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The reproductive biology of *Tricnidactis errans* (Actiniaria, Haliplanellidae) from rocky shore of Mar del Plata (Argentina)

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Abstract: *Tricnidactis errans* from Mar del Plata propagates asexually by pedal laceration. Dynamics of asexual propagation was evaluated. Frequency of laceration and number of lacerates per individual showed a correlation with seasonal changes in mean seawater temperature; the highest rate of fragmentation was observed after the maximum water temperature (February-March). *T. errans* exhibited a clear annual cycle of gametogenesis, but sterile and almost exclusively female specimens were found. Both of them propagate asexually by pedal laceration, producing a similar number of fragments. Asexual reproduction by pedal laceration appears to be the sole mean of propagation in the examined aggregation.

Résumé : *Tricnidactis errans* à Mar del Plata présente une multiplication asexuée par lacération pédieuse. La dynamique de ce processus a été étudiée. La fréquence de lacération et le nombre de fragments produits par individu sont correlés à des changements saisonniers de la température moyenne de la mer ; la production de fragments est maximum après la plus haute température (février-mars). *T. errans* a un cycle annuel de gamétogenèse durant l'été ; cependant à Mar del Plata cette espèce ne montre que des individus stériles et des individus qui sont presque tous femelles. Tous présentent une lacération pédieuse et produisent un nombre similaire de petits fragments. Il semble que la reproduction asexuée par lacération pédieuse soit le seul mode de reproduction dans l'agrégat étudié.

Keywords: Actiniaria, *Tricnidactis errans*, asexual reproduction, pedal laceration.

Introduction

The family Haliplanellidae Hand, 1956 has two monospecific genera: *Haliplanella* Hand, 1956 and *Tricnidactis* Pires, 1988. The single species of the first one, *H. lineata* (Verrill, 1869) is probably the most widely distributed intertidal sea anemone (Stephenson, 1935; Belém & Monteiro, 1977; Minasian & Mariscal, 1979; Dunn, 1982). It relies primarily upon asexual reproduction for recruitment, usually through binary longitudinal fission (Davis, 1919; Minasian, 1976). However this species displays in Japan, both longitudinal fission and pedal laceration (Atoda, 1954, 1973), and only pedal laceration in Malaysia (Dunn, op.cit.); moreover, both sexual and asexual reproductions probably take place in northern Japan (Fukui, 1991).

Tricnidactis errans Pires, 1988 (assigned to the second genus of Haliplanellidae) has been reported only from Guanabara Bay, Rio de Janeiro, reproducing by both pedal laceration and longitudinal fission (Pires, 1988).

Recently, it was found in protected sites from Mar del Plata, at an intermediary level of the intertidal zone, down to the upper limit of the infralittoral; it is somewhat gregarious, coming close to form small aggregations, and is frequently found living on mussels (Excoffon & Zamponi, 1993).

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Aspects such as rate of growth, maximum size attained, and patterns of asexual reproduction are essential characters in describing the life history of sea anemones; they may be central in determining a species' success in a particular habitat (Bucklin, 1987).

The aims of this study on an aggregation of *T. errans* from Mar del Plata, were to establish i) whether short term local recruitment is by asexual or sexual means, ii) the mode and frequency of asexual reproduction, iii) the seasonality of this reproduction and its relationship to the cycle of sexual reproduction.

Materials and methods

Monthly collections of 15 - 30 randomly sampled individuals living on the mytilid *Brachydontes rodriguezi* (d'Orbigny), were taken from a intertidal-subtidal aggregation of *Tricnidactis errans* at Punta Cantera (Mar del Plata, Argentina), (38°05'S and 57°32'W), over a total period of 28 months (February 1989 to May 1991). The studied aggregation is situated in a protected microhabitat, and it is small (no more than 900 cm^2). Mean monthly sea water temperatures were obtained from the mean daily records of water intake from Estación Mareológica, Mar del Plata. Further details on the study area are provided by Genzano (1994).

