

**ASPECTS OF THE LIFE HISTORY
OF A STOLON-BEARING SPECIES OF *EFFLATOUNARIA*
(OCTOCORALLIA : XENIIDAE)**

**ASPECTS DE LA BIOLOGIE
D'UNE ESPECE STOLONIFERE D'*EFFLATOUNARIA*
(OCTOCORALLIA : XENIIDAE)**

Z.D. DINESEN

Australian Institute of Marine Science
P.M.B. 3, T.M.C., Townsville, QUEENSLAND 4810, AUSTRALIA

ABSTRACT

A major component of the soft coral assemblages on outershelf and midshelf reefs off Townsville, central Great Barrier Reef region, is the genus *Efflatounaria*. This xeniid soft coral propagates vegetatively by means of stolons which give rise to daughter colonies.

Subpopulations of an *Efflatounaria* species were studied between December 1980 and June 1982 at two sites at Davies Reef (18°50'S, 147°39'E), one site having overall a comparatively higher density of *Efflatounaria* than the other site. Using maps derived principally from stereophotographs taken at approximately two-monthly intervals, rates of natality (i.e. production of new colonies) and mortality, and changes in relative abundance, were followed in 1 m² plots at 5m and at 10m below l.w.d. (at both sites), and at high and low densities of colonies within plots (at Site 1 only).

Vegetative propagation was observed year-round irrespective of sexual reproductive activity, new autonomous daughter colonies being produced within periods of less than two months. Three-way ANOVAs of standardized natality and mortality data indicated, *inter alia*, a significant effect of density on both natality and mortality rates. This suggests that the species' potential for rapid population increase is not realized, the higher natality rates at high densities being offset by higher mortality rates.

Efflatounaria sp. is dioecious. Release of eggs occurs in early summer (observed early December), and is not fully synchronous but is epidemic over a period of a few days. Following release, eggs remain attached to the colony exterior between the swollen polyps, and planulae are probably brooded here. Most propagules of this *Efflatounaria* species appear to be produced vegetatively, and it seems likely that sexual reproduction serves primarily to promote dispersal, and maintenance of genetic diversity.

RESUME

Le genre *Efflatounaria* est l'un des composants principaux des peuplements d'Alcyonaires dans les récifs situés au milieu et au bord externe de la marge continentale, à Townsville dans la région centrale de la Grande Barrière de. Cet Alcyonaire Xeniidae possède un mode de reproduction végétative par stolons qui donnent naissance à des colonies filles.

Des fractions de populations d'une espèce d'*Efflatounaria* ont été étudiées entre décembre 1980 et juin 1982 dans deux stations à Davies Reef (18°50'S, et 147°39'E), l'une des stations ayant une plus forte densité de population que l'autre. Les taux de natalité (c'est-à-dire la production de nouvelles colonies), de mortalité, et les variations d'abondance relative ont été suivis dans des quadrats de 1 m² à 5 m et 10 m de profondeur dans les deux stations, et dans des zones de forte densité et de faible densité dans la station 1 seulement. Ces données ont été extraites de cartes dressées essentiellement à partir de stéréophotographies prises à intervalles de deux mois environ.

La propagation par voie végétative a été observée toute l'année, indépendamment de toute activité sexuée. Les colonies filles sont produites en moins de deux mois. Une analyse de variance des données standardisées de natalité et de mortalité indique, entre autres, une action significative de la densité sur les taux de natalité et de mortalité. Cela indique que le potentiel de l'espèce pour un accroissement rapide de la population n'est pas réalisé, les taux accrus de natalité aux fortes densités de population étant compensés par des taux accrus de mortalité.

