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Ecologia da reprodução assexuada de *Palythoa caribaeorum* (Zoanthidea : Cnidaria)

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Orientador: Prof. Dr. Luiz Francisco Lembo Duarte

Co-Orientador: Dr. Paul W. Sammarco

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Resumo Geral

O zoantídeo *Palythoa caribaeorum* se reproduz assexuadamente no Canal de São Sebastião, S.P., Brasil, usando quatro mecanismos de fissão e dois mecanismos de fragmentação. Esta variedade de modos, registrada pela primeira vez para a espécie, sugere grande plasticidade fenotípica e alta capacidade das colônias em responder a diferentes limitações do habitat durante seu crescimento. Cerca de 55% da população se reproduz através de fissão e somente 7% por fragmentação. O maior aporte de ramets (novos indivíduos) à população realizou-se por fissão (1304 ramets em um ano), particularmente via fissão marginal "Edge fission", enquanto que o aporte por fragmentação foi consideravelmente menor (64). A contribuição da fissão ao crescimento populacional de *P. caribaeorum* parece ser, portanto, bastante significativa.

A fissão parece ser controlada pela colônia (controle genético), porém sua intensidade muda devido a fatores extrínsecos (bióticos e/ou abióticos), principalmente aqueles relacionados a características do microhabitat em torno das colônias (ex. densidade, tipo e quantidade de recursos: substrato, alimento, etc.). Este tipo de reprodução assexuada ocorreu em colônias de qualquer tamanho com taxa constante e uniforme durante o ano todo (distribuindo a probabilidade de sobrevivência dos ramets no tempo). A freqüência de fissão não diferiu entre: 1) locais com diferentes níveis de estresse (ex. maior turbidez, maior sedimentação, e menos luz), 2) locais com diferenças na mortalidade parcial das colônias, 3)

estações do ano (com flutuação de temperatura) e 4) profundidade (com variação na intensidade de luz).

A fragmentação causada por distúrbios físicos (ex. tormentas) variou no tempo (menor no inverno), mas não no espaço. Já a fragmentação devida à mortalidade parcial foi maior nos locais rasos, onde ocorreu maior incidência de uma doença recentemente descoberta neste estudo.

Mortalidade parcial (< 5% da área total da colônia afetada) ocorreu em 40% da população, sendo maior no local com maior estresse, mas esta nem sempre gerou reprodução assexuada, não sendo, consequentemente um fator determinante na formação de ramets (via fragmentação ou fissão).

A doença, de patógeno desconhecido, registrada pela primeira vez para a ordem Zoanthidea, esteve relacionada diretamente com a temperatura da água e variou no espaço e no tempo. Durante o verão e parte do outono, no pico da reprodução sexuada da espécie, 14 a 20% da população foi infestada. A freqüência da doença e a taxa da reprodução assexuada estiveram diretamente relacionadas ao tamanho da colônia em *P. caribaeorum*. Assim, a doença (provocando perda de tecido, de gônadas, de área de alimentação, e aumentando o gasto energético para combate-la e reparar tecidos) poderia implicar em queda da reprodução e da aptidão da espécie.

A formação de ramets nas colônias pode demorar desde semanas até possivelmente anos. Este estudo mostrou que a dispersão dos mesmos é rápida (3 meses após sua formação) e facilitada pelas correntes, diminuindo no inverno quando o nível de estresse é maior. A maioria dos ramets quantificados foi pequena e, desta forma, sujeita provavelmente a altas taxas de mortalidade. No entanto, a sobrevivência dos ramets e sua contribuição real ao crescimento populacional ainda necessitam ser estudadas.

Abstract

The zoanthid *Palythoa caribaeorum* shows asexual reproduction in the São Sebastião Channel, S.P., Brazil through four mechanisms of fission and two mechanisms of fragmentation. The diversity of reproductive modes in this species reported for the first time, reflected high phenotypic plasticity of the colonies and their ability to respond to constraints imposed by the habitat during it growth. 55% of the population reproduced by fission and 7% by fragmentation. High numbers of ramets were produce through fission (1304 ramets per annum), particularly via "Edge fission", whereas ramets derived by fragmentation were few (64). Fission may be the most important source of ramets to population growth in *P. caribaeorum*.

Fission appeared endogenously controlled by the colonies (genetically programmed), however, it expression was regulated by extrinsic factors (biotic, abiotic), especially them related with the microhabitat around the colonies (e.g. density, type and resource quality: substrate). Fission occurred in colonies of any size, with constant and uniform frequency along the year (spreading the risk through time it may increase ramet survivor). Fission did not varied between 1) sites exposed to different stress level (e.g. higher turbidity, higher sedimentation, and lower light levels), 2) sites experienced different partial colony mortality, 3) seasons (temperature fluctuation), and 4) depths (changing in light intensity).

Fragmentation due physical disturbance (e.g. storms) did change through time (it was lower during the winter), but not in space. Fragmentation due partial colony mortality (e.g. disease) was higher in shallow water, according with the higher incidence of a new disease

discovered here.

40% of the population showed partial colony mortality (< 5% total colony area affected), been higher in the stressful site. Partial mortality did not necessarily induce asexual reproduction, then, it is not an important factor in ramet formation in this study (via fragmentation or fission).

A new disease (pathogen unknown) reported here for the first time for the order Zoanthidea was directly related with water temperature. It degree of infection, however, varied in space and time. 14 to 20% of the population was infected during the summer and early fall, corresponding with gonad maturation time for this species. Disease and asexual reproduction were directly related with colony size in *Palythoa caribaeorum*. Thus, disease (tissue and gonad lost, less feed area, and higher energy expenditure to fight the pathogen and for tissue repairson) may decrease reproduction output and the fitness in this species.

Ramet formation may take weeks to probably years. Ramet dispersal was fast (completed in less than 3 months after it formation) and facilitated by currents. Ramet dispersal was lower during the winter when environmental conditions were harsh. Most ramets were small size; in consequence, they might experience high mortality. Ramet survivor and the real contribution of ramets to the population growth, however, remain unknown at this time.

Introdução Geral

Fatores físicos (distúrbios, temperatura, intensidade luminosa) e fatores bióticos (predação e competição) são importantes isoladamente ou em combinação na estruturação de comunidades de recifes de corais (Done 1983, Harrison e Wallace 1990). Presume-se que as espécies tenham se adaptado e evoluído em resposta à variedade e complexidade de fatores; assim, os diferentes tipos de reprodução exibidos por uma espécie são reflexos das diferentes pressões a que suas populações estão submetidas (Futuyma 1992). A seleção natural tem, portanto, gerado as diversas táticas reprodutivas, no intuito de maximizar o sucesso reprodutivo, durante a vida de um indivíduo, num ambiente particular (Szmant 1986, Richmond 1987, Harrison e Wallace 1990).

O filo Cnidaria tem revelado uma extraordinária diversidade de padrões de reprodução sexuada e assexuada decorrente da alta plasticidade celular, o que lhe confere grande capacidade de adaptação a diversos ambientes (Chia 1976, Highsmith 1982, Sammarco 1982, Walker e Bull 1983, Dinesen 1985, Cairns 1988, Hughes 1989, Shick 1991, Shostak 1993, Ryland 1997).

A reprodução sexuada consiste em uma seqüência de eventos relacionados, cada um dos quais podendo ser individualmente modificado por seleção natural (Bell 1982). Inclui gametogênese, liberação de gametas do tecido parental, fertilização (incluindo recombinação genética), embriogênese e recrutamento larval (Harrison e Wallace 1990). As colônias de Cnidaria são de um modo geral hermafroditas ou gonocóricas, podendo liberar gametas na água para fecundação externa ou incubar plânulas, após fecundação interna, para depois liberá-las no meio (Bell 1982, Fadlallah 1983, Szmant 1986, Harrison e Wallace 1990, Richmond e Hunter 1990). Segundo Richmont e Hunter (1990), variações no tempo e no modo de reprodução entre populações podem representar adaptações a condições locais. A reprodução sexuada é o principal modo de recrutamento para algumas populações (Jackson et al. 1985) e a assexuada pode ser dominante para outras (Highsmith 1982), ou para a mesma espécie no limite de sua distribuição geográfica (Hughes 1989).

A reprodução assexuada foi estudada por Wells (1956). Recentemente tem sido revista para Anthozoa como um todo (Jackson et al. 1985, Hughes 1989, Shostak 1993) e especificamente para anêmonas (Chia 1976, Shick 1991), corais escleractíneos (Highsmith 1982, Cairns 1988, Hughes 1989, Harrison e Wallace 1990) e zoantídeos (Ryland 1997). Existem vários processos básicos de reprodução assexuada em Anthozoa, tais como formação de corpos reprodutivos (gêmulas), poliembrionia, partenogênese ameiótica (=apomíctica), gemação intratentacular, gemação extratentacular, divisão transversa, plânulas assexuadas, fissão e fragmentação de colônias pre-estabelecidas e liberação de pólipos, entre outros (Highsmith 1982, Sammarco 1982, Ayre e Resing 1986, Karlson 1986, Cairns 1988, Hughes 1989, McFadden 1991, Shostak 1993); no entanto em todos eles não acontece recombinação de material genético (Jackson et al. 1985). Além deste espectro de possibilidades reprodutivas, é provável que outros, de origem sexuada ou assexuada, estejam ainda por ser descobertos (Shostak 1993).

Estudos básicos sobre a biologia reprodutiva dos Anthozoa são pouco freqüentes (McFadden 1991), mesmo sabendo-se que a capacidade de uma espécie em colonizar um habitat e de persistir no tempo dependa, em grande parte, do sucesso das estratégias reprodutivas que ela utiliza (Karlson 1986, 1988). Organismos que incorporam reprodução assexuada e sexuada em seus ciclos de vida têm demonstrado muitas vezes grande sucesso

(Begon et al. 1996). Entretanto a contribuição relativa das diferentes estratégias de reprodução à dinâmica populacional de organismos coloniais ainda é desconhecida para a maioria das espécies (Hughes 1989, McFadden 1991, Tanner 1999).

Os estudos de dinâmica populacional de organismos coloniais e clonais são complexos devido a características intrínsecas como: fissão da colônia e fusão entre colônias, senescência não programada e vida longa (Caswell 1989, Hughes 1989, Akçakaya et al. 1997). A fissão (divisão de uma colônia em duas ou mais colônias), por exemplo, não relaciona necessariamente idade e tamanho da colônia, o que diminui a probabilidade de previsão de taxas de reprodução e de sobrevivência, impedindo o uso da idade nos modelos de dinâmica populacional (Hughes e Jackson 1980, Hughes 1984, Hughes e Connell 1987, Hughes 1989, Hughes et al. 1992). Assim, a maximização do valor reprodutivo é quantificada em populações estruturadas pelo tamanho dos indivíduos (matriz transicional) ou pelo estágio de desenvolvimento, mais do que pela idade (Hughes e Connell 1987, Caswell 1989, Hughes et al. 1992, Tanner 1999). Desta forma a reprodução assexuada via fissão, em organismos de crescimento modular tem várias conseqüências ecológicas e evolutivas na dinâmica populacional (Harper 1977, 1981, Jackson et al. 1985, Harper et al. 1986, Hughes 1989, Pedersen e Tuomi 1995, Begon et al. 1996). Vários fatores intrínsecos (ex. tamanho) e extrínsecos (ex. clima), entretanto, podem alterar as taxas reprodutivas e influenciar a aptidão e a dinâmica populacional.

O tamanho da colônia é um fator importante nos modelos de dinâmica populacional, sendo também uma característica fundamental da aptidão dos indivíduos (Begon et al. 1996). Em Anthozoa o tamanho da colônia tem sido positivamente correlacionado com as taxas de fissão, fecundidade e mortalidade (Hughes e Jackson 1985, Szmant-Froelich 1985, McFadden

1997). Qualquer fator que afete direta ou indiretamente o tamanho ou o desenvolvimento do organismo vai ter repercussões negativas na taxa reprodutiva (Tanner 1999).

A taxa de crescimento populacional de organismos clonais é imposta pelo balanço entre ganho de novos indivíduos através de reprodução sexuada (recrutamento de plânulas) e assexuada, e perda de indivíduos por morte ou fusão (Connell 1973, Jackson e Hughes 1985, Hughes 1989, Tanner 1999). Portanto, qualquer diminuição drástica na contribuição relativa de um dos tipos de reprodução ou a ausência de uma das estratégias reprodutivas poderia levar à extinção local da espécie (McFadden 1991). É por isso que o estudo de várias populações submetidas a condições ambientais diversificadas é de grande importância para a compreensão da dinâmica populacional da espécie (Begon et al. 1996). Segundo Kadmon (1993) a heterogeneidade do habitat, com diferenças locais mesmo em pequena escala, implica em diferentes probabilidades de reprodução e sobrevivência. Assim, as taxas demográficas específicas de cada habitat podem ser determinantes da dinâmica de cada população (Pianka 1994). Embora a heterogeneidade ambiental tenha sido enfatizada em pesquisas ecológicas, poucos estudos tentam entender como condições diferentes do habitat (flutuação de variáveis abióticas, estresse, distúrbio) afetam a dinâmica populacional (Kadmon 1993) ou fatores demográficos relacionados com a reprodução (Cook 1978). Além da variação espacial, a taxa reprodutiva também pode mudar temporalmente, sendo constante, cíclica ou irregular. Pode mesmo estar relacionada a características do ciclo de vida como determinados estádios ou tamanhos (Bell 1982, Shostak 1993).

Para a compreensão da dinâmica populacional e da aptidão de um organismo clonal é necessário o conhecimento básico das taxas de reprodução sexuada e assexuada nas diferentes categorias de tamanho das colônias, dos fatores que controlam a intensidade reprodutiva, das taxas de mortalidade nas diferentes classes de tamanho e das mudanças de tamanho das colônias devido a processos como fissão (diminuição da área) e fusão (incremento da área) (Hughes 1984, 1989, Hughes e Jackson 1985, Jackson et al. 1985).

Neste sentido este estudo é o primeiro de uma série que pretende entender a biologia reprodutiva e a dinâmica populacional de *Palythoa caribaeorum* (Cnidaria : Zoanthidea). Assim o presente trabalho teve como objetivo geral a análise qualitativa e quantitativa da reprodução assexuada, e da respectiva contribuição potencial ao crescimento populacional deste zoantídeo, visando também analisar os possíveis fatores que afetam direta ou indiretamente a reprodução assexuada. Desta forma este estudo está apresentado em 4 capítulos que contêm os respectivos objetivos específicos.

Características gerais de Zoanthidea e de *Palythoa caribaeorum*

O Ordem Zoanthidea (Cnidaria) é um grupo importante no ecossistema recifal, sendo os organismos dominantes no início do infralitoral (Suchanek e Green 1981, Ryland 1997). Treze gêneros pertencem aos Zoanthidea *Epizoanthus, Gerardia, Palaeozoanthus, Parazoanthus, Isozoanthus, Thoracactis, Isaurus, Neozoanthus, Acrozoanthus, Sphenopus, Zoanthus, Protopalythoa* e *Palythoa*, mas o número total de espécies existentes é ainda desconhecido (Ryland 1997). Estima-se que no Atlântico Ocidental existem três representantes do gênero *Palythoa*: *P. mammillosa*, *P. variabilis* e *P. caribaeorum* (Attaway e Ciereszko 1974, Sebens 1977, Brattstrom 1980, Suchanek e Green 1981, Fadlallah et al. 1984, Gleibs 1994, Acosta et al. 1998, Gonzalez 1999), mas não se conhece o número de espécies desde gênero no Indo-Pacífico (Ryland 1997).

A maioria dos zoantídeos possui vida longa, é iterópara, hermafrodita, com um ciclo anual de reprodução sexuada, e liberação de gametas na água para fecundação externa. Após fertilização dos ovócitos, o embrião se desenvolve em plânula, a qual é chamada zoantela no gênero *Palythoa*. Vários modos de reprodução assexuada têm sido registrados para os zoantídeos, por exemplo: fissão transversa (*Sphenopus marsupialis*, Soong et al. 1995), gemação (*Isaurus tuberculatus*, Larson e Larson 1982), fragmentação (*Zoanthus, Parazoanthus axinellae*, Karlson 1986, 1988; Dyrynda PEJ in Ryland 1997) e fissão de colônias (*Palythoa caesia*, Tanner 1997, 1999). Embora *P. caribaeorum* seja uma das espécies de zoantídeos com distribuição geográfica mais ampla e maior cobertura do substrato no Atlântico Ocidental, não existem trabalhos sobre suas estratégias de reprodução assexuada, mesmo tendo Fadlallah et al. (1984) sugerido que *P. caribaeorum* poderia investir mais recursos à produção de propágulos assexuados do que à reprodução sexuada (gametas).

O zoantídeo *Palythoa caribaeorum* Duchassaing e Michelotti, 1861 tem sido registrado no Caribe (Attaway e Ciereszko 1974, Brattstrom 1980, Suchanek e Green 1981, Fadlallah et al. 1984, Gleibs 1994, Gonzalez 1999) e no Brasil (ex. Canal de São Sebastião, S.P., Sebens 1977, Gonçalves e Silveira 1996, Migotto 1997). A distribuição de *P. caribaeorum* no Brasil vai desde o Ceará até Santa Catarina, incluindo o arquipélago de Abrolhos, Fernando de Noronha e Atol das Rocas (Echeverría com. pessoal).

É um organismo colonial, séssil, de crescimento indeterminado, incrustante e colonizador primário de substrato rochoso (Sebens 1982, Gleibs 1994). Forma densos agregados de pólipos que chegam a ter vários metros quadrados de área. Suchanek e Green (1981) e Sebens (1982) sugerem que *P. caribaeorum* tem o mais rápido crescimento entre os Anthozoa. A espécie apresenta a toxina "palytoxina" (Gleibs 1994) e é colocada no topo da hierarquia competitiva no sistema recifal (Suchanek e Green 1981). A distribuição vertical da espécie vai desde o nível inferior do mediolitoral, até o máximo de 10m de profundidade (Suchanek e Green 1981), sendo limitada pela disponibilidade de luz devido à simbiose com algas do gênero *Gymnodinium*, as quais proporcionam grande parte da energia que a colônia utiliza em processos básicos de manutenção (Reimer 1971). A perda destas algas é utilizada como indicador de estresse (Williams e Bunkley-Williams 1990, Migotto 1997).

Palythoa caribaeorum é uma espécie funcionalmente protogino-hermafrodita que libera gametas na água para fecundação e desenvolvimento externo de plânulas (Fadlallah et al. 1984, Gleibs 1994, Gonçalves e Silveira 1996; Acosta et al. em preparação). A espécie possui alto esforço reprodutivo em relação a outros zoantídeos (Fadlallah et al. 1984). No Panamá, apresenta um ciclo anual de reprodução de 7 meses (dezembro-junho) com 5 meses de repouso (Fadlallah et al. 1984); na Colômbia a produção de ovos é observada entre junho e outubro (Gleibs 1994); no Brasil (São Sebastião, SP) a época de maturação gonadal ocorre no verão e a liberação de gametas no início do outono (Acosta et al. em preparação). Além disso não se tem registros sobre doenças neste cnidário e seus efeitos na reprodução e/ou mortalidade das colônias.

Objetivos específicos de cada capítulo:

Capítulo I.

Neste capítulo preocupou-se: 1) determinar se o zoantídeo *Palythoa caribaeorum* se reproduz assexuadamente no Canal de São Sebastião, S.P. Brasil. 2) descrever o processo de reprodução assexuada, definindo os mecanismos envolvidos e os fatores que a controlam.

Capítulo II.

Este capítulo teve por objetivo: 1) Estabelecer a contribuição de novos indivíduos (= ramets) gerados pelos diferentes modos de fissão. 2) Avaliar a produção total anual de novos indivíduos ou ramets. 3) Determinar se existem diferenças na freqüência de fissão entre duas populações contrastantes: uma no continente, exposta a maior nível de estresse (alta turbidez, alta sedimentação e baixo nível de luminosidade) e outra na Ilha de São Sebastião, exposta a um nível de estresse moderado. 4) Quantificar diferenças na freqüência de fissão entre populações de diferentes profundidades e em diferentes estações do ano.

Procurou-se também responder as seguintes perguntas: 1) Que percentagem da população exibe fissão? 2) Como a produção de ramets via fissão afeta o crescimento populacional? 3) Em que época do ano ocorre reprodução assexuada? 4) Qual é o tamanho mínimo da colônia para reproduzir-se assexuadamente? 5) Qual o tempo requerido para geração e liberação de um ramet? 6) Em que períodos do ano acontece a liberação de ramets, e que fatores promovem sua dispersão? 7) Qual o tamanho médio dos ramets?

