random in the orientation range observed during succession (0°-180° in 30° orientation-categories moving to the left from 0°, see Fig. 1), and second, that there is no relationship between orientation and age of individuals. The first null hypothesis was tested by means of an one-way table. The second null hypothesis was tested by means of an orientation-category (same as before) by an abundance-at-age (1 month age classes) two-way table.

The construction and analysis of age categories of 1 month and orientation categories of 30°, were considered a good compromise, although arbitrary, between reduction of possible inaccuracy both in age estimation and angle measurements and the need of statistical testing.

RESULTS

Figure 2 shows the recruitment pattern of *Balanus trigonus* onto recruitment plates compared with the numbers of *B. trigonus* found on succession plates. It is clearly visible that the number of competent larvae shows a strong increase during weeks 36 to 52 of the experiment corresponding to the months January to April and thus to the dry season (García and Salzwedel, 1993). It is also interesting to note that recruitment pressure was reflected by the abundance of *B. trigonus* in the succession plates (Pearson correlation was 0.608, n=26, $p<0.05$).

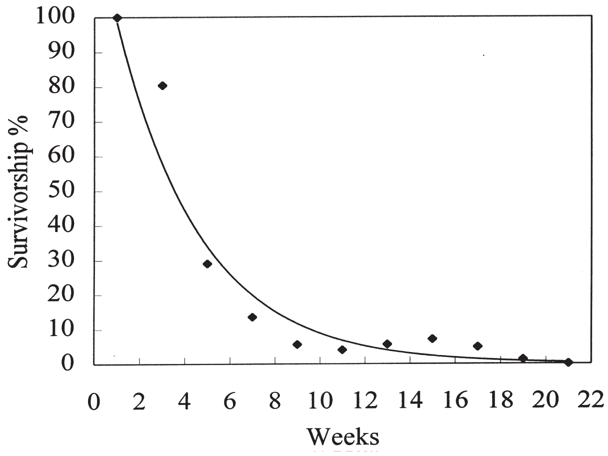

FIG. 4. – Survivorship curve of *Balanus trigonus*. Y = 1700 * EXP (-0.273), $r^2 = 0.939$

A significant association was found between orientation and age classes (chi-square= 61.12, 20 degrees of freedom, p<0.05), thus the null hypothesis that there is no relationship between orientation and age of the individuals can be rejected. Figure 5 shows the pattern of change of orientation of the individuals with age. It can be notice that as individuals grow older there is a substantial reduction in relative numbers of individuals in the orientation category 0°-30° while the contrary occurs with orientation categories 30°-60° and, in particular, in orientation category 60°-90°. Relative numbers in the orientation range 90°-180° remain consistently low and stable as individuals grow older (Figure 5).

Figure 3 shows the growth pattern of *Balanus trigonus*. Maximal mean size of about 6.2 mm carino-rostral distance was reached after 20 weeks. Figure 4 shows the survivorship curve of *B. trigonus* during succession. Note that already by week 3-4 from settlement 50% of the individuals have perished. The probability of surviving increases after week 7 from settlement (Figure 4).

Table 1 presents the overall orientation pattern of *Balanus trigonus* on the succession plates. A number of features can be noticed. Orientation of all individuals was confined to the range of 0°-180°. Inside this range orientation was not random. Orientation categories between 0° and 90° received more individuals than expected by chance while orientation categories between 90° and 180° received less individuals than expected by chance (see 0.95% confidence intervals for cell categories in Table 1).

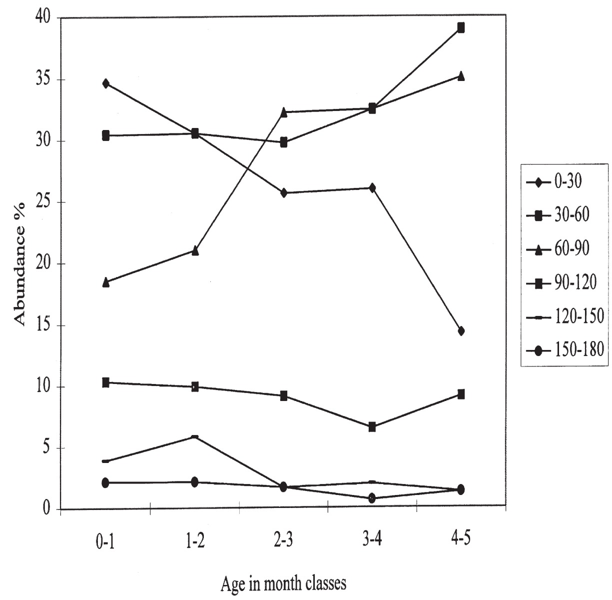

FIG. 5. – Orientation patterns of *Balanus trigonus* for 1 month age. and 30° orientation categories.

TABLE 1. – One-way table of the distribution of *Balanus trigonus* individuals into orientation categories during the colonisation of fouling plates in the Colombian Caribbean. O.C.=orientation category, C.I.= confidence intervals scaled as cell percentage. Ho= each orientation category receives 16.66% of the total of settled individuals.

O. C.	0-30°	30-60°	60-90°	90-120°	120-150°	150-180°	Total
Numbers	967	912	613	296	118	60	2966
Percentage	32.60	31.75	20.67	9.98	3.89	2.02	100
0.95 % C.I.	34.90 30.33	33.02 28.51	22.68 18.72	11.50 8.57	5.01 3.08	2.79 1.39	Ho=16.66% %

DISCUSSION

Continuous but variable recruitment for *Balanus trigonus* throughout the year was found in this study as already showed for other latitudes. In our Caribbean location, the peak of recruitment occurred between January and April. In contrast, the main recruitment peak for this species in Florida (USA) occurs in September-November, with a secondary peak in March-June (Werner, 1967). In North Carolina (USA) the recruitment peak occurs in March-May (Williams *et al*., 1984).