Efflatounaria sp. est dioïque. Les produits sexuels sont émis au début de l'été (observés début décembre). L'émission n'est pas synchrone mais s'étend de façon continue sur une période de plusieurs jours. Après la ponte, les oeufs restent attachés à l'extérieur de la colonie, entre les polypes distendus, et c'est probablement dans cette position que les planula sont incubées. La majorité des propagules de cette espèce d'*Efflatounaria* paraît être produite de manière végétative, et il est vraisemblable que la reproduction sexuée n'a pour rôle principal que la dispersion de l'espèce et le maintien de la variabilité génétique.

INTRODUCTION

Vegetative propagation, leading to an increase in the number of individual animals or colonies, commonly occurs in coral reef invertebrates (Bell, 1982). Several examples of colony propagation by fragmentation have been observed in the Octocorallia (e.g. Cary, 1931; Fishelson, 1973; Tursch and Tursch, 1982; Walker and Bull, 1983), but few instances have been reported of octocoral propagation by means of stolon-like outgrowths (Tursch and Tursch, 1982; Lasker, 1983). Such propagation is conspicuous in the xeniid genus Efflatounaria Gohar, which is a major component of soft coral assemblages on mid-shelf and especially outer-shelf reef slopes in the central Great Barrier Reef region (Dinesen, 1983). In a common species, Efflatounaria sp. (taxonomic description, Dinesen, in prep.) stolons usually arise from near the base of a branch or from the colony stalk. Sometimes series of several daughter colonies are formed, interlinked by straight or divided stolons. The stolons may bear polyps and are then usually attached to the substrate throughout their length. Stolons measure 2-25 mm (usually less than 5 mm) in width, and are usually several cm long (occasionally longer than 25 cm), their length sometimes exceeding the width of the parent colony (Fig. 1a).

This study investigated vegetative propagation, natality and mortality rates, and some aspects of sexual reproduction in Efflatounaria sp., to elucidate the characteristics of the species' life history and possible reasons for its great abundance in some areas.

METHODS

Two study sites were established at Davies Reef (18°50'S, 147°39'E) on the Great Barrier Reef. Site 1, with comparatively high density of Efflatounaria sp., was located on a patch reef about 200 m long on the leeward margin of the lagoon. Site 2, with lower Efflatounaria sp. density, was on a similar patch reef approximately 1 km away, within the lagoon but close to the leeward margin. In mid-December 1980, 1 m² plots were established on hard substrate at about 5 m and 10 m below low water datum. At Site 1, plots were set up with both high density (much greater than 50 colonies per square metre) and low density (less than 20 colonies per square metres) of Efflatounaria sp., but at Site 2 low density plots only could be established. Additionally, 1 m² and 9 m² 'empty' plots were set up at 10 m depth: at Site 1, all Efflatounaria sp. colonies were completely removed from these plots using a knife; at Site 2, these plots were originally devoid of the species. Two replicate were established for each of the above treatments.

Plots were photographed at intervals of about 2 months from December 1980 to June 1982, using twin Nikonos cameras and flashes mounted on a 105 cm high frame constructed of aluminium and PVC piping. Four pairs of centrally overlapping photographs were taken of each square metre, each pair showing an area 70 x 60 cm. Using a stereoscope, a series of maps was drawn for each plot recording the continued existence,

appearance or disappearance of individual colonies and stolons. The precise numbers of colonies and stolons in dense clumps and the presence of very small colonies (less than 2 cm across) were checked by visual inspection underwater. Using standardized, arcsine transformed data, six 3-way ANOVAs were carried out to investigate the effects of density, depth and time (Site 1 treatments only), and site, depth, and time (low density treatments only) on, respectively, numbers of stolons present, natality rates, and mortality rates.

Gonad development was monitored following collection of approximately 40 colonies at 5-10 m from Site 1, at monthly intervals (more frequently in early summer). Reproductive condition was assessed by dissection and from histological sections. Additional field observations were made in summer 1981, principally at Site 1.

RESULTS

Colonizing ability and origin of new colonies

New colonies tended to appear in less crowded areas of plots, stolons sometimes being directed around or even over other benthic organisms, allowing the establishment of daughter colonies on the far side of neighbours.