Capítulo III.

Este capítulo teve por objetivo responder as seguintes perguntas: 1) Existem outros modos de reprodução assexuada em *Palythoa caribaeorum*, além da fissão? 2) Quais, como ocorrem e que fatores os afetam? 3) Que percentagem da população apresenta fragmentação e qual sua contribuição relativa no crescimento populacional? 4) A freqüência de fragmentação é independente do local, da profundidade e da sazonalidade? 5) Em que grau *P. caribaeorum* é afetada por mortalidade parcial das colônias? 6) Qual é a principal causa de mortalidade nas populações de *P. caribaeorum*? 7) A mortalidade parcial é dependente do local e da profundidade? 8) A mortalidade parcial promove reprodução assexuada? e 9) Qual a contribuição relativa da fragmentação *vs*. fissão na produção de ramets?

Capítulo IV.

Neste capítulo houve preocupação em: 1) Descrever a nova doença que afeta colônias de *Palythoa caribaeorum*, explorando os fatores que poderiam promover seu aparecimento e seu efeito na população. 2) Quantificar a ocorrência dessa doença no tempo e no espaço, e determinar se existem diferenças em sua freqüência entre locais contrastantes, entre profundidades, e entre as estações do ano.

Capítulo I

Marine Ecology Progress Series - Submetido para publicação

Asexual Reproduction in a Zoanthid: Variants of Fission

by

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Running Head: Fission in *Palythoa caribaeorum*

Key Words: Asexual reproduction, Brazil, Clones, Fission, Fissiparous, *Palythoa caribaeorum*, Ramets, Zoanthidea.

ABSTRACT

Several populations of the zoanthid *Palythoa caribaeorum* were monitored in a two year study on the São Paulo coast, Brazil. *P. caribaeorum* was found to reproduce asexually *via* two general processes of fission - one involving direct fission, and the other requiring the preliminary production of polyp-groups. Within each of these processes were observed two variants. The first process was characterized by directional growth of tissue, subsequently breaking away and dispersing. It included "Teardrop Formation" and "Polyp Ball Production". In the former, tissue grew into a teardrop form, hanging beyond the edge of the colony then breaking away due to autotomy or *via* the assistance of external forces. In Polyp Ball Production, a small group of polyps (< 9) grew upward and outward from the upper surface of the colony, with its base detached from the substratum. After the coenenchyme connecting neighboring polyps had degenerated, the new ramet was released. The second fission process requires: a) the formation of basal coenenchyme and clearly visible associated crevices through the colony; b) the production of polyp-groups which appear to be independent, but are actually connected to each other by a thin basal coenenchyme, not readily visible; and c) the subsequent severance of the basal coenenchyme between polyp groups, creating truly independent ramets. Two variants of this second fission process were noted: "Edge Fission" and "Pseudo-Colony Lift-Off". The former occurred at the colony edge, where a ramet (characterized by small polyps) remained near the parent colony for several months before dispersal. The latter was observed at the center of large colonies (characterized by large, fertile polyps); there, a polyp-group simultaneously separated itself from neighboring groups and the substratum, then lifted off and drifted away. This paper represents a first report of "Teardrop Formation", "Polyp Ball Production", and "Pseudo-

Colony Lift-Off" for the genus *Palythoa*. It is also the first report of Polyp Ball Production within the Zoanthidea. We were unable to find any analogies of Pseudo-Colony Lift-Off within the Cnidaria. Fission appears to be a conservative trait in this species. Fission also appears to be generally endogenously controlled; its expression co-varied with changes in environmental factors (e.g. substratum limitation), however, suggesting that it may be triggered by exogenous factors as well. The variants of fission described here for *P. caribaeorum* reflect its plasticity in morphology, development, and reproduction. This plasticity allows it to utilize different reproductive methods in response to different environmental conditions and in different habitats, enhancing fitness in this dominant benthic species.

INTRODUCTION

Asexual reproduction is the process by which an increase in colony numbers is achieved without the aid of genetic recombination. The Anthozoa employ a great diversity of reproductive modes, evidencing the extraordinary plasticity of cnidarian tissue (Chia 1976, Cairns 1988, Highsmith 1982, Endean & Cameron 1990, Harrison & Wallace 1990, Shick 1991, Shostak 1993, Ryland 1997). New colonies can be formed asexually in several ways. Some of them are: polyp bail-out (Sammarco 1982), coral polyp expulsion (Kramarsky et al. 1997), detachment of a polyp-group as drifting polyp-balls (Rosen & Taylor 1969), fragmentation of colonies (see review in Highsmith 1982, Brazeau & Lasker 1988), asexually produced planulae (Bell 1982, Ayre & Resing 1986, Shostak 1993), budding (Vaughan & Wells 1943, Chia 1976), pedal laceration (Chia 1976, Cooke 1976, Minasian 1976, Shick 1976, 1991, Bell 1982), and fission (DeVantier & Endean 1989, McFadden 1991, Shick 1991).

Fission, however, can be achieved through several processes such as longitudinal fission (see Schmidt 1970, Chia 1976, Minasian 1976, Francis 1979, Sebens 1979, Crowell & Oates 1980, Brooks & Mariscal 1985, Shick 1991, Shostak 1993), transverse fission (Schmidt 1970, Chia 1976, Crowell & Oates 1980, Cairns 1988, Shick 1991, Soong et al. 1995), binary fission (McFadden 1986, Hughes 1989), and autotomy (constriction and stretching of tissue; Walker & Bull 1983, Hughes 1989, Dahan & Benayahu 1997). Fission represents a major mode of asexual reproduction in a variety of Anthozoa including anemones, zoanthids, soft corals, and hard corals (Chia 1976, Hughes & Jackson 1980,1985, Hughes 1989, Karlson 1991, McFadden 1991, Shostak 1993, Tanner 1997). Whether a single species is able to simultaneously employ several variants of fission, or if it employs additional new pathways to achieve fission still needs to be explored.

Fission is defined as endogenous division of the body into portions that regenerate into separate individuals (Hughes 1989, Karlson 1991). Fission may be controlled by either intrinsic (Sebens 1979) or extrinsic factors (Schmidt 1970, Minasian 1976), or both, and may have evolved as a strategy to escape physical stress (Chia 1976, Shostak 1993). The control of fission in the Zoanthidea *Zoanthus* spp. is considered endogenous (genetically programmed), regulating stolonal elongation, budding of new polyps, and stolonal degeneration (Muirhead & Ryland 1985, Karlson 1991). Disturbance-induced damage and stressful conditions caused by temperature, food availability, currents, storm-related turbulence, oxygen concentration, desiccation, mechanical disturbance, predation, density, and body size, may also promote fission in some anthozoan including zoanthids (Chia 1976, Harper 1977, Sebens 1980a, Shick & Hoffmann 1980, Karlson 1983, DeVantier & Endean 1989, Lin et al. 1992, Tsuchida & Potts 1994, Tanner 1999). It has also been generalized that asexual reproduction has evolved as an escape response to physical stress in harsh, unfavorable, and less stable environments (Minasian 1976, Harper 1977, Cook 1978, Karlson 1983, Mladenov 1996). Although the ultimate causes of fission are difficult to differentiate in most cases (Chia 1976).

Reproductive strategies in the Zoanthidea have been reviewed recently by Ryland (1997). Zoanthids form clones and propagate by fission (Cooke 1976, Yamazato & Isa 1981, Karlson 1991, Soong et al. 1995, Tanner 1996, 1997, 1999), fragmentation (Karlson 1986, 1988a,b, 1991, Ryland 1997), and budding (Larson & Larson 1982, Ryland 1997). In the Indo-Pacific, two zoanthid species of the genus *Palythoa* are known to reproduce asexually *via* fission - *P. caesia* (Tanner 1996, 1997, 1999) and *P. tuberculosa* (Yamazato & Isa 1981). No detailed description of fission in the genus *Palythoa*, however, currently exists. It is not known whether species of the genus *Palythoa* from the western Atlantic reproduce asexually, and if so, how. There, only the genus *Zoanthus* has received attention and been described to reproduce asexually *via* fission and fragmentation (Karlson 1986, 1988a,b, 1991).

Fission is an important process in zoanthids because it is known to be the primary agent of population regulation (*e.g. Palythoa caesia*, Tanner 1997, 1999), and potentially have the largest impact on population structure (*e.g. Zoanthus sociatus* and *Z. solanderi*, Karlson 1991) and genetic variation in a population. McFadden (1991) has shown that fission is important to fitness in the soft coral *Alcyonium* sp. The importance of fission can be under-estimated when quantified if only one or a few of a large number of types of fission employed by the species under study are recognized.

The zoanthid *Palythoa caribaeorum* Duchassaing & Michelotti 1861 is a sessile, colonial organism, common on shallow-reefs between the intertidal to 12 m depth (Sebens 1982). This species can extend over tens to hundreds of square meters over the reef crest and reef flat in the Caribbean and in the coastal areas in Brazil (Fadlallah et al. 1984, Gleibs 1994, Migotto 1997, A. Acosta – chapter 2). It is considered a functional hermaphrodite, which spawns gametes for external fertilization (Fadlallah et al. 1984, Gleibs 1994). The degree of infertility within and between colonies has yet to be explained (Kimura et al. 1972, Karlson 1981, Fadlallah et al. 1984, Ryland & Babcock 1991). To date, its asexual reproduction has not been completely described.

This paper is the first in a series designed to examine the plasticity and importance of asexual processes employed by the zoanthid *Palythoa caribaeorum*, and the means by which it comes to dominate shallow reef areas in the western Atlantic. Before evaluating the implications and ecological significance of fission in *P. caribaeorum* (discussed in detail in Acosta et al. in review – chapter 2), however, it will be necessary to first describe the processes of fission and its various products as observed in the field. This is the primary purpose of this paper.

Here we described in detail morphological characters in *Palythoa caribaeorum* colonies and changes that occur in those characters to facilitate identification, observation, and quantification of asexual reproductive processes in the field at the whole-organism level. Interpretation and use of external diagnostic characters in the zoanthids may assist researchers in understanding ecological, evolutionary, and taxonomic aspects in this group and assessing interspecific and intraspecific variation in colony morphology (Duerden 1898, Walsh & Bowers 1977, Ryland & Babcock 1991, Ryland 1997).

Here, we demonstrate, for the first time, that *Palythoa caribaeorum* reproduces asexually *via* fission in the western Atlantic. We show that this zoanthid has the capability of employing simultaneously two processes of fission, which include four variants of fission termed "Edge Fission", "Pseudo-Colony Lift-Off", "Teardrop Formation", and "Polyp Ball Production". Polyp Ball Production is new for the Zoanthidea, and Pseudo-Colony Lift-Off appears to be new for the Anthozoa. We will also discuss possible controls of fission (*e.g.* endogenous); it's conservativeness as a character in this species, and the adaptive value of this type of reproduction. We have not examined these processes at the cellular, tissue, or physiological levels, and questions pertaining to these levels of resolution remain open at this time.

METHODS

Sampling Periods

This study of *Palythoa caribaeorum* encompassed two years, divided into three periods. During the first six months, a number of colonies were chosen haphazardly along the São Sebastião channel, São Paulo, Brazil. Observations were made daily every other month to examine general patterns of asexual reproductive processes, to determine degree of variation in these processes, to identify different types of fission which might be occurring, and to define variables which would help to document these processes through time. This was followed by a more detailed six-month study where 300 colonies of *P. caribaeorum* were followed daily during December 1996, February 1997, and May 1997. Colonies were selected at two sites and at two depths around random points, defined by a large grid and a random numbers table (Rohlf & Sokal 1995). The two study sites were Praia Portinho, located on São Sebastião Island, and Ponta Recife, on the continental coast (Fig. 1). The two depths were 0.5 - 1.5 m, and 2.5 - 4.0 m. One plot containing an average of 75 colonies was defined randomly at each depth. Sites and depths were chosen to represent a spectrum of environmental conditions under which fission would be occurring. In particular, turbidity, sedimentation, and light varied dramatically between sites and even subtle depth changes in this channel (Acosta et al. 1998). These depths were also selected because of the difficulty experienced in attempting to differentiate individual colonies between 1.5 and 2.5 m. There, they exhibited a very high percent cover (100%), large colony size (> 2 m^2), and low density. Data collected during the first year indicated that quarterly sampling would be sufficient to accurately document all variants of fission through time.

Expanded sampling

Additional populations of *Palythoa caribaeorum* were monitored in a third study period encompassing one year (May 1997 to May 1998). During May 1997, three replicate plots were chosen randomly at each depth and site (as above), with 36 to 85 colonies in each. 579 colonies, including a wide variety of size classes (range: 2.5 x 10^{-5} to 2.1 m^2) were followed, sampling every three months near the end of each season (15 to 45 consecutive days per sampling) - August 1997 (winter), November 1997 (spring), February 1998 (summer), and May 1998 (fall). This sampling scheme was designed to quantify the dominant modes of fission, determine the significance of these processes for *Palythoa* ecology (see Acosta et al. in review - chapter 2), and test hypotheses regarding variations in fission frequency in space and time (Acosta et al. in progress).

The primarily descriptive information presented here is drawn from observations made in all three-study periods.

Palythoa colonies were mapped underwater with the assistance of acrylic tables (since traditional monitored methods failed e.g. marks). Colony size was measured in order to facilitate identification of specific colonies through time. The number, area, and position of the ramets (defined as "a physiologically independent unit, or separated vegetative part of the genet" Harper 1977, 1981) and their pre-cursors polyp- groups (still connected to each other within a colony by a thin basal coenenchyme, also called "assemblage", "polyp clusters", or "aggregation" Karlson 1986, 1988b, Ryland 1997) were identified, measured, and carefully monitored to help describe the details of ongoing fission. Basal coenenchyme is defined as an extension of the column (body walls) - a common tissue that connects the polyps of a colony or fills the spaces between polyps (see Verrill 1869, Duerden 1898, 1890, Calgren 1937, 1954). We defined the processes and variants of fission from which any ramet was derived by following individual colonies and polyp-groups through time.

Pieces of tissue exhibiting active growth, hanging at the edge of the colony (normally at the vertical side of a boulder) were followed particularly closely through time to document the process of "Teardrop Formation" (see below). Individual teardrop pieces in the process of forming (hanging) were differentiated by position, size, and the number of them associated with a given colony. Polyp-groups growing upward and outward from the upper surface of the colony were also followed closely.

Qualitative observations were also made on micro-environmental factors, which could potentially affect fission. These included involvement in competition for space, substrate limitation (availability of substratum for growth), light (top *vs.* side of boulders), evidence of predation, and sexual maturity. Some additional colonies, polyp-groups, and ramets were sampled during March 1997 to help define degree of sexual maturity and reproductive effort (percent of polyps with gonads per colony). Tissue samples were collected at the edge and center of the colony. In some cases, the surfaces of colonies were cut with a knife to simulate crevices. The lesions were monitored to determine whether this disturbance might induce regeneration or fission. Field excursions were also made to other coastal regions in Brazil, Colombia and the Florida Keys to determine whether the process of fission occurred in this species throughout the western Atlantic.

RESULTS

Two general processes of fission were identified in *Palythoa caribaeorum* (Table 1), and each had two variants. These processes, and variants were not part of a continuum in a unidirectional, single-line process. Rather, they were alternative means by which to achieve a single end (*i.e.* ramet production). We have termed these four variants of fission Edge Fission, Pseudo-Colony Lift-Off, Teardrop Formation, and Polyp Ball Production. These variants branch out into different developmental paths, depending upon the specific process by which they were formed, precursor type, ramet position, dispersal time, fecundity, and external factors of influence (Table 1).

The first general fission process in *Palythoa caribaeorum* occurred in two consecutive steps: Pseudo-fission, followed by true fission (Figs. 2a-c & 3c-d).

Pseudo-fission

The prefix "pseudo" means "apparently" or "false". Here, it represents a preliminary step rather than the actual event. "Pseudo-Fission" is the process by which clearly visible crevices appear and spread between polyps, in association with the apparent division of the parent colony into one or several polyp-groups. Pseudo-fission is "apparent" because each polyp-group is still physically inter-connected aborally to neighboring groups and the parent colony *via* a thin, flat, basal coenenchyme.

The first visual external evidence of Pseudo-Fission in the colony surface was the presence of crevices (Figs. 2a-c, 3b & 4c-d). Crevices appeared in one or several parts of the colony. They progressed linearly at first, and then branched throughout the colony. At the bottom of the crevices was a short, flat, connecting basal membrane. The basal coenenchyme tissue was not visible from above without parting the overlying polyps. Basal coenenchyme is the result of vertical constriction of the coenenchyme that connects the polyps. Disappearance of the coenenchyme (probably through resorption or degeneration) progressed from the oral to the aboral side of the colony, until only a small portion of connecting tissue was left between polyps (Fig. 2b). This remaining flat thin tissue was 1-3 mm high and left a gap of 1-10 mm between polyp-groups. The basal coenenchyme was elastic, ranging in length from 1 to, in extreme cases, 10 cm (Fig. 2d & 5b).

When crevices branched throughout the colony, they met and defined one or several polyp-groups within a colony (Figs. 2c & 4c-d). The colony, however, was still recognizable as a single entity. Crevices formed and advanced constantly throughout the year and were a primary characteristic of colonies active in asexual reproduction. Crevices generally continued to form in large colonies until most of the polyp-groups were about the same size. This suggested possible control by the parent colony in the regulation of polyp-group (ramet precursor) size. Once a polyp-group was formed, it was obligated to complete the fission process eventually. All polyp-groups could potentially become autonomous ramets, although the completion of this process could require within weeks, months, or more than 2 years.

Fission

Ramet production occurred when the basal connecting tissue surrounding a given polyp-group became progressively thinner, eventually breaking (Fig. 3a-d). At that point, the new ramet was physically and physiologically independent of the parent colony.

Polyp-groups formed at the edge (Figs. 3c-d & 4a-b) or the center (Fig. 4d) of a colony were observed to become ramets at a higher frequency than those occurring between the edge and the center (see Acosta et al. in review – chapter 2). The fission process does not necessarily involve dispersal of the new ramet. Ramets may remain in place, attached, beside the parental colony (after Edge Fission), or may become detached from the substratum and disperse within a short time (after Pseudo-Colony Lift-Off). Polyp-groups occurring in the area concentric to the center grew slowly into those areas vacated by newly dispersed ramets.

Variants of Fission

Edge Fission

Edge Fission falls within the first general category of fission described above. Polyp-groups occurring at the edge of the colony were usually thin with smaller polyps (Fig. 3a-d) than those towards the center (Fig. 4d). Polyp-groups associated with the edge of the colony were usually less fertile and normally associated with lateral colony growth and competition for space. Ramets were ~0.5 mm - 1.5 cm in height and generally remained attached to the substratum within mm or cm of the parent colony for three to six months before being dispersed (Fig. 3b-d). In many cases, colonies of *Palythoa caribaeorum* utilizing this variant of fission occupied almost all the available substratum in its immediate area. This included the upper surfaces of the boulders and boulder walls. The remaining area (lower part of the boulder wall) was sub-optimal due to low light levels, and high interspecific competition for space with ascidians and sponges. Colonies utilizing this variant of fission had highly variable number of polyp-groups and highly variable degree of crevice development. In addition, they were capable of producing dozens of ramets simultaneously. This mode was apparently the most frequently used by *P. caribaeorum*.

Normally, a ramet formed by Edge Fission was comprised of a number of polyps ($\geq$ 10; Fig. 3b-d); however, rarely we observed $\leq$ 3 polyps (Fig. 4a), even a single polyp (Fig. 4b) isolated at the colony edge, eventually completing the fission process and dispersing. It is not known whether a single polyp can re-attach or not.

Pseudo-Colony Lift-Off

Like Edge Fission, Pseudo-Colony Lift-Off also involved crevice formation and fission (Fig. 4c). It differed from Edge Fission, however. Firstly, in Pseudo-Colony Lift-Off, the precursor polyp-group separated laterally from neighboring polyp-groups and at the same time, it separated itself aborally from the substratum (Fig. 4d). In this case, ramets produced lifted off from the substratum, drifted away, and re-attached elsewhere. Secondly, the parent colony was always large, bearing a larger number of polyp-groups (maximum 400 per colony). Thirdly, Lift-Off generally occurred in colonies with long polyps (2.5 - 6.0 cm in height; Fig. 4d), which were highly fertile (gonad production was observed to occur during the summer and early fall, and spawning occurring during April and May; Acosta et al. in preparation). Fourthly, the ramet was always produced near the center of the colony. Fifth, this type of clone production was less frequent than Edge Fission. Sixth, due the central position of the polyp-group, light limitation and interspecific competition were not limiting factors, as in colonies utilizing Edge Fission. Colonies employing Lift Off could produce several ramets by this or any other variant of fission simultaneously. All colonies utilizing Pseudo-Colony Lift Off were found to occupy the entire substratum available to them; i.e., they were substrate-limited.