January to April corresponds to the dry season in the Colombian Caribbean with a drop in water temperature, an increase in salinity and the highest intensity and velocity of the trade winds causing an upwelling phenomenon (Salzwedel and Müller, 1983). Recruitment here appears to react to an opposite environmental signal compared with what happens in the other two locations: It relates to a change of water temperature from high to low, whereas in Florida and North Carolina it relates to a change from low to high. Thus, this species exhibits the same response to opposed environmental cues. The mechanisms how this happens are worth investigating. One reason why marine organisms synchronize their recruitment with higher water temperatures in the annual cycle is the concomitant reset of primary production, e.g. Starr *et al*., (1990). In our location, however, García and Salzwedel (1993) ruled out increased primary production as the trigger for reproduction and a consequent peak of recruitment (see García and Salzwedel, 1993, for an extended discussion on this point).

The interaction between the recruits and the established populations on the succession plates was discussed by García and Salzwedel (1995). They showed that recruitment pressure by this species was so intense that, regardless of the time of development of the fouling community, recruits were able to settle on the succession plates. They concluded that this was an important regulatory mechanisms in the development of this fouling community. The significant correlation between numbers of recruits on recruitment plates and residents on succession plates shown here confirms this assertion.

Growth rate of *Balanus trigonus* in our Caribbean location was comparable with growth rates in the Florida location. In both cases maximal size was reached in about 20 weeks (Werner, 1967). This contrast with the growth rate reported by Ayling (1976) in New Zealand, where individuals reached a size of over 8 mm in 3.5 weeks (25 days). Ayling (1976) used, as length measurement, the carino-rostral distance as we do in this study. That suggests that the New Zealand population is characterized by faster growing individuals which grow substantially larger than our Caribbean population (on average 6.2 mm in 20 weeks). However, because of the manner we assigned age to the individuals (see Materials and Methods) it can be argued that our growth rate underestimated the actual growth rate in the Caribbean location since there is no guarantee that the five individuals chosen, although the largest on the given plate, actually settled the first day of its exposition. Moreover, there are indications that new surfaces need some acclimation time to become attractive to larvae (Wahl, 1989). In any case, no individual was found in the study with a carino-rostral length over 8 mm. Only a comparative study tailored to that purpose would help to unravel the causes of this apparently wide variation, whether they are genetic or due to environmental conditions.

An aspect in which Ayling's (1976) observations and our observations tend to coincide is in the survivorship pattern. Mortality pressure, however, was apparently heavier in New Zealand (50% mortality after 1-2 weeks against the same mortality proportion after 3-4 weeks in our Caribbean location). But, as the case was with growth rate and because of the same reasons, the estimated mortality rate in the Caribbean location probably underestimates the actual mortality rate. If so, this would put both observations even closer.

Orientation patterns at settlement of our Caribbean population resembled those in New Zealand. As our plates were placed vertically and their surface had a random contour, we expected that the barnacles would settle with the carinal end upwards towards the light, i.e. 90º from the horizon (see Figure 1), following Crisp and Bougert (1985, and references therein), who stated that light is the second strongest stimulus of orientation at settlement in barnacles, after the direction of surface grooves. However, individuals in the age category 0-1 month settled over-proportionally in the orientation range 0º-60º (over 65% of individuals of that age in the year, Figure 5) as well as 64% of individuals of all ages (Table 1). In New Zealand, 61% (calculated from Ayling, 1976: Figure 5) of the individuals that settled in a period of three weeks on plates placed vertically like ours, settled also in approximately this orientation (exchanged axes in

Ayling's Figure 5). Taking into account that the results of Ayling (1976) were achieved conditioning the surge movement to be vertical (i.e., parallel to the light stimulus) and her general conclusion, that water movement is the primary orientation stimulus for this species (individuals orientate at 90º of water surge), it is not unreasonable to suggest that there was a vertical surge movement in our Caribbean location which together with the concurrent light stimulus, caused an orientation pattern of individuals resembling that in New Zealand. In fact, García (1991) states that the plates were placed facing into the current. Therefore, this aspect of the natural history of *Balanus trigonus* seems to be a basic feature of the species, regardless of the location.

Otway and Underwood (1987) studying the intertidal barnacle *Tesseropora rosea* mentioned three possible processes that may give rise to orientation in barnacles: (1) settlement behaviour, as already treated here, (2) rotational growth after settlement (e.g. Crisp, 1953), and (3) differential mortality. There is no report of the second process occurring in *Balanus trigonus*. Own observations of the bases of detached individuals of variable size in no case showed torsion of the radial canals.

The orientation pattern did vary between age classes (see results). The significant decline of the relative representation of individuals in the orientation category 0º-30º during aging suggest that orientation was a factor of differential mortality. The increase in the relative representation of individuals in the orientation range 30º-90º as individuals grow older, suggests an advantage for the individuals so orientated, while the stability in the relative representation of the individuals oriented in the other categories suggests that mortality operated in them independently of orientation. Thus, there seems to be a basis to assume with Ayling (1976), that orientation can in effect be both optimal and suboptimal in *Balanus trigonus*.

The life history features described confirm the general opinion (e.g. Werner, 1967; Ayling, 1976) of *Balanus trigonus* being a so called r-selected species, i.e. an opportunistic, fast growing, and early reproducing species that suffers substantial mortality. More experimental and comparative studies are necessary to complete the picture of the biology of *Balanus trigonus,* a species that because of its widespread presence and sessile habit could become a model species for latitudinal variation in a sublittoral benthic r-selected organism.

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