Since this study commenced, it has been shown that some soft coral species are capable of colony movement (Benayahu and Loya, 1981; La Barre and Coll, 1982). However, there is strong circumstantial evidence against this having occurred in Efflatounaria sp. New colonies were generally much smaller and more than 50% were first observed still linked to other colonies. Distinctive colonies remained in exactly the same location throughout the study. Furthermore, since stolons provide an efficient means of invading nearby available space, it may be argued that movement of established colonies would be superfluous.

In this species of Efflatounaria stolons often degenerate rapidly, and consequently no attempt was made to determine whether new colonies without stolon linkages arose vegetatively or from planulae (although Lasker (1983) has attempted with questionable success to do so for populations of Briareum asbestinum). However, observations indicate that most new colonies of Efflatounaria sp. arose vegetatively. Most appeared relatively close to existing Efflatounaria sp. colonies, and the majority were first observed still linked by stolons. Although some newly-settled 1-3 polyp stage xeniids (about 1 cm across; Fig. 1b) were detected at Site 1 in March 1982, none was found in any of the study plots despite rigorous inspection. Since Efflatounaria sp. colonies can attain a size of several cm across within a few months, any substantial settlement following 1980 and 1981 spawnings should have been detected, but natality rates showed no seasonal trends (see below). Moreover, only 12 new colonies appeared in cleared plots, all at plot perimeters and adjacent or still linked to colonies outside the plots. Empty plots at Site 2 remained free of Efflatounaria sp. throughout.