In a second general form of fission, pseudo-fission was not a pre-requisite for ramet formation. Instead, tissue growth was promoted at specific points within the colony within a period of several weeks or months before they became physically independent and dispersed (Figs. 5a & 6a). These pieces of tissue were commonly not attached to the substratum (Fig. 5a,c) but were connected to neighboring polyps *via* coenenchyme (Fig. 6a). Two variants of fission using this general process were “Teardrop Formation”, and “Polyp-Ball Production” (term already utilized in the Scleractinia by Rosen & Taylor 1969, Dahan & Benayahu 1997).

Teardrop Formation

This variant of fission occurred exclusively at the colony edge (Fig. 5a-d). In all cases, colonies did not have substratum available for lateral growth (Fig. 5a,c,d). In addition, colonies growing on the upper part of large boulders were usually several centimeters above the sediment or hard bottom (20 - 150 cm). Under these conditions, the parent colony directed polyp growth (*via* budding) at specific points along the colony edge; that is, not the entire colony perimeter was involved in this process. One or several portions of tissue per colony continued to grow without attachment to the substratum, hanging at the colony edge. These formations can reach 2 - 8 cm wide and several centimeters long (1 - 100 cm; Fig. 5a,c), but normally they were small in size and teardrop shaped before being dispersed. As in Edge Fission, these teardrop formations were exposed to lower light levels and sometimes interspecific competition for space with other sessile benthic organisms. Eventually the formation broke away from the parent colony *via* autotomy (*i.e.* tissue degeneration of the thinnest portion of the Teardrop), its own weight, or external forces (*e.g.* currents or storms). Ramet formation and ramet dispersal took place at that same time. Teardrop Formation was common, and the ramet released was fertile.

Colonies exhibiting Teardrop Formation generally also bore crevices. These crevices, however, rarely occurred at the thinnest portion of the teardrop, or within teardrop formations, and did not play a role in ramet formation and dispersal. Colonies using this strategy possessed a very elastic basal coenenchyme (Fig. 5b). Colonies utilizing Teardrop Formation could also reproduce simultaneously by either one or both of the variants previously described.

Teardrop Formation did not always result in ramet formation and release. Sometimes the tissue hanging at the edge of a boulder continued to grow towards the bottom (Fig. 5c), attach, and expand into a neighboring microhabitat (Fig. 5d). Dissociation from the parent colony was optional, with the formation sometimes reaching > 100 cm.

Polyp Ball Production

The sequence of events leading to Polyp Ball Production varied somewhat from that described in Teardrop Formation. In Polyp Ball Production, a large single polyp initially grows upward and outward from the surface of the colony, then starts budding into a "ball shape" (Fig. 6a-b). This small, closely associated group of polyps (< 9), emerging from the colony surface in such a way that its base was not attached to the substratum (Fig. 6b). The ball, however, remain connected to neighboring polyps through coenenchyme. Eventually, the connecting coenenchyme degenerated, freeing the polyp-ball from the parental colony (Fig. 6c), to be dispersed by currents. "Polyp balls" were released generally from the interior of the colony. It is not known whether these polyp balls were sexually mature or not.

Polyp-Ball Production did not require as much time for ramet formation as some of the other fission variants. This is probably because it was not dependent upon the formation of crevices in the colony (as in Edge Fission), or detachment from the substratum (as in Pseudo-Colony Lift Off).

Polyp-Ball Production did not seem to be affected by substratum limitation, light, and competition for space; however, substratum irregularities (micro-topography) may affect this process, helping to explain its lack of fixation to the substratum. Colonies producing ramets via this mean exhibited bumps in their surface due to irregularities in the substratum, previously occupied by encrusting organisms (*e.g.* bivalves, barnacles, etc.).

These variations of fission should not, be confused with fusion. The former occurs within a colony, while the latter occurs between colonies. Ramets already separated by fission never fused again with the parent colony, irrespective of the fission mode which produced them. Crevice formation within a colony appears to be irreversible, along with the formation of polyp-groups, which are normally followed by fission.

The artificial lesions made to the colonies, which involved both polyps and coenenchyme regenerated completely, without leaving any scars or basal coenenchyme between polyps.

General observations

Frequency of fission was low or absent where there was active, intraspecific competition for space. Fission and ramet release were frequent at the colony edge, under conditions of interspecific competition for space with such epibiota as *Palythoa variabilis, Zoanthus sociatus, Z. solanderi, Sargassum* sp., and several species of ascidians, sponges, and other algae. No colonies were observed to suffer from the effects of predation during the study.

DISCUSSION

Edge Fission

Edge fission is similar to several reproductive processes described elsewhere. Duerden (1898) indicated that new individuals of *Palythoa mammillosa* arise mostly alongside those at the periphery of the colony (A. Acosta pers. obs.). Calgren (1937) observed one colony of *P. howesii* dividing into two parts; they were in communication only at their bases. Yamazato & Isa (1981) briefly documented apparent fission occurring at the colony edge in the zoanthid *P. tuberculosa*. Tanner (1997, 1999) and Ryland (1997) described the formation of ramets in *P. caesia* through frequent lateral constrictions (shrinkage), resulting in numerous, small, nodular clumps. These observations provide valuable background, but the low number of specimens observed, or the absence of detailed descriptions restricts our ability to make a detailed comparison of these zoanthids. It does seem, however, that Edge Fission is widely employed by the genus *Palythoa*.

Edge Fission may promote specific colony shape or size for energetic (McFadden 1986) or physiological reasons. It is known that small colony size rather than extensive sheets are maintained in *Isaurus, Protopalythoa, Zoanthus,* and *Palythoa caesia* through asexual reproductive mechanisms such as fragmentation or fission (Ryland 1997). In *P. tuberculosa*, colonies retain constant ratios of circumference to area, employing constant rates of growth and fission (Yamazato & Isa 1981). It appears that colony size in *P. caribaeorum* populations may be regulated by frequency of Edge Fission, depending upon environmental conditions and habitat. Large colonies of densely packed *P. caribaeorum* covering several square meters at 1.5-2.5 m depth were observed to exhibit low rates of Edge Fission. By contrast, a high number of small colonies, also densely packed at 3.5–5.0 m depth, exhibited maximal Edge

Fission rates, maintaining small colony sizes there. At the deeper site, populations may experience less favorable environmental conditions (e.g. low light levels, low productivity). It is known that *Palythoa* colonies have difficulty sustaining positive energy production in slightly deeper (3.4 m) vs. shallow (1.4 m) water (Tun et al. 1997). Deeper colonies also experience starvation due to diapause during the winter (long period of dormancy of *P. caribaeorum*, where colonies develop a characteristic mucus coat; Acosta et al. in review – chapter 4). Low energy and starvation may favor the formation of clones (Stephenson 1935, Minasian 1976, Smith & Lenhoff 1976, Sebens 1979). In *P. caribaeorum* Edge Fission may decrease the total maintenance cost of the colony (see Shick 1976, Bucklin 1987), keep colonies at a size optimal for filter-feeding (McFadden 1986, Hughes 1989), and increase genet survivorship by spreading the risk over a larger number of ramets as hypothesized by Cook (1978) and Stoner (1989). Edge Fission may be utilized as an escape response under unfavorable conditions as proposed earlier (Rosen & Taylor 1969, Chia 1976, Smith & Lenhoff 1976, Cook 1978, Sebens 1980b, Endean & Cameron 1990, Shostak 1993), then, fitness is served by fission (or fragmentation) rather than by further growth of the colonies (Sebens 1979, Stoner 1989). Where fission is maximized, it may be at considerable cost to the colony in terms of tissue growth (Minasian 1982).

Further studies will hopefully reveal whether constant shrinkage of *P. caribaeorum* colonies *via* Edge Fission is maximized in particular habitats depending upon food supply (Okamura 1985, McFadden 1986, Johnson & Sebens 1993, Anthony 1997), net energetic input (Minasian 1982), colony growth rates (Yamazato & Isa 1981, Minasian 1982), density (see Tanner 1999), or increases colony mortality.

Release of a single polyp *via* fission from a *Palythoa caribaeorum* colony has two analogies in zoanthids and stony corals. In *Zoanthus sociatus* and *Z. solanderi*, stolonal degeneration (basal coenenchyme in *P. caribaeorum*) resulted in the dispersal of single polyps (Karlson 1986). Expulsion of single polyps in scleractinian corals may help colonies to escape environmental stress, as is known to occur in some scleractinian corals. In "Polyp Bail-Out" (Sammarco 1982), the parent colony isolates and separates its polyps from each other and then releases them; in "Coral Polyp Expulsion" (Kramarsky et al. 1997), a polyp along with its skeleton is expelled from a healthy parent colony.

Detached modules or polyps represent the most common form of asexual reproduction in the Metazoa, being employed by 18 of the 34 phyla (Jackson et al. 1985, Hughes 1989). Most of the ramets produced by fission in *Palythoa caribaeorum* here, however, were polyp-groups, which probably have a higher rate of survival than a single polyp because of their size refuge (Sammarco 1982, Karlson 1986, 1988a), but lower dispersal capabilities due to their increased weight and negative buoyancy.

Pseudo-Colony Lift-Off

An extensive review of the literature did not reveal any analogs of Pseudo-Colony Lift-Off. Ramets produced by this process were sexually mature and exhibited the highest reproductive effort compared to the other variants of fission described here (Acosta et al. in progress), making them more valuable to the parent colony in terms of fitness. It is unknown at this time, however, whether ramets remained fertile during and after settlement. In addition, it is not known whether a trade-off exists in the parent colony between the cost of lost space of reproductive polyps, and the gain in overall population growth.

Teardrop Formation

With respect to Teardrop Formation, we found one analog in British populations of *Parazoanthus axinellae*. Colonies growing on rock faces (at 20 m depth) produce thread-like, club-tipped stolons, which hang vertically, breaking off (due to water movement) and dispersing (P.E.J. Dyrynda, *c.f.* Ryland 1997). These formations are associated with substratum limitations. In Teardrop Formation, the tissue also continues growing beyond the edge of the colony when there is no more available substratum for attachment. Some large colonies of the scleractinian coral *Porites* have a related growth response (DeVantier & Endean 1989). Fission in *Porites* occurs as undisturbed growth results in ledge formations around lower portions of large colonies; outward growth of the ledge shade and kill the tissue directly beneath, causing tissues near the base of the colony to become isolated from the parent. This type of ramet is formed, however, through partial colony mortality and not autotomy (intrinsic), as in *Palythoa caribaeorum*.

Autotomy of growing tips is also known to occur in the Octocorallia (Lasker 1983, Dinesen 1985), the gorgonian octocoral *Junceella fragilis* (see Walker & Bull 1983), and the alcyonacean octocoral *Dendronephthya hemprichi* (see Dahan & Benayahu 1997). In these octocorals, as well as in *Palythoa caribaeorum*, the high level of ramet production in large colonies appeared to be under endogenous control (Walker & Bull 1983, Dahan & Benayahu 1997). In *P. caribaeorum*, however, ramets were not formed from older pre-existing parent tissue, as in octocorals, but from new tissue growing at the edge of the colony. Walsh & Bowers (1977) suggested that polyps are budded from extensions of the gastrodermal canals (= basal coenenchyme) rather than from old polyps, which may be the case in *P. caribaeorum*.

Traditionally, *Palythoa caribaeorum* has not been considered to possess stolons; only basal coenenchyme (Duerden 1898). In several *Zoanthus* species, stolons act like a runner or root-like projections, from which new polyps bud (M'Murrich 1889, Karlson 1986, 1988a,b). The basal coenenchyme in *P. caribaeorum* was observed to be highly plastic. It is possible that under certain conditions, it could act as a runner to explore and colonize new habitats.

Polyp-Ball Production

Polyp-Ball Production represents a new report for *Palythoa caribaeorum* and for zoanthids in general. Duerden (1898) earlier description of this species indicated that the colony's upper surface is almost uniform, with polyps immersed in a thick coenenchyme, extending only a few millimeters above it (see also Haddon & Shackleton 1891). The surface of some *P. caribaeorum* colonies is irregular, exhibiting "bumps" that correspond to several "polyps balls" rising above the upper level of the coenenchyme (particularly in Angra dos Reis, Rio de Janeiro, Brazil; A. Acosta pers. obs.). "Polyp-Ball" production was initially described in a scleractinian coral (Scheer 1959, 1960, Rosen & Taylor 1969), and is reported to be associated with unfavorable environments and sandy habitats in *Goniopora stokesi.* This is the first report of its occurrence in the Zoanthidea.

Each variant of fission described here is independent. The variants are not sequential, and each has its own characteristics, some of which occur only in a subset of modes. For example, the formation of crevices was not a pre-requisite to Polyp-Ball Production or Teardrop Formation; it was an obligate, integrated step, however, in Edge Fission and in Pseudo-Colony Lift-Off.

Palythoa caribaeorum utilizes a variety of asexual reproductive strategies, including fission and fragmentation (Acosta et al. 1998), to increase the probability of survival in this unstable environment, or to colonize space under favorable conditions. Intrinsic and extrinsic factors may differentially stimulate each of the specific developmental pathways and the production of ramets, with different ecological consequences for ramet dispersal, survival, and colonization.

Endogenous Control

Fission in *Palythoa caribaeorum* appears to be under endogenous control, as evidenced by the following: 1) ability of the colony to produce morphological and perhaps physiological changes through manipulation of the coenenchyme; 2) production of polyp-groups of specific shapes and sizes; 3) breakage of basal connecting tissue around a specific polyp-group to create a ramet, while neighbor polyp-groups remain connected; 4) simultaneous detachment of a polyp-group from their neighbors and substratum; 5) tissue growth directed into a specific shape to facilitate breakage or colonization of proximal microhabitats; and 6) regeneration to lesions-like crevices produced artificially, while the basal coenenchyme created by the colony is an irreversible process.

These observations agree with Karlson's (1991) results for *Zoanthus* spp. In cnidarian and in other invertebrates, such as asteroids, fission processes, tissue resorption, and stolon degeneration are considered to be under endogenous control, by processes not yet fully understood (Mladenov et al. 1983, Walker & Bull 1983, Wilkie et al. 1984, Muirhead & Ryland 1985, Karlson 1986, Hughes 1989, McFadden 1991, Dahan & Benayahu 1997).

Exogenous Control of Fission

There is correlative evidence suggesting that fission in *Palythoa caribaeorum* can be triggered by environmental stress (abiotic, biotic, anthropogenic) or that exogenous factors (*e.g.* low light levels, substratum limitation, competition for space, and density) may help to regulate expression of this character as documented in zoanthids, sea anemones, asteroids, holothuroids, polychaetes, and plants (Minasian 1976, 1982, Johnson & Shick 1977, Abrahamson 1979, Sebens 1980b, Cook 1983, 1985, Hunter 1984, McFadden 1986, Shick 1991, Mladenov 1996, Tanner 1999).

Light Limitation

Most *Palythoa caribaeorum* colonies in the study area colonized almost all-available substratum, including sub-optimal space on the walls of the boulders. In this microhabitat, characterized by low light conditions and interspecific competition for space, most ramets were produced *via* Edge Fission. Continuous darkness has been shown to increase rates of asexual reproduction in animals (Smith & Lenhoff 1976, Calow et al. 1979, Sebens 1980a, Hunter 1984, Mladenov 1996), and increased shading has produced similar effects in plants (Abrahamson 1979). The effects of light limitation in *P. caribaeorum* were reflected in their vertical distribution, which declined dramatically with depth (Suchanek & Green 1981, Sebens 1982). Low light levels in relatively deeper waters may not only increase fission rate, but also promote ramet detachment in *P. caribaeorum*, as has been suggested to occur in *Porites* (DeVantier & Endean 1989).

Competition for Space

With few exceptions, most of the interspecific competitive interactions observed resulted in "stand-offs", as noted previously for this species (Karlson 1980, Suchanek & Green 1981, Bastidas & Bone 1996). Oliver (1984) stated that complex biological interactions provide a major potential selective force for fission, enhancing success of the genet (also see Sebens 1982, Jackson et al. 1985).

Fission in this zoanthid may allow the colony to escape prolonged, intense competition for space. The adaptive advantage here would be greater energy efficiency, enhanced population growth in a potentially more favorable habitat (Cook 1978, Karlson 1983, Mladenov 1996).

By contrast, intraspecific competition for space seems to suppress fission in areas dominated by *Palythoa caribaeorum*. Fusion, however, did occur under these conditions (A. Acosta unp. data). These observations agree with Tanner's (1997) observations that fission was density-dependent, decreasing at higher densities in *P. caesia*. The percentage of variation in fission explained by density (impacting intraspecific competition) was low, however - 3.9%, suggesting that other factors were involved. These negative impacts of density on fission and growth have also been observed in scleractinian corals (Fadlallah 1982), soft corals (Karlson et al. 1996), fissiparous asteroids (Mladenov 1996), polychaetes, rotifers, *Daphnia* spp., and *Hydra* sp. (see Mladenov 1996).

Substratum Limitation

Fission appears to be enhanced by substrate limitation. Teardrop formation was clearly a response to substrate limitation. Substrate limitation may also promote fission in large and probably older colonies by stimulating Pseudo-Colony Lift Off. We hypothesize that once a colony has monopolized all available horizontal substratum, it begins to grow vertically -sometimes up to 6 cm in height in this Brazilian population. This is an unusual polyp size for this species, which has only been observed to reach 1 - 2 cm in the Caribbean (Duerden 1898, Gleibs 1994, A. Acosta pers. obs.). After maximal lateral and vertical expansion, colonies have nowhere left to grow, and Pseudo-Colony Lift-Off may provide space for the colony by removing pieces of tissue, while effecting dispersal as well. This mode of fission not only enhances ramet dispersal, and population growth, but permits the colony to continue growth through re-colonization of vacated areas.

Fission as a Conservative Trait

The fission processes observed here in *Palythoa caribaeorum* were not exclusive to the study populations. Preliminary observations at other sites in Brazil and in the Caribbean (Colombia - Gonzalez 1999; Puerto Rico - R. Urueña pers. com.; Florida Keys - A. Acosta pers. obs.) indicate that fission is present in this species over a wide geographical range. Although *P. caribaeorum* populations from the Caribbean and southern Brazil have been isolated for long period of evolutionary time by the Amazon and Orinoco rivers, they both exhibit Edge Fission, Teardrop formation, and Pseudo-Colony Lift Off (see Gonzalez 1999). That is, these variants of fission appear to be a conservative trait in this species. This would be strong evidence for a single western Atlantic species. Further observations are required to determine whether Polyp Ball is also exhibited in populations that are more northerly.

Advantages of Fission in *Palythoa*

The selective advantages of fission for *P. caribaeorum,* fall into a number of categories, as follows: 1) Fission can increase fitness in the parent colony by producing clonal copies (Hughes 1989, McFadden 1991). Simultaneously, fission decreases risk of mortality of the genet in large populations, spreading the risk of mortality among ramets, especially in unpredictable environments (Cook 1978). 2) Fission results in an increase in the local dominance of well-adapted genotypes (Williams 1975). As long as environmental conditions remain within the same range, the offspring will enjoy the same level of success that the parent had. 3) Fission permits clones of a genet to escape local selective factors, poor quality micro-habitats, or environmental stress (Hunter 1984). 4) Fission may enhance colony growth in *P. caribaeorum* by freeing up space within the colony, or through directional growth. 5) It increases the probability of survival for a reproductive propagule, since ramets are larger than sexually produced larvae (Karlson 1988b). 6) Fission probably requires less energy than sexual reproduction, as has been proposed previously by Francis (1979) and others (Fadlallah 1982, Hunter 1984, Karlson 1986). 7) Fission may regulate population size, clonal structure, and size distribution in *P. caribaeorum*, as has been demonstrated for other zoanthids (Karlson 1991, McFadden 1991, Tanner 1997). 8) Fission may helps to maximized nutrient intake through a reduction in colony size (McFadden 1986).

There are also potential selective disadvantages for fission. These include 1) a decrease in local genetic diversity in short period of time; 2) Inability of the population to adapt to eventually changing environments (Levins 1968); and 3) Lower dispersal abilities.

Four new variants of fission have been described here for the first time in the zoanthid *Palythoa caribaeorum*: Edge Fission, Pseudo-Colony Lift-Off, Teardrop Formation, and Polyp Ball Production. The morphological symptoms of those processes should be useful tools for identifying ongoing asexual reproduction in the field, and quantifying it. Fission appears to be genetically controlled, but external forces may regulate its expression as well. The diversity of the types of fission observed suggest that these processes play a major role in this species, contributing fitness by enhancing reproductive potential.