Individuals were anaesthetized and fixed in 5 % formalin in sea water. The following morphological characteristics were measured: pedal disc diameter, number of complete mesenteries, number of incomplete mesenteries, number of tentacles and number of siphonoglyphs. Individuals were examined for the presence of recognisable gonad, and gonad squashes were analized for sex determination.

Estimations of the number of fragments produced by individuals with a pedal disc diameter > 7 mm was made and the monthly mean number of pedal lacerates per individual was calculated.

Means of individual size and number of pedal lacerates in sterile and fertile individuals were compared with a Student's t-test and a non-parametric Mann-Whitney Test, respectively (Sokal & Rohlf, 1981).

Results

Asexual reproduction by pedal laceration occurred throughout the year in the studied aggregation from Mar del Plata, as indicated by the presence of lacerated fragments near individuals of *Tricnidactis errans* (fig. 1) .

A total of 344 specimens was analized, and 205 of them had pedal lacerates. They were divided into four size classes (fig. 2), ranging in pedal disc diameter from 1.0 to 19.9 mm. The species appears to be gonochoristic (Excoffon & Zamponi, 1993), but the sampled population contained mainly female and immature individuals. All the individuals

Figure 1. Individuals of *T. errans* and fragments asexually produced by pedal laceration (arrow), on a mytilid *Brachydontes rodriguezi*. Bar = 2.5 mm.

Figure 1. Plusieurs individus de *Tricnidactis errans* et de petits fragments produits par lacération pédieuse (flèche), fixés sur une coquille du bivalve *Brachydontes rodriguezi*. Echelle = 2,5 mm.

less than 5.0 mm across were sexually immature. The size range for female anemones was 5.0 - 19.9 mm; mean sizes were for immature 7.3 ± 2.0 mm (n = 219) and for females 8.7 ± 1.5 mm (n = 72). These figures are significantly different ($P<0.01$; $t = 5.48$).

The internal symmetry of most specimens was irregular implying that they were asexually produced, with the 2nd

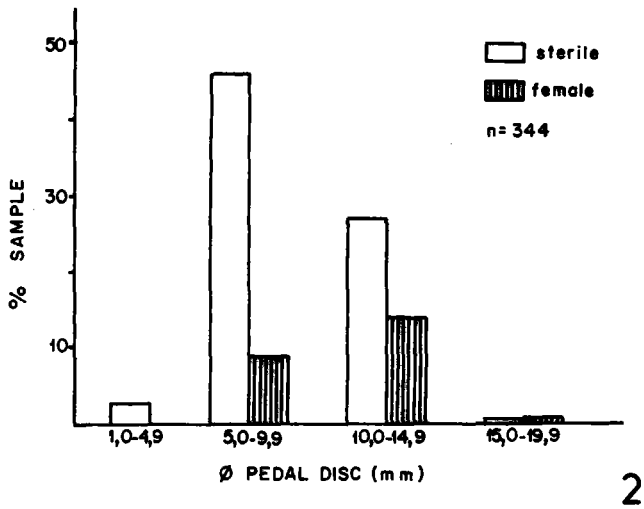

Figure 2. Sexual composition of the studied population of *T. errans* in the four size classes.

Figure 2. Proportions des individus immatures et des femelles dans la population étudiée de *T. errans*, dans les quatre classes de taille.