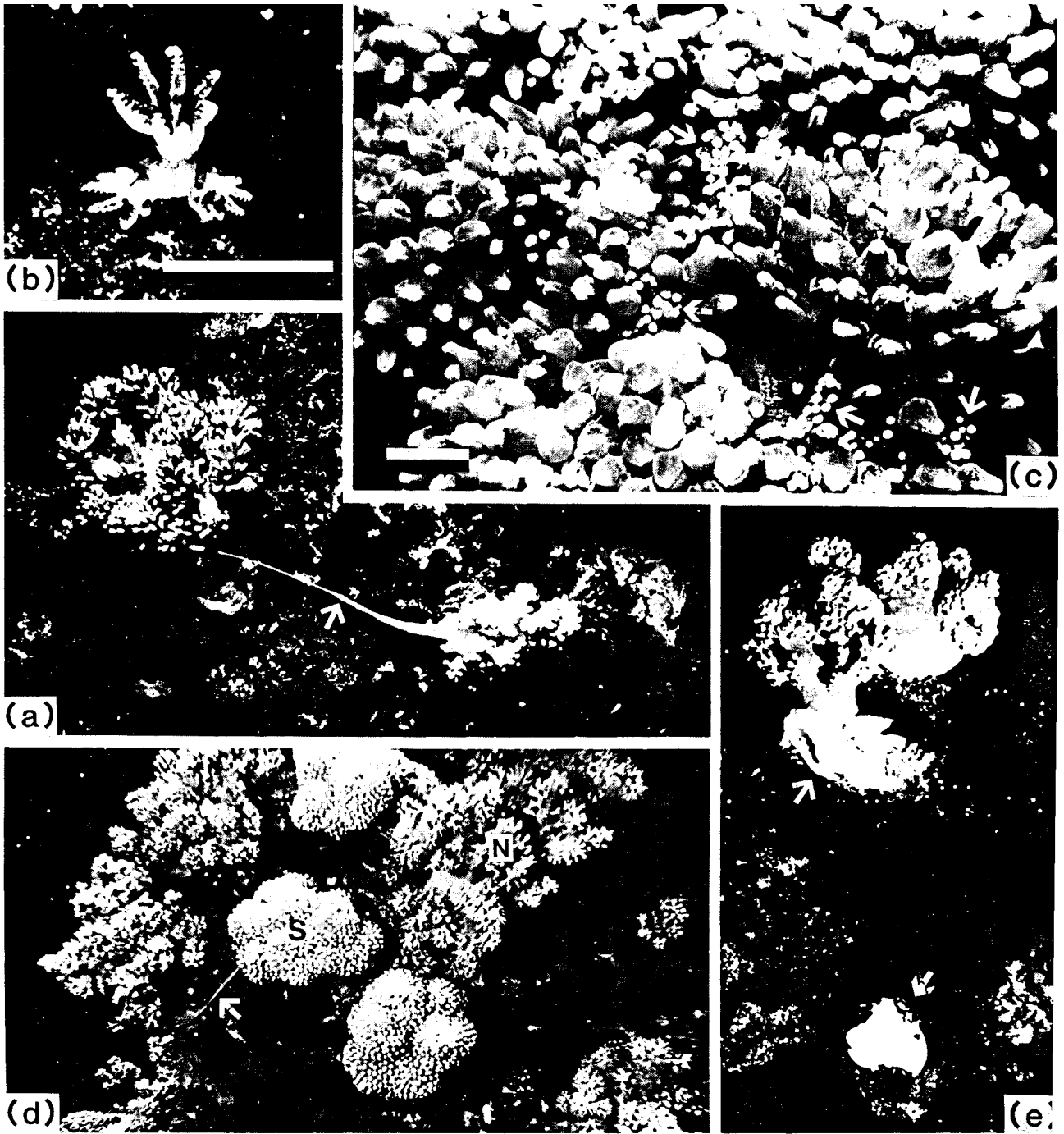


Figure 1. Eflatounaria sp. at Site 1, Davies Reef. 1a: Parent and daughter Eflatounaria sp. colonies, linked by narrow, degenerating stolon (marked with arrow). 1b: Three polyp stage xeniid, probably Eflatounaria sp. 1c: 'Swollen' Eflatounaria sp. colonies with eggs (marked with arrows) partially concealed between polyps. 1d: 'Swollen', egg-laden Eflatounaria sp. colony (marked S) linked by stolon to daughter colony (marked with arrow). Compare appearance of 'swollen' colonies to 'normal' colonies (marked N), polyps of the latter having expanded tentacles. 1e: Group of Eflatounaria sp. colonies, some of which (marked with arrows) have been eaten off down to the base by predators. Scale bar in 1b and 1c indicates approximately 1 cm.

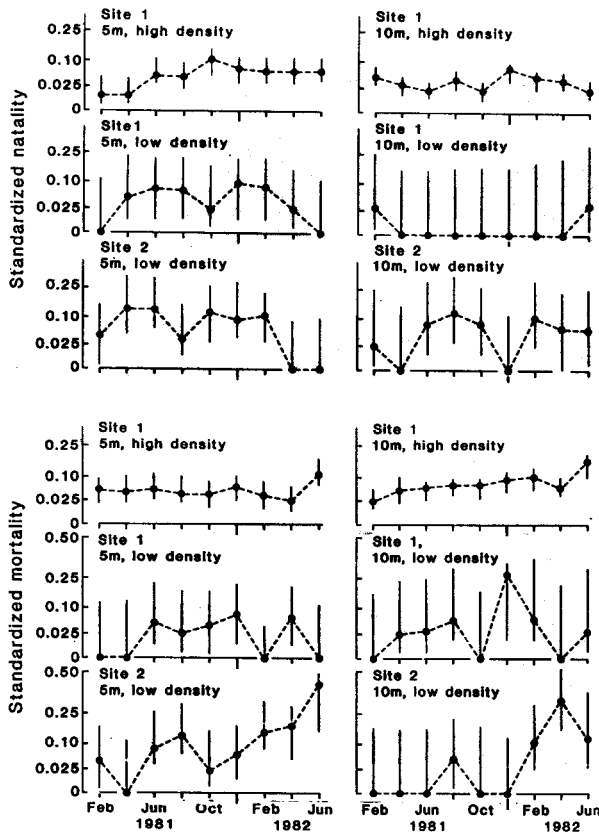


Figure 2. Standardized natality and mortality rates. Plotted after arcsine transformation of data.