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Figure Legends

Figure 1. Study sites in the São Sebastião channel, São Paulo coast, Brazil. (1) Ponta Recife, on the mainland; (2) Praia Portinho, on offshore island. "T" represents the Terminal Maritimo Almirante Barroso (TEBAR).

Figure 2. Asexual reproduction *via* fission in *Palythoa caribaeorum.* (a) Colony exhibiting crevices spreading throughout the surface, delimiting a polyp-group; (b) Crevice isolating two polyp-groups; thin basal coenenchyme at the base of the crevice; cuticle protecting polyps exposed; polyp diameter 0.8 - 1 cm; (c) Three polyp-groups within a colony separated by crevices and connected by basal coenenchyme; (d) An example of plasticity in the basal coenenchyme, extending 8 cm while connecting two polyp-group that have become separated. Polyps at the upper left belong to *Zoanthus* sp. colony.

Figure 3. Edge Fission in *Palythoa caribaeorum.* (a) Parental colony (upper right) still connected by basal coenenchyme to a polyp-group (middle left) at the colony edge. (b) Parent colony and a newly formed ramet, produced at the edge of the colony. Note the crevice in the surface of the colony. (c) Parent colony and a new physically isolated (smaller) ramet (below). (d) Edge Fission. Ramet at the colony edge in a substrate-limited situation. Ramet may remain near the parent colony for weeks or months prior to actually dispersing. Polyps in all colonies shown here are 1.0–1.5 cm in height.

Figure 4. (a) Three polyps being separated from the parent colony; at this point, they remained attached to the parent colony by a white basal coenenchyme. (b) One

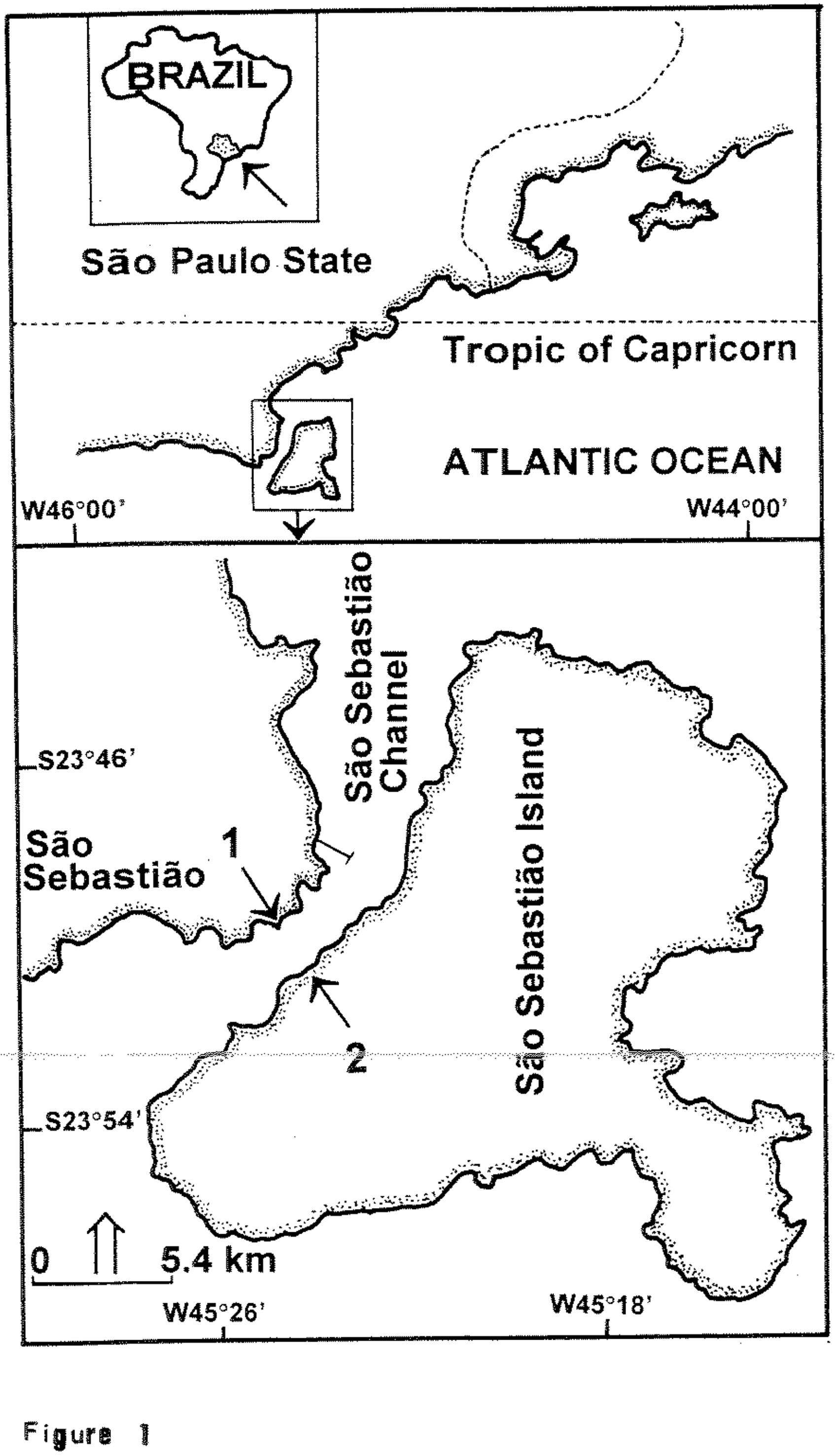
solitary polyp being isolated from the parent colony at the colony edge *via* Edge Fission. Polyp diameter = 0.8 cm. (c) Crevices dividing a colony into several polyp-groups; (d) "Pseudo-Colony Lift-Off". Note how one polyp-group (upper center) becomes an independent ramet *via* the simultaneous loss of connective basal coenenchyme to the neighboring groups and detachment from the substratum; colony thickness = 4.5 cm.

Figure 5. Fission *via* Teardrop Formation. (a) Tissue grows beyond the substratum; note two different colonies, each one exhibiting teardrop tissue hanging at the edge of the parent colony, detached from the substratum; (b) The basal coenenchyme extending and breaking during autotomy, facilitating break-away of a Teardrop-piece from the parent colony. (c) Teardrop tissue hanging at the colony edge (boulder wall) and growing toward the sand bottom. (d) Teardrop tissue which was not released; instead, the tissue grew, attached and colonized the substrate. Polyp diameter = 1 cm.

Figure 6. Polyp Ball Production. (a) A group of 9 polyps growing up and outward from the colony surface (center left). (b) A polyp ball remains connected to neighboring polyps *via* distal coenenchyme, but not attached to the substratum. (c) Polyp ball being release from the parent colony, after separation of the coenenchyme.

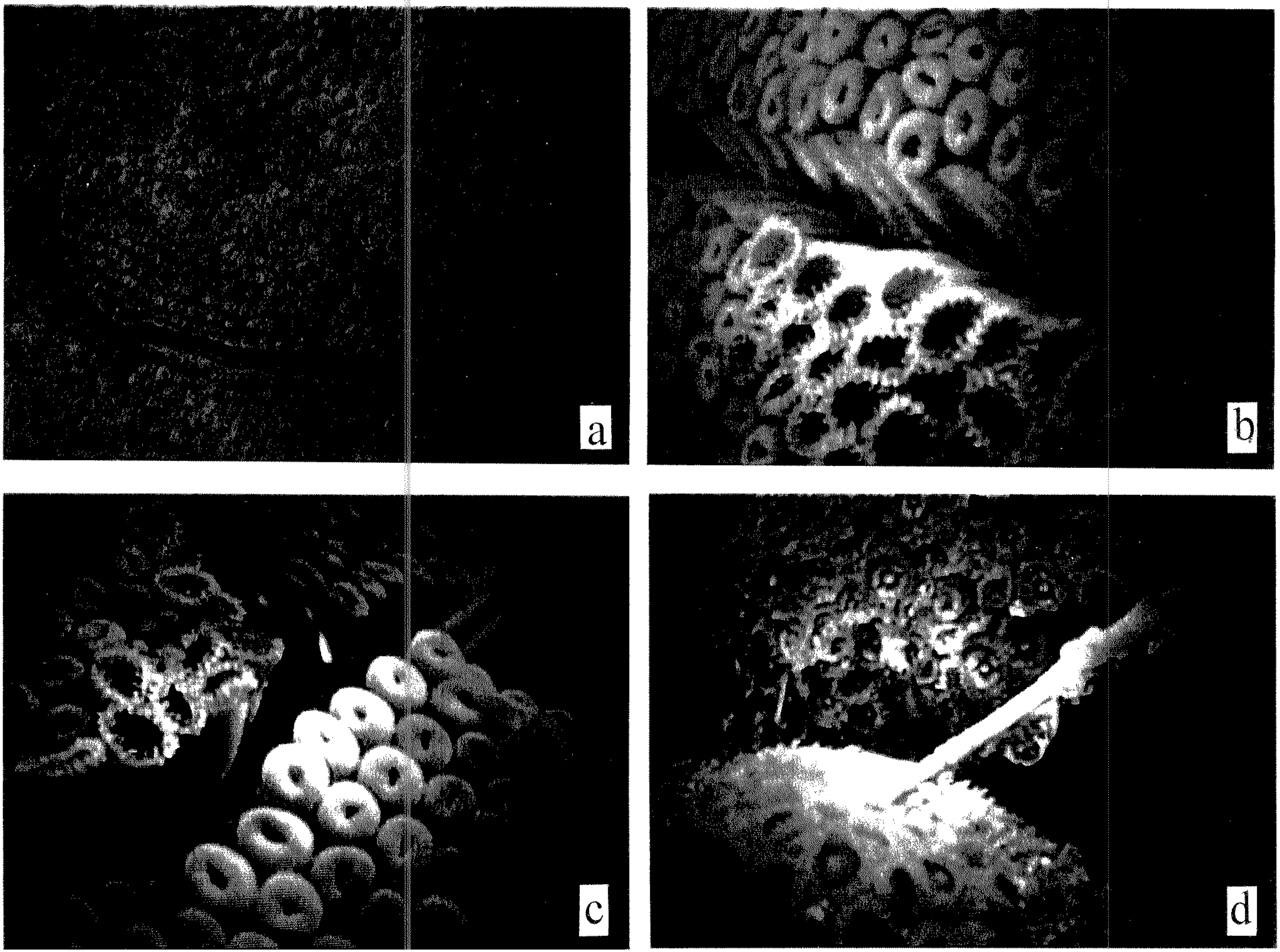
Table Legends

Table 1. Comparisons of the four variants of fission found in *Palythoa caribaeorum*.



BRAZIL
São Paulo State
Tropic of Capricorn
ATLANTIC OCEAN
W46°00'
W44°00'
São Sebastião Channel
São Sebastião Island
S23°46'
São Sebastião
1
2
S23°54'
0
5.4 km
W45°26'
W45°18'

Figure 1


a
b
c
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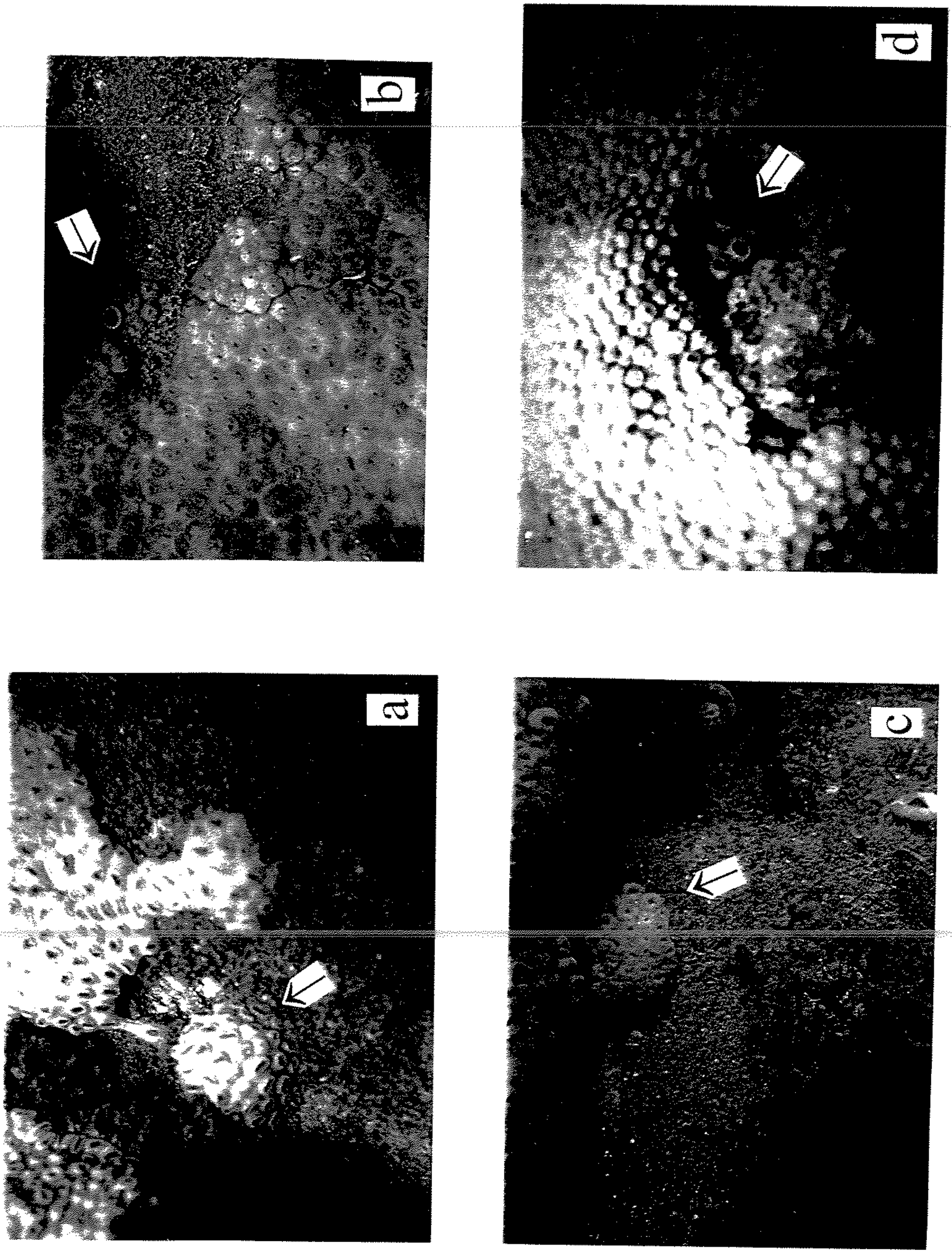
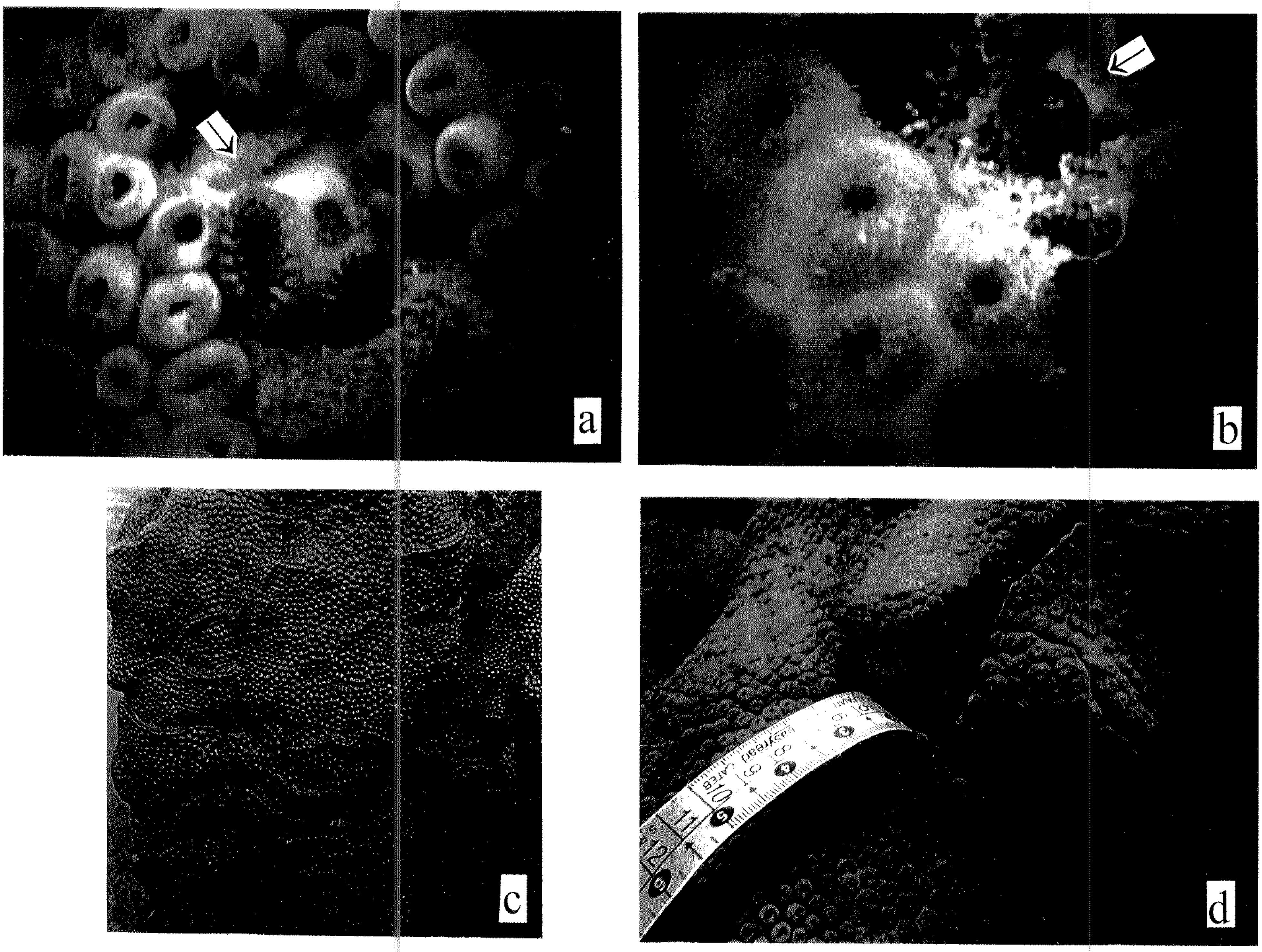