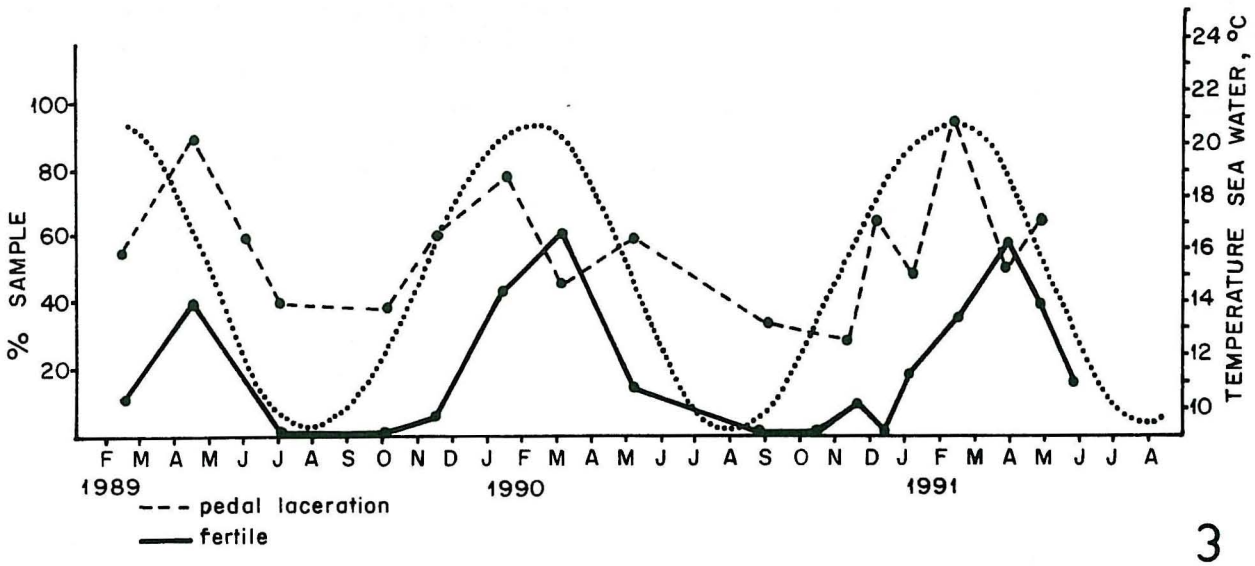

Figure 3. Percentages of female (= fertile) and asexually reproducing *T. errans* through the year, between February 1989 and May 1991, and mean sea water temperature over the same period (dotted line).

Figure 3. Variations quantitatives, chez *T. errans*, des pourcentages de spécimens femelles (= fertiles) et de spécimens montrant une lacération pédieuse, entre février 1989 et mai 1991. La ligne en pointillés indique la température moyenne de l'eau de mer.

and 3rd cycles fertile (Excoffon & Zamponi, 1993). However, *T. errans* exhibited a well defined annual cycle of gametogenesis, during December to May (fig. 3), but the proportion of sexually mature individuals in *T. errans* was only 62 %, and almost all of them were females. Both immature and females propagate asexually by pedal laceration: during the summer months (December to April), the proportion of individuals with lacerated fragments increased rapidly, from 29 % to 96 %, and was strongly temperature dependent (fig. 3). Similarly, mean numbers of recently