Production of stolons and daughter colonies

New autonomous colonies some 2-5 cm across commonly appeared within less than 2 months. 78% of stolons observed were recorded only once, and most daughter colonies apparently become autonomous within less than 4 months. In the various treatments, 50-75% of stolons observed gave rise to daughter colonies, but this may be an underestimate as some stolons presumably arose and decayed in the intervals between photographic sampling. 3-way ANOVAs revealed no significant effects of density, site, depth, or time on standardized numbers of stolons.

Natality and mortality rates

Up to 11 new colonies per square metre appeared within less than 2 months. Standardized natality and mortality rates for each treatment are shown in Fig. 2. Although rates vary among treatments, there is no obvious seasonality in either natality or mortality rates. Results of 3-way ANOVAs are given in Table 1. These indicate that density had a highly significant effect on natality and mortality rates, both being higher at high densities. In both ANOVAs using natality data, depth was also found to have a significant effect on natality rates, these being greater at 5 m than at 10 m. The significant effect of site on natality rates in low density plots

Table 1. 3-way ANOVAs of standardized natality and mortality rates. After arcsine transformation. * $p = <0.05$; ** $p = <0.01$; *** $p = <0.001$; NS Not significant.

Site 1 data only		
	Natality	Mortality
Main effects		
Density	***	***
Depth	*	NS
Time	NS	NS
Interactions		
Density/Depth	NS	NS
Density/Time	NS	NS
Depth/Time	NS	NS
Density/Depth/Time	NS	NS
Low density data only		
	Natality	Mortality
Main effects		
Site	**	*
Depth	*	NS
Time	NS	**
Interactions		
Site/Depth	NS	NS
Site/Time	NS	**
Depth/Time	NS	NS
Site/Depth/Time	NS	NS

(greater at Site 2) is surprising. The interactive effect of site and time on mortality rates in low density treatments is attributed to the fact that while mortality rates were on average higher at Site 2, times at which mortality rates were greatest here did not coincide with times of peak mortality in similar plots at Site 1.

Fluctuations from initial abundance in terms of both increases and decreases were most marked at Site 2. Here also the continued survival of colonies originally present was much lower, with less than 25% of such colonies persisting throughout the study, compared with 45-60% survival in treatments at Site 1.

Sexual reproduction

Oocytes begin to develop in April and are clearly evident by June. Testis bundles and/or sperm were detected by histological examination only in specimens without oocytes, collected in October-December, and the species is presumed dioecious. Eggs are generally about 1 mm across or larger at maturity, sometimes contain zooxanthellae, are released through the mouth, and remain in mucous bundles attached to the colony exterior, partially concealed among the polyps (Fig. 1c). Tentacles are withdrawn but anthocodia greatly enlarged (Figs 1c, 1d) and these 'swollen' colonies are easily distinguishable from 'normal' colonies from a distance of several m (Fig. 1d). Such 'swollen' colonies may be linked to daughter colonies (Fig. 1d), some also egg-laden; small autonomous colonies about 3-4 cm across were observed in reproductive condition.

Spawning is not fully synchronous but is largely epidemic. A few spawning colonies were first observed at Site 1 on 4 December 1981; by 8 December 1981 (3 days after the moon's first quarter) some 35-40% of colonies on the Site 1 patch reef were 'swollen' and carrying externally-adhering eggs. Most colonies had returned to 'normal' by 16 December 1981, and no samples collected on 19 December 1981, were reproductively active.