Fig 3


a
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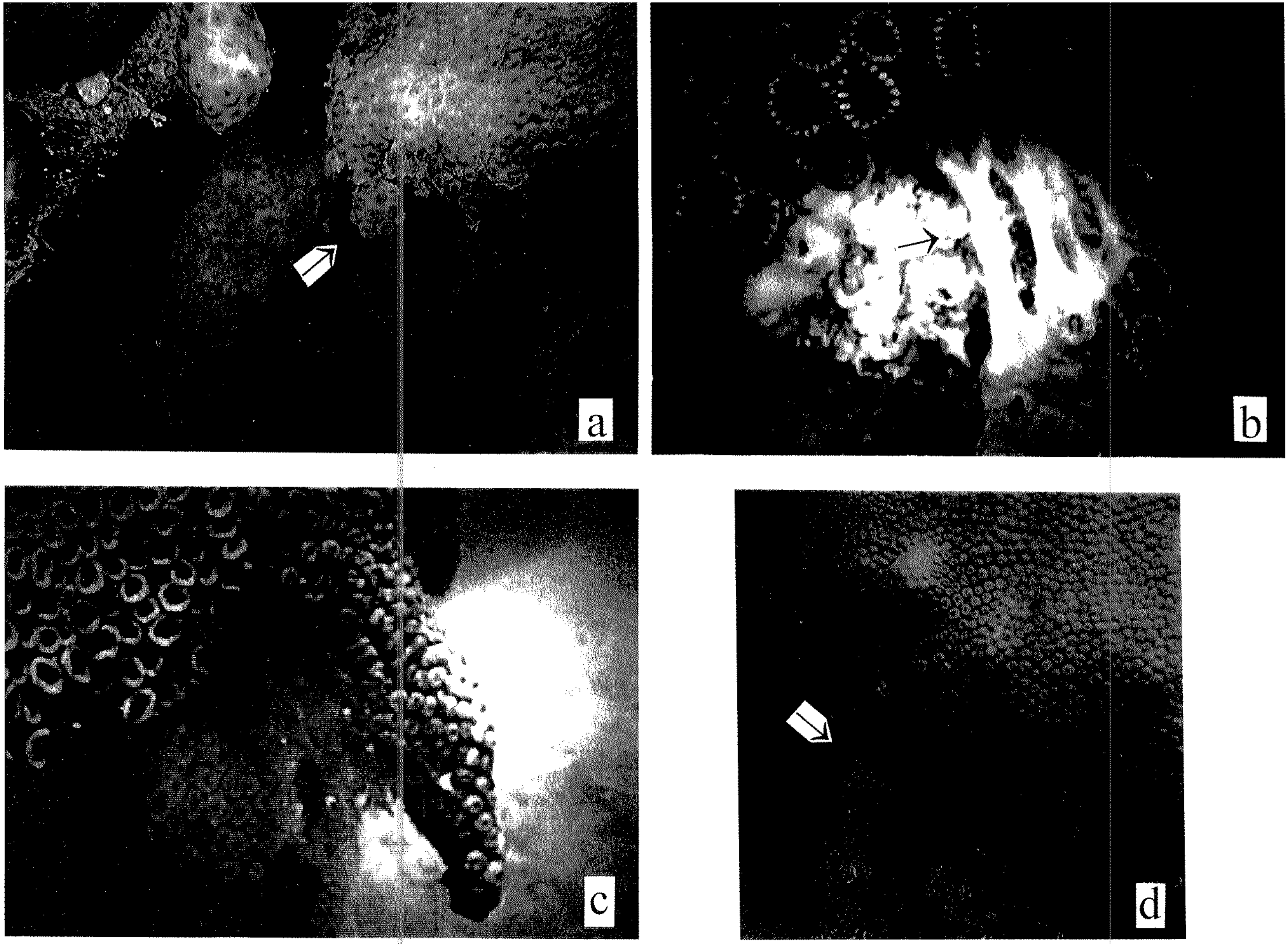
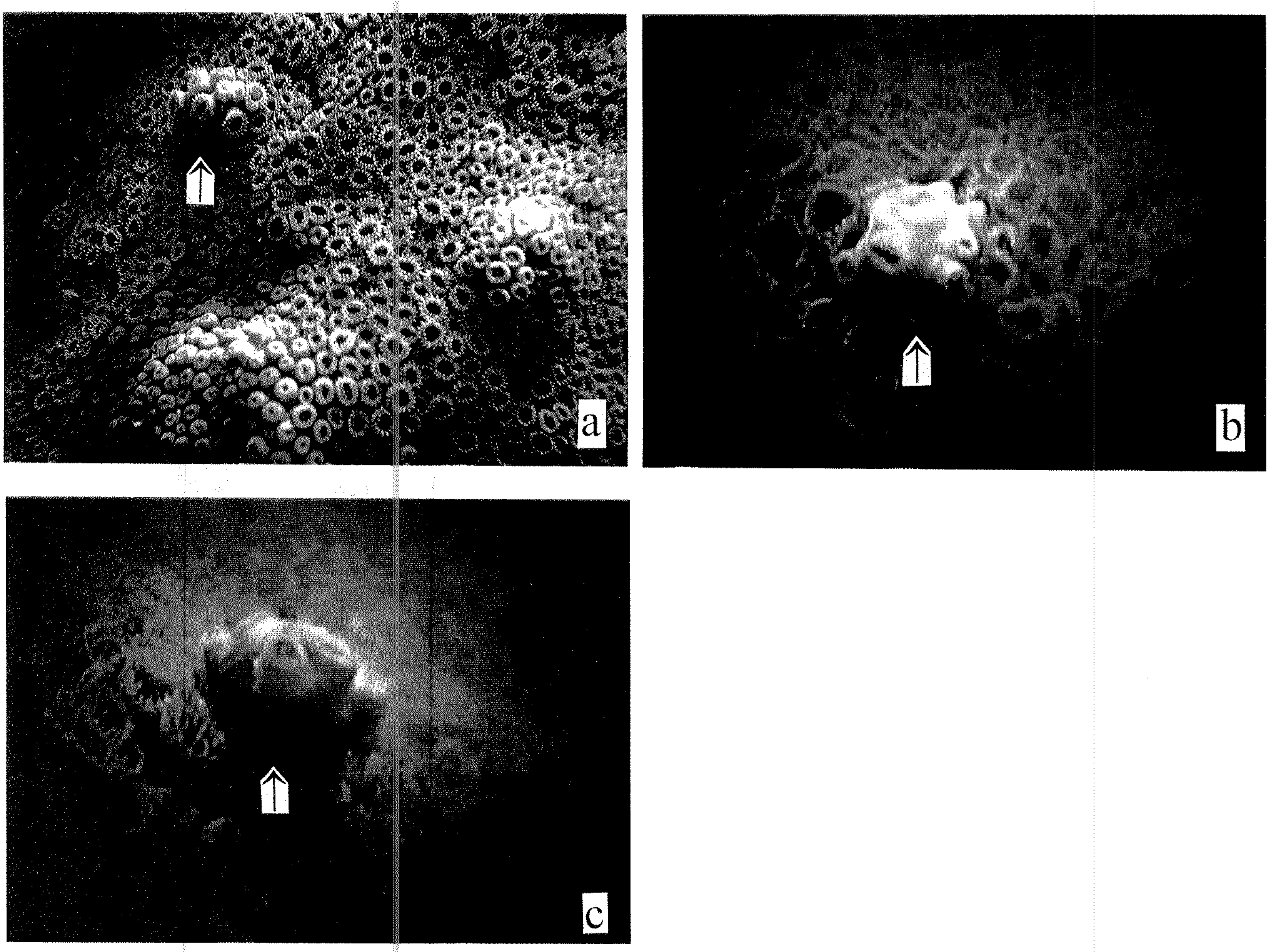


Fig 5


a
b
c

	Edge Fission	Pseudo-Colony Lift-Off	Teardrop Formation	Polyp-Ball Production
Process 1.				
Pseudo-Fission followed by fission	Yes (obligatory)	Yes (obligatory)	No	No
Ramet precursor	Pseudo-Colony	Pseudo-Colony		
Precursor position in the colony	Edge	Center		
Precursor Attachment to the substratum	Yes	Yes		
Precu. promote separation from the substratum	No	Yes		
Fission (breakage)	Basal Coenenchyme	Basal Coenenchyme		
Process 2.				
Directional Tissue Growth followed by fission	No	No	Yes	Yes
Ramet Precursor			Teardrop tissue	Emerging Polyps Ball-Shape
Precursor position in the colony			Edge	Commonly center
Precursor Attachment to the substratum			No - Hanging	No, only to neighbor polyps
Fission (breakage)			Autotomy or extrinsic	Distal Coenenchyme
Frequency of Fission Process	Frequent	Common	Common	Rare
Ramet Dispersal	Remain besides the parent for weeks or months	Diperse Almost Immediately	Disperse Immediately	Disperse Immediately
Sexual Maturity of the Ramet	Mature	Mature	Mature	?
****Reprodutive effort**				
(% polyps with gonad, n)	Medium (42%, n = 240)	High (68%,n = 170)	Medium (38%, n = 90)	?
Relative Ramet Size	Medium	Large	Small	Small
Ramet Polyp Size	Small	Large (>2.5 to 6cm)	Small	Normal (1 - 1.5 cm)
Presence of Exogenous Factors				
Substratum limitation	yes/ not necessarily	yes	yes	Not necessarily
Light limitation	yes	no	yes	no
Interespecific competition for space	yes	no	yes (avoided while hanging)	no
Intraspecific competition for space	not (inhibited)	no (different genotypes within the colony?)	no	no
Substratum irregularity (*e.g.* shells)	no	no	no	yes
Fission variant enhanced by	Low-medium density or % cover	Large colonies with substratum limitation	Any colony with substratum limitation growing in boulders above the bottom	Substratum irregularities

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* Tissue can continue its growing, be fixed, and explore new micro-habitats.

** Source Acosta et al. in progress

Capítulo II

Marine Ecology Progress Series - Submetido para publicação

Asexual Reproduction in a Zoanthid : Quantitative Aspects of Fission

by

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Running Head: Fission in *Palythoa caribaeorum*

Key Words: Asexual reproduction, Brazil, Clones, Fission, *Palythoa caribaeorum*, Ramets, Seasonal Variation, Zoanthidea.

ABSTRACT

Asexual reproduction plays an important role in the life history, population dynamics, and genetic structure of invertebrates. Several populations of the zoanthid *Palythoa caribaeorum* were followed and quantified for one year on the São Paulo coast, Brazil. The dominant variants of fission were measured in these populations, including Edge-Fission, Pseudo-Colony Lift-Off, and Teardrop Formation (these fission processes have been described for this species elsewhere in a sister study). We also examined whether there were significant differences in the frequency of fission between moderately *vs.* highly stressed environments, with respect to depth and season. The impact on ramet production on population growth was also assessed. Edge Fission was the predominant form of asexual reproduction in this species. 55% of the monitored colonies ($n_t = 579$) exhibited at least one variant of fission, yielding 1,304 ramets in the period of one year. Fission occurred all year-round and in colonies of all sizes. The minimum size of a colony reproducing by fission was 5 cm^2. The frequency of fission increased with colony size. There was no significant difference in ramet production between different study sites, nor did it vary between depths or seasons. The time required to produce a ramet varied between colonies, requiring 3–12 months, with equal probability. Release of a ramet, once formed, however, generally occurred within three months of production. Ramet release also occurred all year, although it decreased significantly during the winter when environmental conditions were harsh. Currents may assist ramet release and dispersal. 80% of the ramets produced were between 0.25 and 36 cm^2 in area, irrespective of variant of production. The adaptive value of fission for *P. caribaeorum* lies in its contribution to the number of clone-mates. These variants of

fission represent a critical and important form of asexual reproduction, which helps to explain the evolutionary success of this species in the western Atlantic.

INTRODUCTION

The population dynamics of most clonal animals and plants are driven by the births and deaths of asexually produced individuals (ramets), while recruitment of sexual propagules into the population is an infrequent event (Harper 1977, Cook 1985, Jackson 1985, Eriksson 1989, Shostak 1993). The heavy reliance of some benthic invertebrate populations on vegetative reproduction affects their distribution, abundance, ecology, and genetic diversity (Lasker 1983, McFadden 1997, Tanner 1999). Asexual reproduction is considered most adaptive when it is associated with populating habitat space near the parent when fitness heritability may be high. It is also adaptive when associated with rapid colonization of new space when favorable conditions occur in an unstable environment; sexual reproduction, on the other hand, is considered adaptive when associated with dispersal of offspring to distant, unpredictable habitats (Williams 1975, Glesener & Tilman 1978, Bell 1982, Shostak 1993).

Fission is a biological characteristic, which has been selected over evolutionary time and incorporated into the life history of sea anemones, fungiid corals, octocorals, bryozoans, and other Metazoa (Francis 1973, 1979, Chia 1976, Highsmith 1982, Sebens 1982a, Jackson & Coates 1986, Lasker 1983, 1988, Hughes 1989, McFadden 1991, Shostak 1993). The impetus for fission may be intrinsic or extrinsic, and the organism's response is a function of complex interactions between environmental and genetic constraints on colony morphology (Cameron & Endean 1985, Devantier & Endean 1989). Fission is known to have effects at the population level in a number of benthic marine species, and may affect such factors as demography (Cook 1983, Hughes 1988, Hughes & Jackson 1985, Shick 1991), population size (Tanner 1997, 1999), size distribution, fitness (McFadden 1991), genet longevity

(McFadden 1997), and genetic structure (Hoffmann 1987, Mladenov & Emson 1990, Karlson 1991, Shaw 1991, Hughes et al. 1992, Hunter 1993, Burnett et al. 1994, 1995, McFadden 1997, Vrijenhoek 1998). At the individual level, fission may assist in maximizing nutrient intake (by increasing surface : volume ratios through the creation of smaller colonies; MacFadden 1986, Anthony 1997), energy input (Minasian 1982), colony growth (Yamazato & Isa 1981), or asexual reproduction output – due to changes in transition sizes (Tanner 1999).

Fission is an important process in the Zoanthidea because it is the primary agent of regulating populations (*e.g. Palythoa caesia*; Tanner 1997, 1999), and their structure (*e.g. Zoanthus sociatus* and *Z. solanderi* Karlson 1991, *P. caesia* Burnett et al. 1994).

The distribution and predominance of the zoanthid *Palythoa caribaeorum* on the western Atlantic may be explained by the following: 1) its high tolerance to environmental variability (Cooke 1976, Sebens 1982b); 2) high growth rate (Suchanek & Green 1981); 3) interspecific competitive abilities with respect to space (Suchanek & Green 1981, Gleibs 1994); 4) toughened skeleton due to inorganic matter incorporated into its tissues (Haywick & Muller 1997); 5) toxins (palytoxin) which act as predator deterrents (Gleibs 1994); and 6) reproductive abilities (Fadlallah et al. 1984, Gleibs 1994, Acosta et al. 1997, 1998a,b, Acosta et al. in review – chapter 1). The relative contributions of new propagules derived from sexual *vs.* asexual reproduction have not yet been determined for *P. caribaeorum*. Nevertheless, the reproductive effort of *P. caribaeorum* seems to be high when compared to *Zoanthus sociatus* and *Z. solanderi* (Fadlallah et al. 1984). In this study, the importance and contribution of asexual reproduction for *P. caribaeorum* will be examined.

Palythoa caribaeorum reproduces asexually *via* four variations of fission (Acosta et al. in review – chapter 1) and two types of fragmentation (after partial colony mortality and due physical disturbance; Acosta et al. in review – chapter 3). Only 7.2% of the population exhibited fragmentation, producing 64 new ramets after a year period (Acosta et al. in review – chapter 3). In contrast with other zoanthids and scleractinian corals (Highsmith 1982, Karlson 1986), fragmentation in *P. caribaeorum* does not appear to play a critical role in ramet production and population growth in São Paulo populations, Brazil (Acosta et al. in review – chapter 3). Data collected during the summer on the Santa Marta coast of Colombia suggests that fission in *P. caribaeorum* is important in terms of population growth (Gonzalez 1999). Tanner (1997) found that fission played an important role in reproduction in *P. caesia.*

Three variants of fission recently described - "Edge Fission", "Pseudo Colony Lift Off", and "Teardrop Formation" - appear to be common in Brazilian populations of *P. caribaeorum* (Acosta et al. 1998a, Acosta et al. in review – chapter 1). Polyp Ball Production appears to be rare (Acosta et al. in review – chapter 1). Edge Fission and Pseudo-Colony Lift-Off are variants of fission which require crevice-formation in the colony, where polyp-groups are formed, being connected to each other by a thin basal coenenchyme (see for the use of basal coenenchyme Duerden 1898). This is followed by fission or physical separation from the parent colony *via* the severing of interconnective basal coenenchyme surrounding a polyp-group. Edge Fission is the separation of a polyp-group at the colony edge, where the new ramet remains beside the parent colony before dispersing. Pseudo-Colony Lift-Off occurs at the center of large colonies (bearing large-fertile polyps), where a polyp–group separates itself simultaneously from neighboring polyp-groups and the substratum, then lifts off and drifts away. Teardrop Formation employs a different process. Here, the colony promotes directed tissue growth into a teardrop form in such a way that it hangs beyond the edge of the colony and then breaks off due to autotomy or external forces.

There are no data regarding the production of ramets on a per annum basis for *Palythoa caribaeorum*, let alone for each variant of fission. *Palythoa caesia* is known to produce a constant supply of ramets *via* asexual reproduction (Tanner 1997), as do scleractinian corals (Fadlallah 1981) and other groups (Schmidt 1970, Sebens 1980b, Minasian 1982, McFadden 1991, Lin et al. 1992, Chao & Tsai 1995). In addition, no information exists on seasonal variation in ramet formation and ramet dispersal, ramet size, and the role of fission in the population growth of *P. caribaeorum*. Information related to these topics has been reported for a variety of other species, however, including zoanthids (see Connell 1973, Highsmith 1982, Hughes 1984, Wulff 1985, Karlson 1986, 1988b, Lasker 1990, Karlson 1991, McFadden 1991, Dahan & Benayahu 1997, Ryland 1997, Tanner 1999).

It has been suggested that some organisms respond to physical stress and partial colony mortality through an increase in fission rate (Schmidt 1970, Chia 1976, Harper 1977, Johnson & Shick 1977, Cook 1978, Minasian & Mariscal 1979, Shick & Hoffmann 1980, Lasker 1990, Shostak 1993). Here, we attempted to determine whether there are significant differences in fission rate between populations of *P. caribaeorum* in moderately *vs.* highly stressed environments (i.e. under different light and sedimentation regimes), and also with respect to different depth and seasons.

Here we present quantitative data regarding three of the aforementioned variants of fission. We will demonstrate that: 1) fission is commonly used by *Palythoa caribaeorum* in Brazil, and may make a significant contribution to population growth; 2) fission occurs all year-round in this species and in colonies of any size; 3) Edge Fission is the most common form of fission in this species; 4) the frequency of fission remains constant through time, despite seasonal and environmental fluctuations associated with the environment; and 5) ramet size is generally constant, irrespective of the variant of fission which produced the ramet. We will also discuss whether the rate of fission decreases when energy is channeled into sexual reproduction, as proposed by Minasian (1982) and Herberts (1987), in light of the results presented here.

METHODS

Study Site

Populations of *Palythoa caribaeorum* were studied on the São Paulo coast, Brazil, near the southern latitudinal limit of its geographical distribution (23° S.). Study sites were located on both sides of the São Sebastião channel (Fig. 1). This region is subject to frequent polar disturbances and associated cold fronts and storms. The local currents are forced mainly by winds (equatorial or poleward) and shelf circulation (Carelli 1995, Castro Fo 1990). Surface seawater temperatures (SSTs) and salinities fluctuate widely throughout the year (15-31°C; 22-36‰; CEBIMar 1991). The summer (rainy season, December 21 to March 21) is characterized by high SSTs (26.2°C), low salinities, and low current velocities (< 0.2 m s^{-1}), predominantly SW (Carelli 1995). The average current velocity during the winter, spring, and autumn is 0.4 - 0.6 m s^{-1}, predominantly NE (Carelli 1995). Winter temperatures averaged 21.3°C, with high wind and waves (Castro Fo 1990). Tidal currents are 0.03 m s^{-1} (Carelli 1995) with a mean tidal flux of 0.66 m. Turbidity is relatively high (visibility < 4.3m, annual mean; Acosta et al. in review – chapter 2 and 4).

The shores bordering the channel are characterized by alternating sandy and rocky beaches; in addition sand, debris, and boulders of various sizes, creating a three-dimensionally complex hard-bottom. *Palythoa caribaeorum* colonies commonly grew as a single large unit over the boulders.

Sampling

Populations of *Palythoa caribaeorum* were monitored closely at two sites. Praia Portinho (PPo), on São Sebastião Island, and Ponta Recife (PR; Fig. 1), and at two depths in the sub-tidal - 0.5-1.5 m, and 2.5-4.0 m. Sites and depths were chosen to represent different environmental conditions under which this process of fission would be occurring. In May 1997, three random replicate plots were delineated at each depth (n = 12), with 36-85 colonies in each. Colonies were selected around random points, defined by a large grid and a random numbers table (Rohlf & Sokal 1995). *In toto*, 579 colonies, including a wide variety of size classes (range: 2.5×10^{-5} m^2 to 2.1 m^2), were monitored for one year (from May 1997 to May 1998). Colonies were quantified every three months near the end of each season (each sampling of 15 to 45 days depending of environmental conditions) - August 1997 (end of winter), November 1997 (spring), February 1998 (summer), and May 1998 (fall). Colonies were mapped using acrylic tables, noting the position of all polyp-groups and ramets to measure changes through time. Percent-cover of *P. caribaeorum* was quantified *via* a random-point technique along a chain transect, sampling 100 points per depth.