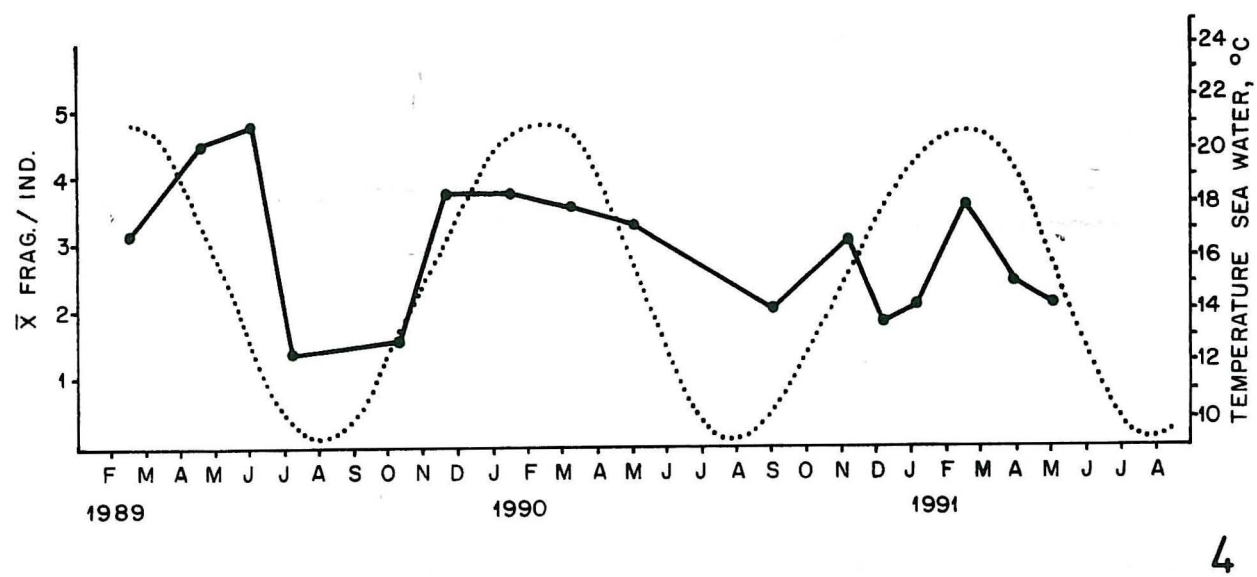

Figure 4. Mean number of recently lacerated fragments per individual, in monthly samples of *T. errans* collected between February 1989 and May 1991, and mean sea water temperature over the same period (dotted line).

Figure 4. Moyennes du nombre de fragments récents produits par individu de *T. errans*, entre février 1989 et mai 1991. La ligne en pointillés indique la température moyenne de l'eau de mer.

lacerated fragments varied from 1.3 to 4.0 fragments per individual, peaking between November and May (fig. 4).

The mean number of pedal lacerates of immature and fertile individuals were compared for the samples collected in February and April 1989, January and Mars 1990, Mars and April 1991. The rates of pedal laceration of both sterile and fertile *T. errans* were nearly constant for these periods; mean number of fragments from sterile specimens was 1.77, and from fertile specimens 2.17. These differences were not significant ($P<0.05$) by the Mann-Whitney Test.

Discussion

In *Tricnidactis errans* from Mar del Plata the only asexual reproduction method observed was pedal laceration, while both longitudinal fission and pedal laceration was suggested for the same species by Pires (1988) in a population from Rio de Janeiro.

While *T. errans* reproduces asexually throughout the year, *Pseudoparactis tenuicollis* Mc Murrich, 1904, reproduces actively by pedal laceration only in spring in Mar del Plata. In this species, the number of lacerated pieces from one adult varies from 1 to 6 with an average of two fragments (Zamponi, 1979).

Miyawaki (1952) considered temperature as an important factor in the process of longitudinal fission in *H. lineata*, a species that belongs to the same family as *T. errans*. Atoda (1973) reported, in *H. lineata*, the increase of pedal laceration when sea water temperature rises, and a decrease of laceration when this parameter goes down below 20°C. These data have been confirmed by Minasian (1979, 1982), Minasian & Mariscal (1979) who, after considering the significant increase of fission in *H. lineata* exposed to very small changes in temperature, within a very narrow range, concluded that temperature is the main exogenous factor which affects the fission rate.

In *T. errans*, the increase in number of asexually reproducing individuals and of fragments produced by pedal laceration are related to increasing temperatures during summer. Thus, the population growth by this asexual mechanism during this period is extremely important.

Other exogenous factors that, together with temperature, affect the fission activity in sea anemones are the availability of food or feeding frequency and the cyclic periods of emersion (Johnson & Shick, 1977).

Minasian (1979) observed that in *Haliplanella lineata* the fission rate is optimized at the expense of gametogenesis, an idea already expressed by Uchida (1932) who related asexual reproduction to young specimens and sexual reproduction to adults. Conversely, in *Gonactinia prolifera* Sars, 1851, sterile as well as fertile specimens have asexual reproduction (Chia, *et al.*, 1989), as observed in *Tricnidactis errans*.