Eggs may be fertilized internally, or possibly externally, and planulae are probably brooded externally among the polyps. Surface brooding has been noted in two other soft coral species, the tropical alcyoniid Parerythro-podium fulvum fulvum (see Benayahu and Loya, 1983) and the temperate nephtheid Capnella gaboensis (see Farrant, this congress). It was not possible to study planular development and behaviour in Efflatounaria sp., since no planulae could be detected on more than 40 'swollen' colonies collected, all eggs sampled appeared to be unfertilized, and all attempts to fertilize eggs were unsuccessful.

DISCUSSION

Efflatounaria sp. can rapidly produce daughter colonies which are capable of colonizing available substrate in the close vicinity of parent colonies. The negligible invasion of cleared plots suggests that a longer period is required to colonize larger areas. From the evidence of this study it seems that most propagules arise vegetatively, and this is consistent with observations on clone-forming grasses, of which most offspring are vegetatively produced (Harper, 1977). It appears that sexually-derived colonies of Efflatounaria sp., once settled in a suitable environment, then form extensive clones which may result in a locally very high abundance of the species. Higher standardized natality rates at high densities indicate that established colonies in a favourable environment are especially active in producing vegetative offspring. At such high densities, however, these natality rates tend to be offset by higher mortality rates. Causes of mortality are not known, but for crowded colonies there may be competition for food (at least some Efflatounaria seem to be planktivorous, Lewis, 1982); or for light (at high densities, natality rates were higher at 5 m than at 10 m, suggesting that light assists vegetative propagation and/or growth in this hermatypic species). Although the species contains terpenoid compounds (Bowden et al., 1983), some predators are capable of consuming it. While a colony may tolerate minor damage, to branch tips for example, major damage such as loss of entire branches usually seems to destroy the colony's integrity (pers. obs.). Sometimes colonies are eaten off down to the base (Fig. 1e), presumably by larger vertebrate predators such as fish or turtles, and these colonies cannot regenerate.

While natality and mortality rates varied among treatments, the overall situation of high or low density, within plots and at the two sites, remained unchanged. However, the lower survival of colonies originally present in Site

2 plots suggests that this environment is less favourable for survival of Efflatounaria sp. Lasker (1983) attributed some differences in vegetative output and abundance of Briareum asbestinum to availability of suitable substrate. In this case water movement is a more likely factor. Although Efflatounaria sp. occurs in a variety of habitats it favours areas with moderate to strong currents, perhaps because of increased food supply. Although the two study sites are similar in many respects, Site 1, adjacent to a large break in the lagoon margin, experiences considerably more tidal water movement than Site 2.

Although one might have expected effort to be channelled seasonally into sexual or asexual propagation, Efflatounaria sp. shows no such seasonality and can simultaneously produce gametes and vegetative offspring. The small size of some sexually reproducing colonies indicates that at least some colonies become mature at an early age, i.e. less than 1 yr.

Some life history characteristics of Efflatounaria sp., such as fast growth rate, potential for rapid invasion of available space, early sexual maturity, and growth pattern consistent with it being a poor space defender (see Coates and Jackson, in press), are characteristics generally attributed to opportunistic species. However, its mode of sexual reproduction with externally-adhering eggs and apparent surface brooding of planulae, suggests that planulae are demersal, and other studies (e.g. Gohar, 1940; Benayahu and Loya, 1984) have indicated that brooded xeniid planulae settle soon after being shed and are not therefore widely distributed. Benayahu and Loya (1984) consider that despite its limited dispersal, the Red Sea xeniid Xenia macrospiculata is an opportunistic species. However, the substantial capacity for vegetative propagation demonstrated by Efflatounaria sp. would surely be best complemented by a wider dispersal of sexual propagules, to enhance the genetic diversity of local populations and allow colonization of more distant habitats. Further research will be required to determine the dispersal capabilities of this species, and whether recruitment of sexually-derived propagules is generally as low as it appeared in this study.

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* Present address : Queensland National Parks and Wildlife Service, P.O.
Box 5391, Townsville M.C., QLD 4810, Australia.