The morphological characters of the *Palythoa caribaeorum* colonies and changes in them through time, described in Acosta et al. (in review – chapter 1), were used to facilitate quantification of the asexual reproductive process in the field. The dynamics of the fission processes, ramet production, and ramet release in general were assessed using the following variables: 1) *Colony size* - expressed in area (maximum colony length x maximum width); this character was also used to facilitate re-location and identification of specific colonies; we define a colony as a group of polyps physically independent from other groups, even if comprised itself of tens or hundreds of inter-connected polyp-groups, or even if separated only by a few millimeters from the other groups. 2) *Cumulative length of crevices.* Crevices occur externally in the colony surface. Actively forming crevices (*i.e.* those actively spreading throughout the colony) were monitored, being measured with a cloth tape, in order to follow pseudo-fission in progress (fully developed crevices already defining polyp-groups were not included). 3) *Number and area of polyp-groups* - precursors of true ramets. 4) *Number and area of "teardrop formation"* - tissue exhibiting active growth, hanging from the colony edge. 5) *Time required for ramet formation* – period of development from initiation of the fission process (or from t_0, at initiation of the study) to development of a true ramet. 6) *Number of ramets produced per colony, and variant of fission from which they were derived.* This included ramets produced and released between samplings (comparing the total number of polyp-groups, tissue pieces, and ramets per colony per sampling period; Fig. 2). A ramet was considered to be a group of polyps physically disconnected from the parent colony. The presence or absence of basal coenenchyme connecting tissue around the ramet was verified using a small plastic knife, which was used to pry the polyp-groups apart. 7) *Ramet area*, in order to: a) determine the mean size of the ramets produced by the variants of fission observed here, along with an estimate of variance; b) to facilitate identification and re-location of the ramets and thus determine how long a ramet remained associated with its parent colony prior to dispersal (*e.g.* Edge Fission); and c) determine any seasonal trend in ramet dispersal. 8)

Temporal variation of ramet production – seasonal variations in the fission process. 9) *Area of partial mortality*. Partial mortality was considered any portion of the colony exhibiting lesions or skeletal remnants (*e.g.* caused by disease; Acosta, in review – chapter 4). The area of partial mortality was calculated using the diameter of the affected area (in some cases, maximum length x width).

Measurements of abiotic variables included assessment of incident light using a Secchi disc (measured at both sites from February 1997 to May 1998), and PVC sediment traps, using 12 traps per site (35 cm length x 5 cm diameter, from January 1997 to May 1998) fixed to the bottom and collected seasonally (mgs. dry weight m^{-2} day^{-1}). Intensity of illumination was also quantified several times per week during fall and winter 1997 using a Rigo Submarine Illuminometer at 1.5 and 3 m depth at each site. Seawater surface temperature, salinity, and precipitation were measured daily (8 am and 4 pm.) at the Centro de Biologia Marinha (CEBIMar - USP), located on the continent close to PR. One additional thermometer (min-max) was installed at 1.5 and 3 m depth at both sites to record temperature extremes.

For purposes of normalization, data were log-transformed prior to analysis by parametric statistics (Sokal & Rohlf 1995). Bartlett's and F_{max} Tests for Homogeneity of variances were performed on the data to insure homoscedasticity. Data were analyzed by one-way ANOVA, followed by *a posteriori* tests (Tukey-Kramer test). Differences between means were tested *via* one-way ANOVA's on the following data sets: 1) number of ramets produced per colony *vs.* variants of fission from which they were produced; also *vs.* seasons, sites, depths, habitats (PPo shallow, PPo deeper, PR shallow, PR deeper), and colony size. The size classes defined were small ($\leq$50 cm diameter), medium (51-150 cm), and large (>150 cm). 2) Cumulative length of crevices, number of polyp-groups, partial colony mortality, and ramet size were also compared individually to the three variants of fission occurring in the colonies bearing these characters. 3) Area of partial colony mortality *vs*. the variant of fission occurring in that colony, and *vs*. colony size. 4) Area of tissue lost due to release of ramets *vs*. the variant of fission from which they were derived; also, *vs*. temporal changes in sedimentation rates, water turbidity, temperature, and intensity of illumination. A two-way Model-I ANOVA was also performed on data regarding mean ramet production, colony size, cumulative length of crevices, number of polyps groups per colony, and partial colony mortality as dependent variables with respect to sites and depths.

The total number of colonies exhibiting a particular variant of fission, the number of ramets produced by each variant, and the frequency of colonies requiring 3, 6, 9 or 12 months to produce ramets were compared *via* G-test using William's correction (Sokal & Rohlf 1995). Seasonal changes in ramet dispersal were similarly compared. The relationship between colony area and number of ramet produced per colony was analyzed through linear regression.

RESULTS

Frequency of Fission

Fission was common in *Palythoa caribaeorum*, occurring in 55% of the 579 colonies monitored over the period of one year. An additional 19.2% of the population exhibited signs of fission in progress, such as active crevice formation and an increase in the number of polyp-groups. These yielded a total of 74.2% of the population actively exhibiting fission.

Of those colonies exhibiting fission (n = 320) 47.8 to 74.1% were observed to reproduce asexually by more than one variant, either simultaneously or sequentially (Table 1, Fig. 2).

The total number of ramets produced and released within one year for 320 colonies was 1,304. This was almost twice the total number of polyp groups (767) produced within those colonies over the same time. This was in addition to the 1,772 polyp-groups, already present in the population at the beginning of the study. Clearly, this represents a high rate of fission.

Quantitative Comparisons of the Three Variants of Fission

The number of colonies exhibiting one variant of fission or other varied significantly from each other ($p < 0.001$, G-test with William's correction; Table 1 & Fig. 3), with Edge Fission having the highest frequency (Fig. 3). There was also a significant difference in the number of ramets produced by each of these variants of fission ($p < 0.001$, G-test with William's correction; Fig. 3), and for the mean number of ramets produced per colony for each variant ($p < 0.001$, one-way ANOVA; Table 1). Once again, Edge Fission yielded the highest number of ramets per colony ($p < 0.05$, Tukey-Kramer Test; Fig. 3).

Colonies using Edge Fission, Pseudo-Colony Lift-Off, or Teardrop Formation, respectively, were found to be significantly different with respect to mean values of the following (Fig. 4): 1) cumulative length of crevices produced per colony ($p < 0.001$, one-way ANOVA); 2) number of polyp-groups per colony ($p < 0.05$); 3) area of partial mortality per colony ($p < 0.001$); and 4) size of parent colony ($p < 0.05$). *A posteriori* test indicated that fission by Teardrop Formation had significantly higher levels of all of the above factors than

Edge Fission or Pseudo-Colony Lift-Off ($p < 0.05$, Tukey-Kramer Test). This result supports differences previously found between these variants of fission. Additional details comparing fission variants are presented in Table 1.

Reproductive Size

Fission occurred in colonies of all sizes, ranging from 5 cm^2 to 2.17 m^2, and all colony thicknesses, from 0.5 mm to 6.0 cm high. The minimum size for colonies reproducing *via* Edge Fission, Pseudo-Colony Lift-Off, and Teardrop Formation was 5.0 cm^2, 97.0 cm^2, and 89 cm^2, respectively. A positive and highly significant linear relationship was found to occur between colony area and number of ramets produced per colony ($p < 0.001$, linear regression, $n = 311$, Fig. 5). Larger colonies exhibited more fission than smaller ones. The minimum colony size observed for fission was 5 cm^2; the minimum average colony size estimated by the regression model to produce one ramet ($Y = 1$) was 61.5 cm^2.

The mean number of ramets produced per colony and the mean area of partial mortality were significantly different between small, medium, and large colonies ($p < 0.01$, one-way ANOVA $n = 320$). Larger colonies exhibited higher frequencies of fission and partial mortality than medium and small colonies ($p < 0.05$, Tukey-Kramer Test).

Ramet Size

Mean ramet size did not vary significantly between the three variants of fission ($p > 0.05$, one-way ANOVA; Table 1). Size-frequency analyzes indicated that 80% of the ramets were between 0.25 and 36 cm^2, irrespective of reproductive variant (Fig. 6). The largest ramet observed 1,518 cm^2 was produced *via* Pseudo-Colony Lift-Off (Table 1).

Temporal Variation

There was no seasonal variation in any of the following: mean cumulative length of crevices, mean number of polyp-groups, and mean number of ramet produced per colony ($p > 0.05$, one-way ANOVA; Fig. 7a,b,c).

There was no significant difference between the frequencies of colonies requiring 3, 6, 9, or 12 months to produce ramets ($p > 0.05$, G-test with William's correction; Fig. 8a), suggesting a constant production rate. Once a ramet was formed (*e.g. via* Edge Fission), however, a significantly greater proportion of colonies released them within three months ($p < 0.001$, G-test with William's correction; Fig. 8b).

Ramet dispersal, however, did vary significantly with respect to time ($p < 0.001$, G-test with William´s correction; Fig. 7d). The frequency of ramet dispersed was lower in the winter than in the other seasons.

In most cases, currents and wave action were the principal forces of dispersal for ramets. The ramets were slightly negatively buoyant and were transported along the bottom. They survived without attachment to the substratum, even on sand. When a newly produced ramet encountered a suitable place for settlement, it expanded its polyps to stabilize itself. Reattachment was slow, usually requiring weeks or months, and was dependent upon degree of water movement.

Variation between Sites and Depths

There was no significant variation between sites or depths with respect to any of the following characters: mean colony size, mean area of partial colony mortality, mean cumulative length of crevices, mean number of polyp-groups, and mean number of ramets produced per colony ($p > 0.05$, one-way ANOVA; Table 2a).

The mean number of polyp-groups per colony did vary significantly, however, with respect to depths ($p = 0.014$, one-way ANOVA) and habitat ($p < 0.05$, one-way ANOVA). The number of polyp groups was higher in deeper water (7.9 +/- 14.8, $n = 153$) than in shallow water (5.3 +/- 7.2, $n = 167$; $p < 0.05$, Tukey-Kramer Test). The mean number of polyp-groups was highest at the PR-deeper site, followed by PPo-deeper, PPo-shallow, and PR-shallow ($p < 0.05$, Tukey-Kramer Test, Table 2a).

No significant variation was found between sites and depths in any of the following variables: mean number of ramets produced per colony, mean cumulative length of crevices, mean number of polyp-groups, and mean area of partial colony mortality ($p > 0.05$, two-way model-I ANOVA; Table 2b). Nor were any significant higher-order interactions noted.

Partial Mortality

Partial mortality accounted for < 5.3% of the area in colonies exhibiting all three variants of fission (Table 1). In colonies reproducing by fission, the mean area of ramets produced and dispersed per colony was significantly higher than the area lost due to partial colony mortality ($p < 0.001$, one-way ANOVA; Table 1). The same pattern was also true under conditions of Edge Fission and Teardrop Formation, respectively ($p < 0.001$, one-way ANOVA). This was not the case, however, for Pseudo-Colony Lift-Off ($p > 0.05$, one-way ANOVA).

Other sessile epibenthic invertebrates rarely colonized substrate which was freed up as a consequence of partial mortality or ramet dispersal. These areas were generally re-occupied slowly *via* colony growth.

Cover of *Palythoa caribaeorum*

P. caribaeorum was the dominant benthic organism in the study area. It accounted for 37-65% of the hard cover in shallow (0.5-1.5 m) and deeper (2.5-4.0 m) waters, respectively.

Abiotic Factors

Mean sedimentation rates varied significantly through time ($p < 0.01$, one-way ANOVA), being higher in the winter (124.5 +/- 145 mg cm^{-2} day^{-1}, n = 37) than in the other seasons (15.1 to 16.5 +/- 12.5 mg cm^{-2} day^{-1}, n = 82; $p < 0.01$, Tukey-Kramer Test). The maximum sediment value was observed during the winter in a 15-day period of continuous storms (483.5 mg cm^{-2} day^{-1}). Mean Secchi disc values averaged between 3.5 and 4.3 +/- 2.0 m (n = 129) throughout the year, and were not significantly different between seasons ($p > 0.05$, one-way ANOVA).

The two sites differed in mean sedimentation rate ($p < 0.01$, one-way ANOVA, n = 134) and light levels ($p < 0.05$, one-way ANOVA, n = 130). PR possessed a higher sedimentation rate (62.8 +/- 114 mg cm^{-2} day^{-1} at PR *vs.* 35.1 +/- 70.4 mg cm^{-2} day^{-1} at PPo) and lower light levels (3.5 +/- 1.7 m *vs.* 4.8 +/- 1.8 m, Secchi disc) than PPo ($p < 0.05$, T′-Tukey-Kramer- GT2 methods). The mean annual water temperature was not significantly different between sites (23.0 +/- 2.1°C; $p > 0.05$, one-way ANOVA, n = 112), with minimum value during the winter 15.5°C and maximum during the summer 29.3°C (n = 143).

Intensity of illumination differed significantly between depths ($p < 0.05$, one-way ANOVA), whether data for sites were pooled or analyzed separately. The shallow water sites received higher mean levels of light (2,043 +/- 1,084 lux, n = 50) than deeper ones (1,259 +/- 866 lux, n = 50, $p < 0.05$, Tukey-Kramer Test). PPo received a higher intensity of illumination than PR at both depths. Mean sedimentation rates did not vary significantly between depths (55.7 +/- 108.6 mg cm^{-2} day^{-1} shallow *vs.* 42.3 +/- 80.8 mg cm^{-2} day^{-1} deeper, $p > 0.05$, one-way ANOVA, n = 134) when sites were pooled.

DISCUSSION

Impact of Fission on Population Growth

The total number of ramets (1,304) produced by 320 of the 579 monitored colonies could potentially increase the population size at least two-fold in a short time, if all survived. The number of ramets and the potential ramets represented by new polyp-groups (767), produced during the period of a year, could potentially increase the population size by 225%. 74.2% of the population in Brazil exhibited active fission. This agrees with the results of Gonzalez (1999), who found that 273 of 383 Colombian *Palythoa caribaeorum* colonies exhibited fission (71%) and produced 1,474 ramets *via* the same three variants of fission. Although Gonzalez's data correspond to a single set of samples in space and time, they are even higher than those reported here for Brazil. In Colombia, the population size might increase by as much as 384% during a summer (Gonzalez 1999). There are several possible explanations for the observed geographical differences, and one is related to densitydependence (Tanner 1999). Populations in Colombia are less dense and have a lower cover (19%) than populations in Brazil; thus, according to Tanner's (1999) hypotheses, they may be expected to reproduce more by fission. The Colombian populations also had a lower mean size, in further supporting this premise (see Acosta et al. in review). Differences in environmental conditions, such as a higher intensity of interspecific competition for space with scleractinian corals, and higher levels of predation from the fire worm *Hermodice carunculata* in Colombia, may also have influenced fission rates differentially (Acosta et al. in review).

The genus *Palythoa* is generally considered to have a high rate of asexual reproduction (Cooke 1976). The results here support this premise, but the high rates of fission observed in *P. caribaeorum* are more than three times those observed by Tanner (1997) in *P. caesia*. This suggests species-specific differences in fission rates.

Estimates of mortality before and after settlement of ramets are not known at this time for *Palythoa caribaeorum*. The large number of ramets produced in *P. caribaeorum*, and the diversity of fission variants employed suggest that fission may have a substantial impact on population growth, facilitating colonization and expansion of genets into nearby available space. We propose that *P. caribaeorum* may be more heavily dependent upon vegetative *vs.* sexual reproduction. Settlement of propagules from asexual was higher than from sexual larvae in the study plots (A. Acosta, unp. data). The large production of clones here is also associated with a high degree of fertility in *P. caribaeorum* (Acosta et al. in progress). This contrasts with reports of high infertility for this species in the Caribbean, and in zoanthids such as *P. tuberculosa* (Kimura et al. 1972, Fadlallah et al. 1984, Ryland & Babcock 1991; Ryland 1997). McFadden (1991) found that in the temperate soft coral *Alcyonium* sp., reproduction is primarily by asexual ramets, and sexual propagules rarely enter the population. This also seems to be the case with *P. caribaeorum*. She predicted that sexual reproduction had a negligible impact on fitness and that if asexual reproduction by fission were eliminated, fitness would be greatly reduced, leading to rapid extinction of the population.

Differential Ramet Production Rates

Edge fission produced the highest number of ramets in comparison to the other variants of fission. The differences in fission rates appeared to be related to habitat, colony condition, and ecological interactions (Acosta et al. in review – chapter 1). Edge Fission occurred independent of substrate type, substrate limitation, colony size, topography, or interspecific competition. It occurred less frequently, however, under conditions of high density or high cover. Pseudo-Colony Lift Off occurred only in large colonies experiencing substrate limitation. Teardrop Formation occurred only under specific conditions such as when a colony was growing on boulders several centimeters above a sand-bottom and was substrate-limited (A. Acosta, in review – chapter 1). Teardrop Formation occurred, however, independent of colony size. Pseudo-Colony Lift Off and Teardrop Formation occurred under more restricted conditions and may be bioenergetically more expensive than Edge Fission, which could in part explain its lower observed frequency.

Minimal Colony Size Required for Fission

There does not appear to be any minimal colony size for fission. Most of the smaller colonies were reproduced *via* Edge Fission (5 cm^2). The ability to undergo fission at a small colony size seems to be common within the *Palythoa* genus. Gonzalez (1999) reported that Edge Fission occurs in Colombian *P. caribaeorum* colonies as small as 4 cm^2 in area. Using a linear regression model, she predicts that the average minimal colony size for fission in *P. caribaeorum* would be 10 cm^2 in area. In Brazil, we found that a minimal average size for such would be 61.5 cm^2. Tanner (1997) indicated that colonies of *P. caesia* divide by fission in size classes of <10 cm^2 (also see Haddon & Shackleton 1891).

There are some advantages associated with initiating asexual reproduction at a small colony size. These include maintaining a small parent colony size; preserving optimal morphological dimensions (Hughes 1989); increasing metabolic rate to promote rapid growth and reproduction (Stoner 1989, Ryland & Warner 1986, Hughes 1989); increasing efficiency of food capture (McFadden 1986); increasing genet size (Chia 1976, Coates & Jackson 1985); and escaping from constraints associated with size (metabolic rate and body mass; Hughes 1989, Acosta et al. in review – chapter 1). Fission is, however, disadvantageous when it repeatedly divides the body into sub-optimal sizes (Sebens 1982a) and keeps individual colony size below the threshold for sexual maturation (Minasian 1982, Bucklin 1987, Stoner 1989). The few studies of sexual reproduction in *Palythoa caribaeorum*, which have been done thus far do not provide details on colony size (Fadlallah et al. 1984, Gleibs 1994, Goncalves & Silveira 1996) and particularly the minimum colony size required for sexual reproduction. Preliminary results from Acosta et al. (in progress) revealed for *P. caribaeorum* that colonies as small as 7 cm^2 and ramets as small as 4 cm^2 (derived from Edge Fission) were mature. *P. caribaeorum* begins to reproduce both sexually and asexually at a very small colony size. In *P. tuberculosa,* colonies 5 - 15 cm in length were already fertile (Kimura et al.

1972, Yamazato et al. 1973). Karlson (1986) suggests that the zoanthid *Zoanthus solanderi* may reproduce sexually at a small size.

Fission rates increased with colony size in *Palythoa caribaeorum*. This agrees with other reports regarding *P. caribaeorum* (Gonzalez 1999), *P. caesia* (Tanner 1997), the soft coral *Alcyonium* sp. (McFadden 1991), and asteroids (Ottesen & Lucas 1982). Several biotic (*e.g.* competition for space, density, Karlson 1980, 1983, Karlson et al. 1996) and abiotic (*e.g.* substrate type) factors, however, may limit colony size and, with it, the maximum potential for asexual reproduction (see Tanner 1999). It seems that *P. caribaeorum* may enhance its own fitness by limiting colony size (Gonzalez 1999, Acosta et al. in progress), and the employment of both sexual and asexual reproductive strategies may help to explain its dominance of shallow benthic areas such as those studied here.

Size Selection and Survival of Ramets

80% of the ramets produced by the three variants of fission were between 0.25 to 36 cm^2 in area. This supports related observations that crevice and polyp-group formation is controlled by the colony (Acosta et al. in review – chapter 1). Fission appears to be an important part of the life history, partially because of its direct effect on ramet size. The size-range observed is probably optimal for successful dispersal and survival of the ramets. It is possible that a "trade-off" exists between ramet size, distance of dispersal, and survival, as has been suggested for sponges (Wulff 1985). The relative advantage of small ramets is that they can be carried over longer distances by local currents. In contrast, large ramets may travel short distances because of their increased weight but may have a longer survival time (due to a larger feeding area, or greater lipid reserves), as has been observed in *Zoanthus solanderi* (Karlson 1986, 1988b).

Ramet survival is known to be a function of size in a number of plants and other clonal organisms (Connell 1973, Highsmith et al. 1980, Hughes & Jackson 1980, Newell et al. 1981, Highsmith 1982, Hughes 1984, Benayahu & Loya 1985, Farrant 1987, Klainman 1990, Lasker 1990, Dahan & Benayahu 1997). Mortality rates for ramets are not yet known in *Palythoa caribaeorum*. If ramet survival is size-dependent in this zoanthid, then a high mortality of ramets may be expected in the lower size classes of *P. caribaeorum*, which are the most common. Ramet production over a wide size spectrum (>36 to 1,518 cm^2) may help to compensate for size-dependent mortality. Low recruitment of ramets in the plots (A. Acosta unp. data) may be explained by high mortality or high dispersal of ramets. Another explanation of the pattern observed here in ramet size is the energetic requirements of production on the part of the parent colony, as has been discussed by other investigators (see Shick 1976, Sebens 1980a, 1982a, Minasian 1982, McFadden 1986, Tun et al. 1997, Acosta et al. in review – chapter 1).