Another outstanding aspect was that the size of the dividing specimens did not affect the number of produced fragments. Although there was a significant difference in basal diameters between fertile and sterile specimens, the numbers of fragments produced by both groups were similar. Minasian (1976) also found that fission in *Haliplanella lineata* was independent of size and this was also observed in *Anthopleura elegantissima* Brandt (Francis, 1976).

In *Sagartia elegans* (Dalyell), a gonochoric sea anemone that also propagates asexually by pedal laceration, the proportion of sexually mature individuals was only 63 % (Shaw, 1989), as in *T. errans*. This author suggests that this is almost certainly the result of pedal laceration, which produces individuals below the minimum size required to support gonad production.

Fertile specimens in the aggregation studied here consists almost exclusively of females. Although the species is gonochoric, male specimens were very rare (only 2 individuals out of a total of 346) and they probably are tranferred from other aggregations. Actually, the sampled population of *T. errans* is higher than a few other subtidal aggregations of the same species, located at a distance between 20 and 70 meters and with individuals of both sexes (personal unpublished data). A transfer of male specimens could be explained by the fact that the species is epibiotic, usually living on the mytilid *Brachydontes rodriguezi* which could be dislodged by wave exposure and carried along by currents in other places.

In *Haliplanella lineata*, the frequent occurrence of local populations comprising individuals of only one sex appears to result from asexually produced descendants from a few founder specimens (unisexuality of clones) (Shick, 1991).

In the light of such data it has been concluded that during winter months the studied aggregation of *T. errans* consists of immature individuals, the third of which reproducing asexually and producing a reduced number of fragments (mean of about 1.5 fragments per individual). When sea water temperature rises, the proportion of specimens with pedal laceration increases as does the number of fragments produced. During this period, gametogenesis in the largest individuals starts and fertile specimens (females), are found, the majority of them reproducing asexually. Although being larger and investing energy in the production of gametes, they still produce a number of fragments similar to that of sterile specimens.

In the intertidal of Mar del Plata, *Tricnidactis errans* appears to spread strictly by asexual reproduction to form clones, the sexes being represented in separate populations; this pattern is similar to that of others sea anemones Mesomyaria (Schmidt, 1972), such as *Haliplanella lineata* (Shick and Lamb, 1977) and *Metridium exilis* Hand (Bucklin, 1987).

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References

Atoda, K., 1954. The development of the sea anemone, Diadumene luciae, reproduced by pedal laceration. *Scientific Reports of the Tohoku University*, **2** : 123-129.

Atoda, K., 1973. Pedal laceration of the sea anemone, *Haliplanella luciae*. *Publications of the Seto Marine Biological Laboratory (Proceedings of the Second International Symposium on Cnidaria)*, **20** : 299-310.

Belém, M.J.C. & D.C. Monteiro, 1977. Contribuições ao conhecimento da fauna de cnidarios do Rio de Janeiro. II. *Haliplanella luciae* (Verrill, 1898) (Actiniaria, Acontiaria) uma nova ocorrencia no Brasil. *Avulso Universidad Federal do Rio de Janeiro. Departamento de Zoologia,* **26** : 1-19.

Bucklin, A., 1987. Growth and asexual reproduction of the sea anemone *Metridium*: comparative laboratory studies of three species. *Journal of Experimental Marine Biology and Ecology,* **110** : 41-52.

Chia, F.S., J. Lützen & I. Svane, 1989. Sexual reproduction and larval morphology of the primitive anthozoan *Gonactinia prolifera* M. Sars. *Journal of Experimental Marine Biology and Ecology*, **127** : 13-24.

Davis, D.W., 1919. Asexual multiplication and regeneration in *Sagartia luciae* (Verrill). *Journal of Experimental Zoology*, **28** : 161-263.

Dunn, D.G., 1982. Sexual reproduction of two intertidal sea anemones (Coelenterata: Actiniaria) in Malaysia. *Biotropica*, **14** : 262-271.

Excoffon, A.C. & M.O. Zamponi, 1993. Anémonas de Mar del Plata y localidades vecinas. IV. *Tricnidactis errans* Pires, 1988 (Actiniaria, Haliplanellidae). *Iheringia*, **75** : 47-53.

Francis, L., 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima. Biological Bulletin*, **150** : 361-376.

Fukui, Y., 1991. Embryonic and larval development of the sea anemone *Haliplanella lineata* from Japan. *Hydrobiologia*, **216/217** : 137-142.

Genzano, G.N., 1994. La comunidad hidroide del intermareal de Mar del Plata (Argentina). I. Estacionalidad, abundancia y períodos reproductivos. *Cahiers de Biologie Marine*, **35** : 289-303.

Johnson, L.L. & J.M. Shick, 1977. Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Verrill) in laboratory culture. *Journal of Experimental Marine Biology and Ecology*, **28** : 141-149.

Minasian, L.L., 1976. Characteristics of asexual reproduction in the sea anemone *Haliplanella luciae* (Verrill) reared in the laboratory. In *Coelenterate Ecology and Behaviour* (G.O.Mackie ed), pp 289-298. Plenum Press: New York.

Minasian, L.L., 1979. The effects of exogenous factors on morphology and asexual reproduction in laboratory cultures of the intertidal sea anemone, *Haliplanella luciae* (Verrill) (Anthozoa: Actiniaria) from Delaware. *Journal of Experimental Marine Biology and Ecology*, **40** : 235-246.

Minasian, L.L., 1982. The relationship of size and biomass to fission rate in a clon of the sea anemone, *Haliplanella luciae* (Verrill). *Ibid.*, **58** : 151-162.

Minasian, L.L. & R.N. Mariscal, 1979. Characteristics and regulation of fission activity in clonal cultures of the cosmopolitan sea anemone, *Haliplanella luciae* (Verrill). *Biological Bulletin*, **157** : 478-493.

Miyawaki, M., 1952. Temperature as a factor influencing upon the fission of the orange-striped sea anemone *Diadumene luciae. Journal of the Faculty of Science, Hokkaido Imperial University*, **11** : 77-80.

Pires, D.O., 1988. *Tricnidactis errans*, n. gen., n. sp. (Cnidaria: Actiniaria, Haliplanellidae) from Guanabara Bay, Rio de Janeiro, Brazil. *Revista Brasileira de Biologia*, **48** : 507-516.

Schmidt, H. 1972. Prodromus zu einer Monographie der Mediterranen Aktinien. *Zoologica*, Stuttgart, 42, **121** : 1-146.

Shaw, P.W., 1989. Seasonal patterns and possible long-term effectiveness of sexual reproduction in three species of sagartiid sea anemones. In *Reproduction, Genetics and Distributions of Marine Organisms* (Ryland and Tyler ed), pp 189-199. Olsen and Olsen: Fredensborg.

Shick, J.M. 1991. *A Functional Biology of Sea Anemones.* Chapman & Hall: New York. 395 pp.

Shick, J.M. & A.N. Lamb, 1977. Asexual reproduction and genetic population structure in the colonizing sea anemone *Haliplanella luciae. Biological Bulletin*, **153** : 604-617.

Sokal, R.R. & F.J. Rohlfs, 1981. *Biometry*, W.H.Freeman and Co : San Francisco. 859 pp.

Stephenson, T.A., 1935. *The British Sea Anemones.* London, Ray Society II, XI, 426 pp., 19 pls.

Uchida, T., 1932. Occurrence in Japan of *Diadumene luciae*, a remarkable actinian of rapid dispersal. *Journal of the Faculty of Science, Hokkaido Imperial University*, Ser. 6, **2** : 69-85.

Zamponi, M.O., 1979. El desarrollo asexual de *Pseudoparactis tenuicollis* Mc Murrich, 1904 (Actiniaria: Actinostolidae) y algunas consideraciones sobre su ecología. *Acta Zoológica Lilloana*, **35** : 595-602.