Time Required for Ramet Formation

The time required for ramet formation *via* fission in *Palythoa caribaeorum* varied between 3 and 12 months. Depending upon the specific requirements of the colony, however, the relative position of the polyp-group, and environmental factors, the timing of completion of fission (from crevice formation to true ramets) may require years (A. Acosta, pers. obs.). This is in part because fission process can stop at any time at any stage. The time required to complete a fission event depends upon the species considered, and varies between days to years (Benayahu & Loya 1985, Dinesen 1985, Farrant 1987, Klainman 1990, Mladenov 1996, Dahan & Benayahu 1997). It would appear that *P. caribaeorum* colonies are capable of completing the ramet-formation process over a broad range of time-periods.

Temporal and Site-Specific Variation in Fission

Fission process in *Palythoa caribaeorum* provides a year-round supply of ramets, as it does in the scleractinian coral *Astrangia lajollaensis* (Fadlallah 1981). In anemones and other groups (*e.g.* holothurians), abiotic factors such as temperature have been shown to control fission rates, increasing with increases in temperature and decreasing at extreme low temperatures as 15 °C (Schmidt 1970, Atoda 1973, Johnson & Shick 1977, Minasian 1979, Minasian 1982, Emson & Mladenov 1987, Chao & Tsai 1995). *P. caribaeorum* populations produced ramets even during the winter. Low water temperatures 15 - 17°C, high turbidity, and high sedimentation, characterized winter. Sedimentation rate was one order of magnitude higher than in the other seasons (considered sub-lethal for scleractinian corals; Pastorok & Bilyard 1985, Rogers 1990). Clearly, fluctuations in some environmental variables have no effect on ramet production rate in the population.

Similarly, the degree of environmental stress between different sites (levels of turbidity, light and sedimentation) or different depths (levels of light) did not affect ramet production in *Palythoa caribaeorum* populations. We could not find any evidence to support hypotheses related to increased ramet production in response to higher environmental stress, at least under the conditions studied here.

The high number of polyp-groups per colony observed at the deeper site in PR, however, is difficult to explain. Low light levels and low food availability (Sebens 1977, 1982a, Tsuchida & Potts 1994, Acosta et al. in review – chapter 1) might enhance fission in these habitats (see Steen & Muscatine 1984) by limiting energy input (Sebens 1980a). The evidence here suggests that the specific microhabitat of a colony (*e.g.* substrate, see Acosta et al. in review – chapter 1; density, see Tanner 1999) or a occurrence in a marginal habitat may play an important role in affecting frequency of fission in this zoanthid.

The constant production of asexually produced ramets by *Palythoa caribaeorum* populations may increase the chances of survival in some ramets by spreading the risk of mortality through time and space in this variable environment. On the other hand, simultaneous sexual reproduction in this species will help to maintain levels of genetic variability.

Ramet production did not decrease during the summer when gonads are maturing in *Palythoa caribaeorum* (Cooke 1976, Fadlallah et al. 1984, Acosta 1999a,b, Acosta et al. in progress), which contrasts with Herberts (1987) report that, in a temperate zoanthid, initial stages of gametogenesis inhibit asexual reproduction. Nor did the data here support the predictions of Minasian & Mariscal (1979) and Minasian (1982) that gonadal development should be accompanied by a decrease in the rate of fission for sea anemone. Acosta (1999a,b) suggested that energy must be channeled into gonad production and into fighting a disease that attacks *P. caribaeorum* during the summer; however, despite this, the rate of fission was maintained, suggesting that the cost of fission is low and that asexual reproduction is critical for this species. The reproductive success and population growth afforded by maximizing fission while continuing to produce sexual gametes (Kimura et al. 1972, Fadlallah et al. 1984) could allow survival and maintain of *P. caribaeorum* populations in this environment, characterized by frequent disturbance.

Temporal Variation in Ramet Dispersal

There are several external factors which may stimulate release of the ramet, as in plants (Hartnett & Bazzaz 1983, Hester et al. 1994). A combination of factors related to marginal microhabitats, such as high levels of interspecific competition, low light levels, lack of appropriate substratum for colonization, etc. may help to explain the short time required for ramet dispersal.

A small number of colonies were found to release ramets during the winter. This is counter-intuitive, since one would expect storm waves and high currents, normally associated with that season, to facilitate ramet release (see Dahan & Benayahu 1997, Carelli 1995). This suggests that control of ramet-release (detachment from the substratum) may be under endogenous control, keeping the ramet from exposure to a harsh environment. This, however, remains to be experimentally demonstrated.

Partial Mortality *vs.* Fission

Cook (1978), Karlson (1988a), and Shick (1991) stated that the frequency of asexual reproduction should bear some relation to the source of mortality. In *Palythoa caribaeorum,* total colony mortality was low (Acosta pers. obs.), while partial colony mortality was measurable. The total area lost in *Palythoa* populations due to partial mortality was much smaller than the total area lost in the population *via* fission (Table 1). *P. caribaeorum* colonies experiencing high levels of partial colony mortality also appeared to have higher frequencies of fission. This may be because frequency of fission is also positively correlated with colony size. As proposed by Harper (1977) and Lasker (1990), asexual reproduction may represent an escape mechanism from mortality. Thus, it is possible that *P. caribaeorum* colonies respond to a specific degree of tissue lost by producing at least an equivalent area in ramets dispersed (spreading the risk), enhancing the chance of survival of the genet to a more favorable environment.

Advantages of Ramet Production *via* Fission in *Palythoa*

Fission provides a number of selective advantages for *Palythoa caribaeorum,* including the following: 1) Fission may increase fitness in the parent colony by producing a large number of clonal copies which can themselves reproduce, increasing the number of gametes representing the parental genotype (Hughes 1989). The use of different modes of fission and the production of high number of ramets in *P. caribaeorum*, spreads the risk of mortality of the genet in large populations (Cook 1978), especially in unpredictable environments. 2) Fission in *P. caribaeorum* provides a year-round supply of ramets; in contrast, sexual propagules are produced only in a particular season. 3) This process of fission probably requires less energy than sexual reproduction (Francis 1979, Fadlallah 1982, Hunter 1984, Karlson 1986). 4) Fission at any colony size may represent a strategy by which to overcome certain constraints encountered while growing and expanding. 5) Fission may result in an increase in the local dominance of well-adapted genotypes (Williams 1975).

Fission plays an important role in the life cycle of this species, contributing to its success in the tropical shallow waters of the western Atlantic. Future topics for research might include the effectiveness of fission through quantification of dispersal, success of settlement, ramet survival, and ultimate contribution to population growth, as well as genetic variation of *Palythoa caribaeorum* populations.

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Figure Legends

Figure 1. Study sites in the São Sebastião channel, São Paulo coast, Brazil. 1. Ponta Recife, located on the mainland. 2. Praia Portinho, on an offshore island. T represents the Terminal Maritimo Almirante Barroso (TEBAR).

Figure 2. Example of the dynamics of fission in a typical colony of *Palythoa caribaeorum*, sampled every three months for a period of 18 months. The number of new ramets formed by Edge Fission, Teardrop Formation, and Pseudo-Colony Lift-Off is shown, along with ramet dispersal and number of polyp-groups at any one time. The colony starts at t_0 with 22 polyp-groups, and 2 ramets produced *via* Edge Fission. After 18 months, this colony has 21 polyp-groups (six of which are new), 1 teardrop-tissue formation, and has produced and released 10 ramets - five of them *via* Edge Fission, four *via* Pseudo-Colony Lift-Off, and one *via* Teardrop Formation. When crevices meet, a polyp-group is formed; ramets are formed from a polyp-group, which separate from the parent colony. Thus, note that the number of polyp-groups decreases with ramet formation and increases when crevices meet.

Figure 3. Total number of ramets produced by a given form of fission in *Palythoa caribaeorum* - “Edge-Fission”, “Pseudo-Colony Lift-Off” and “Teardrop Formation”, respectively. Number of parent colonies exhibiting a given reproductive variant shown by open bar; number of ramets produced by those

colonies shown by shaded bar. Any given colony may reproduce by one or more variants of fission simultaneously. $n_i = 320$ (total number of parent colonies exhibiting fission); 1,358 (total number of ramets produced); 247 (total number of parent colonies exhibiting Edge Fission); 948 (total number of ramets produced by Edge Fission); 137 (total number of parent colonies exhibiting Pseudo-Colony Lift-Off); 262 (total number of ramets produced by Pseudo-Colony Lift-Off); 58 (total number of parent colonies exhibiting Teardrop Formation); and 84 (total number of ramets produced by Teardrop Formation).

Figure 4. Comparison between colonies exhibiting Edge Fission ($n = 247$), Pseudo-Colony Lift-Off ($n = 137$), and Teardrop Formation ($n = 58$). Mean value per colony given for (a) length of crevices (cm); (b) abundance of polyp-groups; (c) area of partial colony mortality; and (d) parent colony size. Bars represent 95% confidence intervals.

Figure 5. Linear regression between annual number of ramets produced per colony and colony area (cm^2). Data transformed by of Log_{10} for purposes of normalization. $\mathrm{Log}_{10}(Y) = 0.3281 * \mathrm{Log}_{10} X - 0.5869$, $p < 0.001$, $n = 311$; 95% confidence limits for the slope 0.2601 and 0.3961. When $Y = 1$, $X = 61.5\ cm^2$, with confidence limits of $30.3\text{-}180.4\ cm^2$.

Figure 6. Size-frequency distribution of ramets produced by all variants of fission. Bars represent 95% confidence intervals.

Figure 7. Temporal changes in stages of fission in *Palythoa caribaeorum*. Data represent the percentage of colonies exhibiting an increase in (a) cumulative length of crevices; (b) number of polyp-groups; (c) number of ramets produced; and (d) number of ramets released. The biological process proceeds from the top to the bottom of the figure. Bars represent 95% confidence intervals. Note that ramet release is the only character varying significantly through time, with the lowest release rate during the winter.

Figure 8. Frequency of colonies requiring 3, 6, 9, or 12 months, respectively, for ramet (a) production, and (b) release. Bars represent 95% confidence intervals. n = 320. No significant difference in time required by a colony to produce a ramet (3 - 12 months; $p > 0.05$, G-test with William's correction). Significantly greater proportion of parent colonies releasing ramets within three months, *vs.* 6, 9, or 12 months ($p < 0.001$, G-test with William's correction).

Table Legends

Table 1. Comparisons of abundance and relative frequencies of *Palythoa caribaeorum* colonies exhibiting various characters associated with fission. The three variants of fission considered here are Edge Fission, Pseudo-Colony Lift-Off, and Teardrop Formation. Note that any given colony may reproduce by one or more variants of fission; thus, totals may be disparate. Under "Estimated Cumulative Area of Ramets", the cumulative area of ramets produced was calculated based upon 1,304 ramets known to be released over the period of a year, and also from the size frequency distribution data calculated from a subset of 524 ramets, measured in the field.

Table 2. A. A comparison of Sites and depths, with respect mean colony size, cumulative length of crevices, number of polyp-groups, ramet production, and partial colony mortality. B. Summaries of ANOVA results when comparing sites and depths for: mean number of ramets produced per colony, mean cumulative length of crevices, mean number of polyp-groups, and mean area of partial colony mortality.

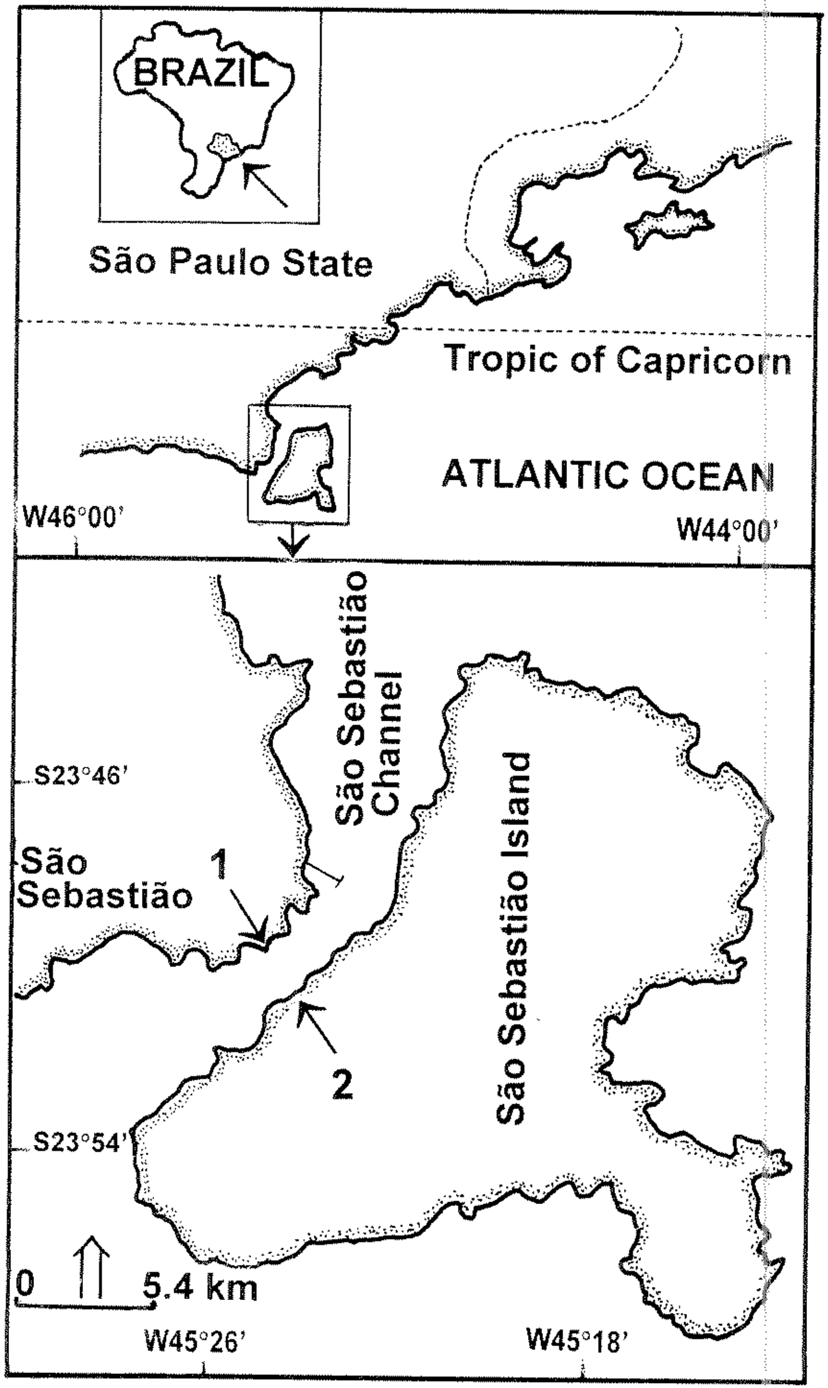

BRAZIL
São Paulo State
Tropic of Capricorn
ATLANTIC OCEAN
W46°00'
W44°00'
São Sebastião Channel
S23°46'
São Sebastião
1
São Sebastião Island
2
S23°54'
0
5.4 km
W45°26'
W45°18'

Fig 1

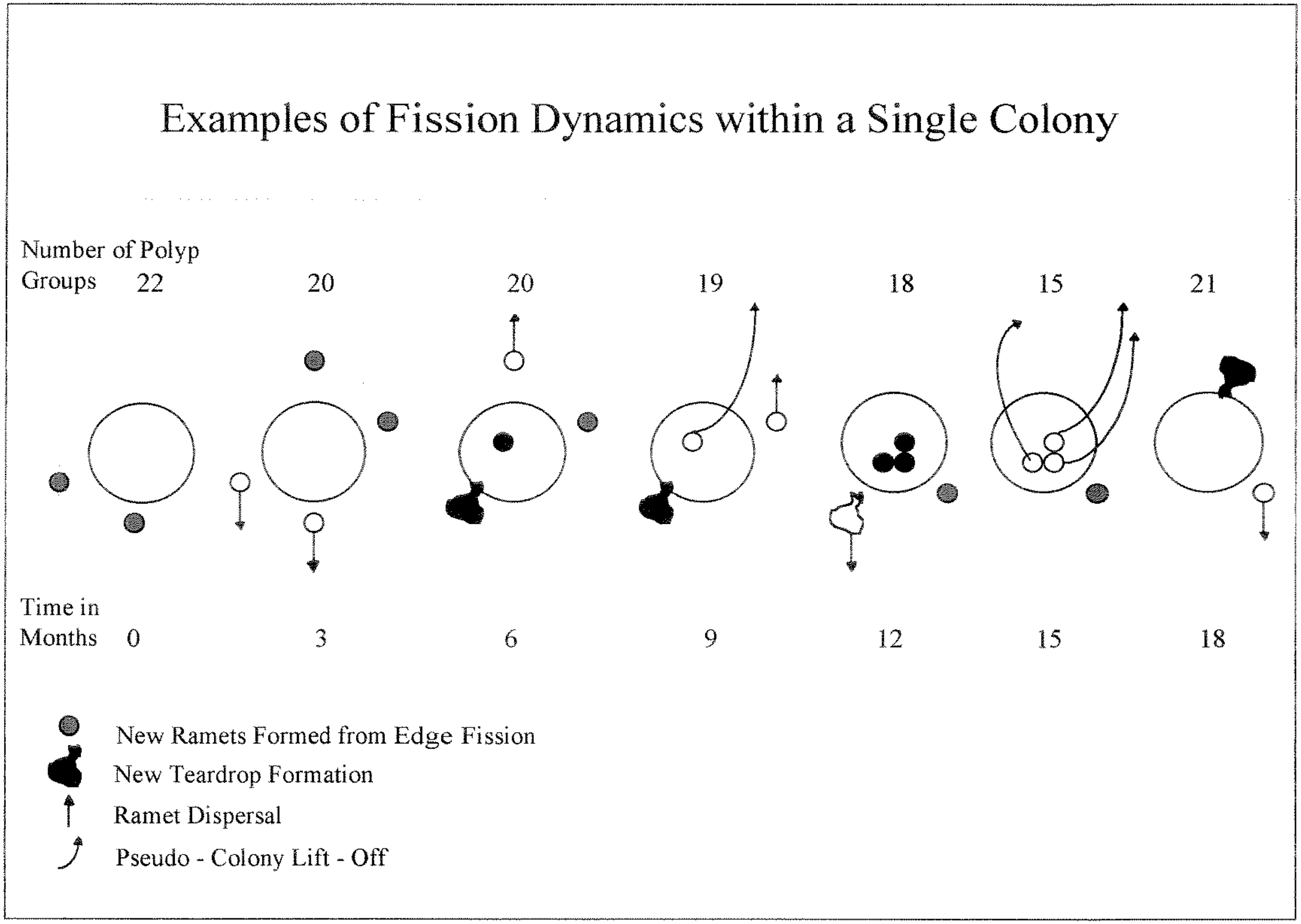

Examples of Fission Dynamics within a Single Colony
Number of Polyp Groups
22
20
20
19
18
15
21
Time in Months
0
3
6
9
12
15
18
● New Ramets Formed from Edge Fission
New Teardrop Formation
↑ Ramet Dispersal
Pseudo - Colony Lift - Off

Fig 2

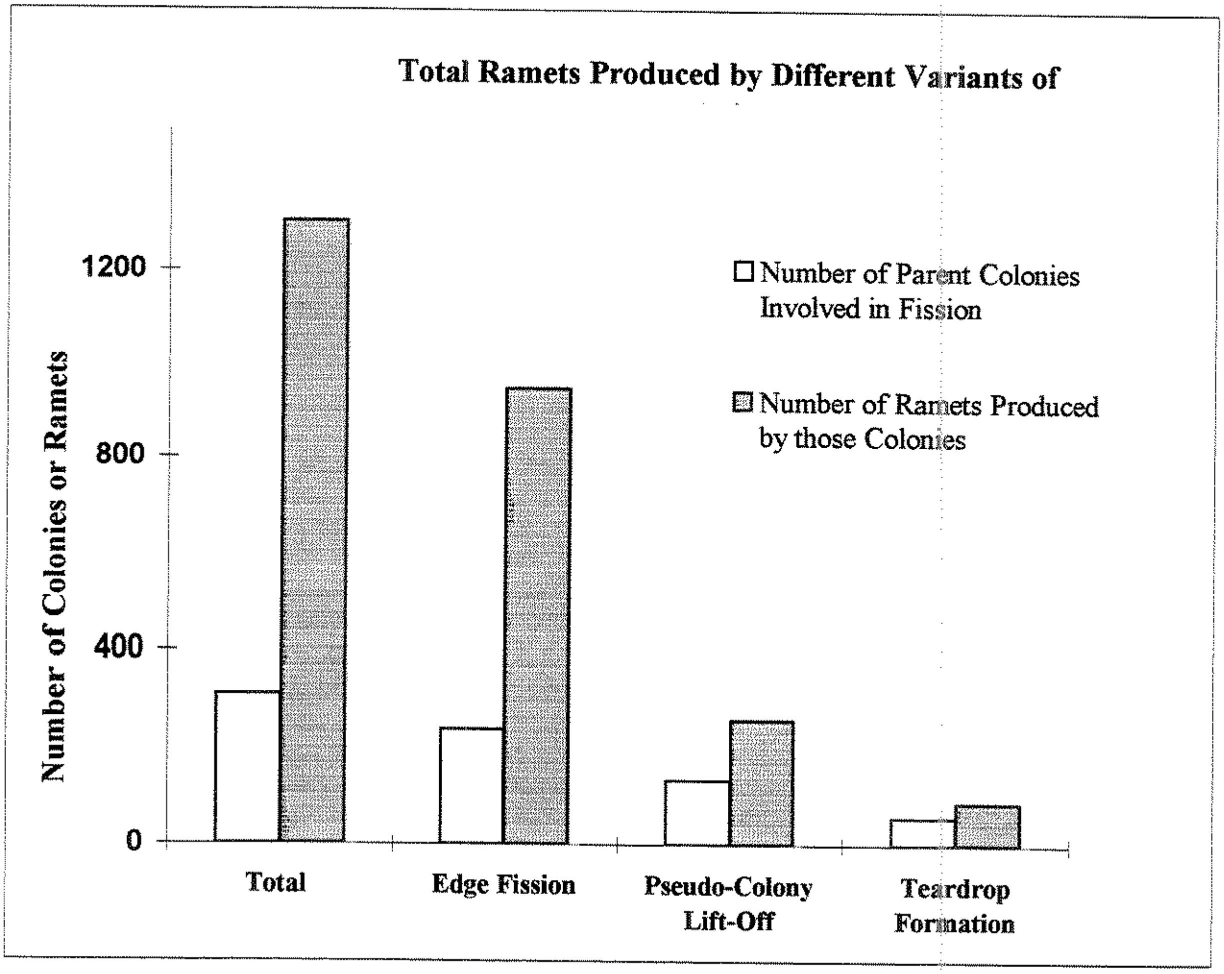

Total Ramets Produced by Different Variants of
Number of Colonies or Ramets
1200
800
400
0
☐ Number of Parent Colonies Involved in Fission
▨ Number of Ramets Produced by those Colonies
Total
Edge Fission
Pseudo-Colony Lift-Off
Teardrop Formation

Fig 3

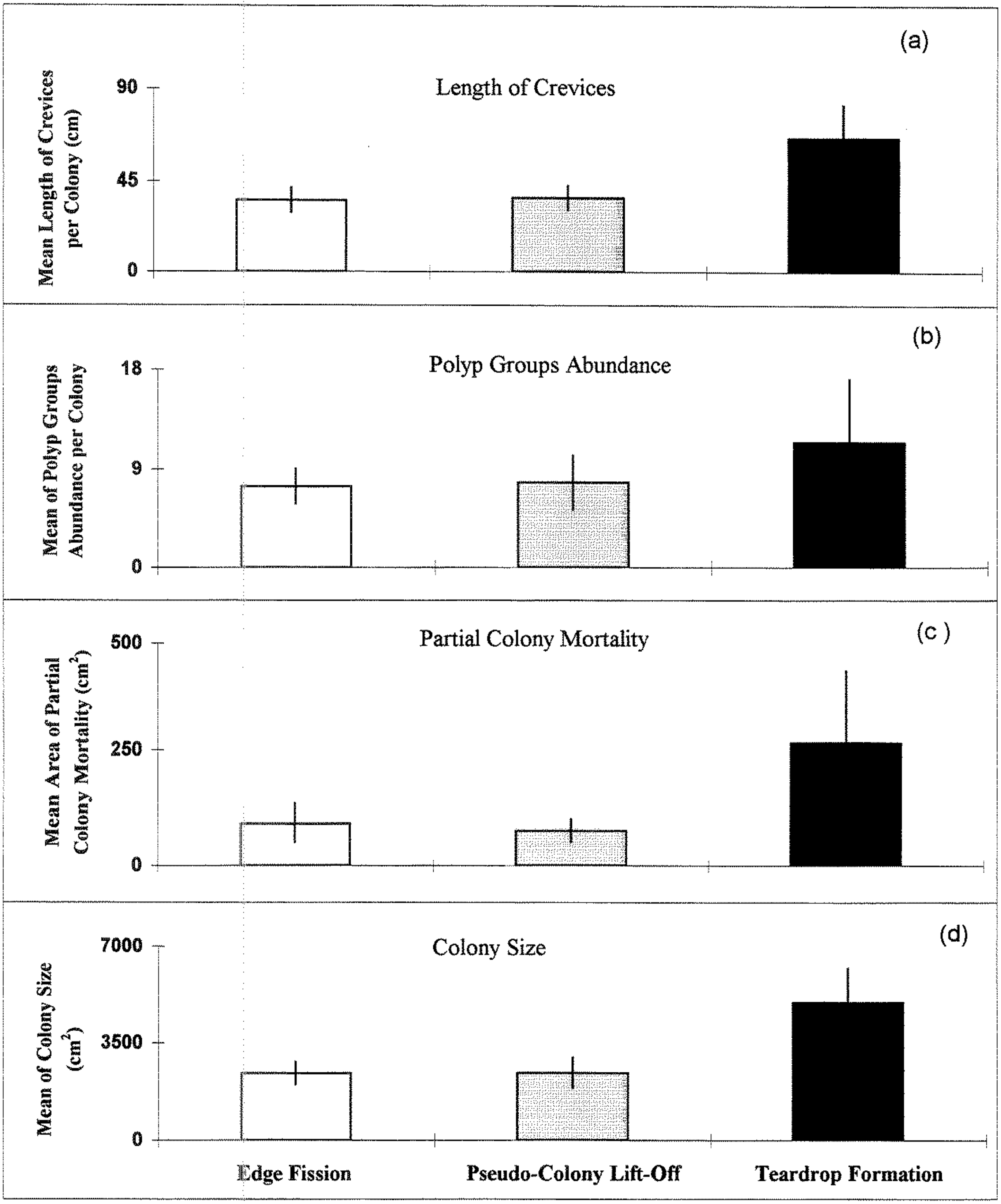

(a)
Length of Crevices
Mean Length of Crevices per Colony (cm)
90
45
0
(b)
Polyp Groups Abundance
Mean of Polyp Groups Abundance per Colony
18
9
0
(c)
Partial Colony Mortality
Mean Area of Partial Colony Mortality (cm^2)
500
250
0
(d)
Colony Size
Mean of Colony Size (cm^2)
7000
3500
0
Edge Fission
Pseudo-Colony Lift-Off
Teardrop Formation

Fig 4

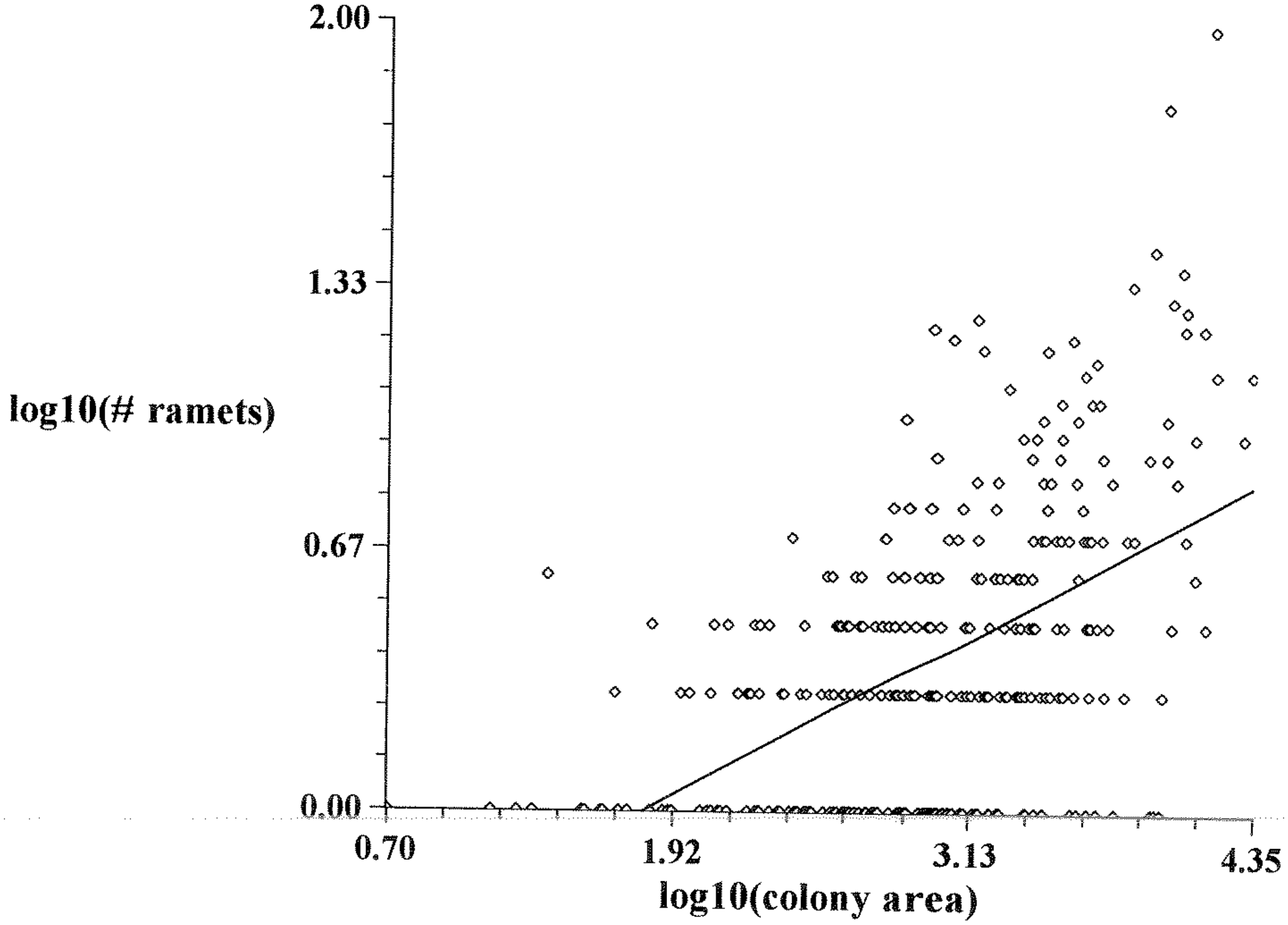

2.00
1.33
0.67
0.00
log10(# ramets)
0.70
1.92
3.13
4.35
log10(colony area)

Fig 5

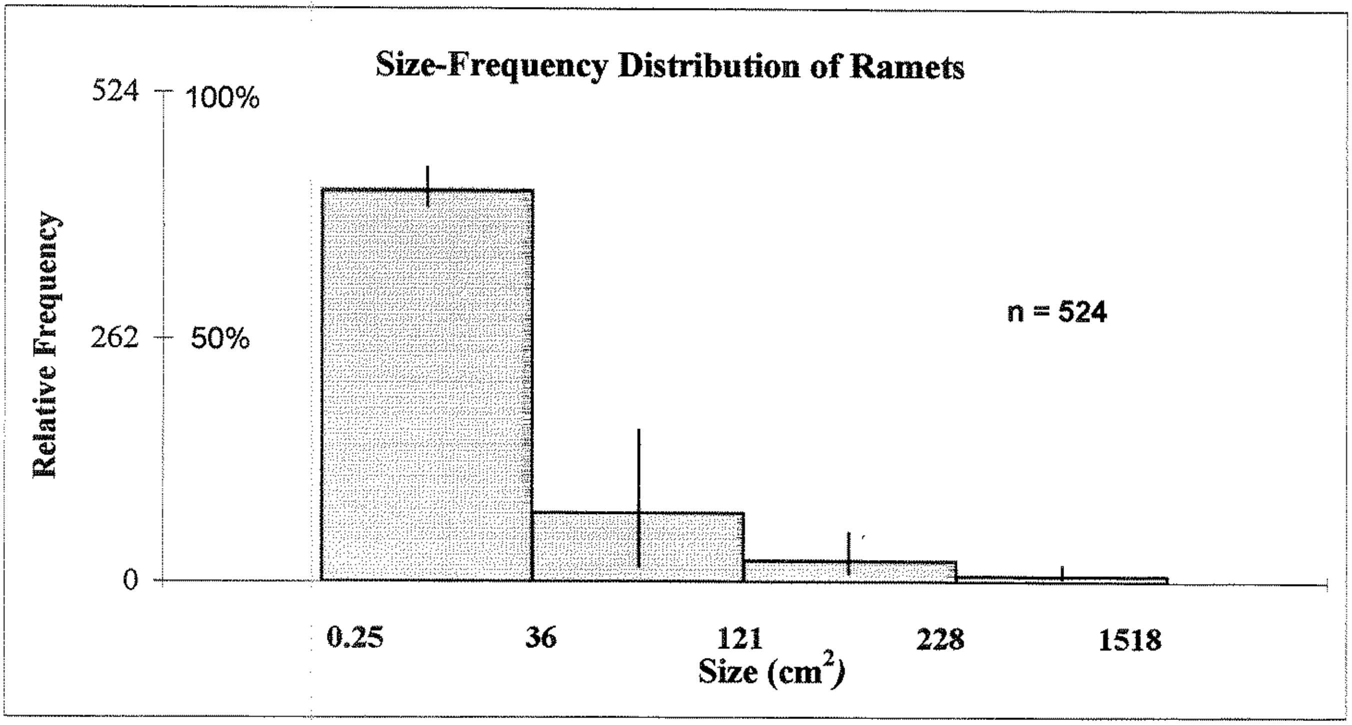

Size-Frequency Distribution of Ramets
Relative Frequency
524
100%
262
50%
0
n = 524
0.25
36
121
228
1518
Size (cm^2)

Fig 6

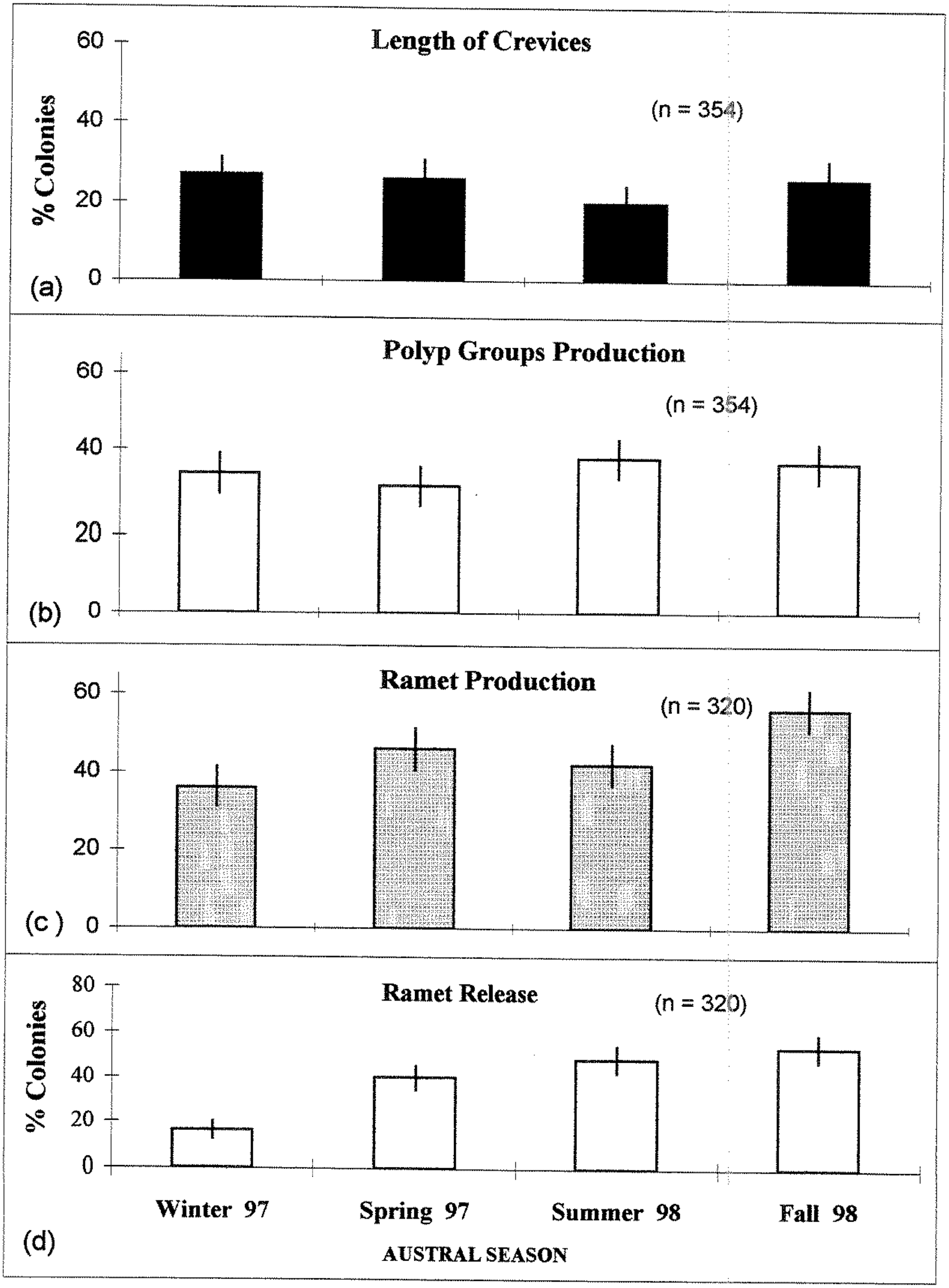
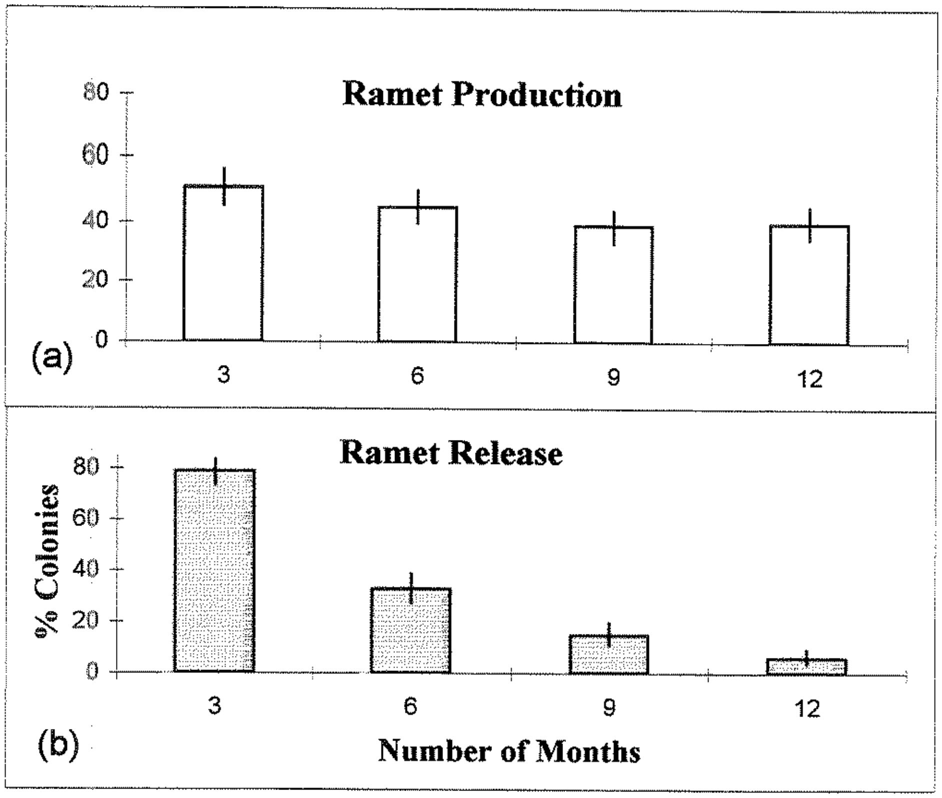

Length of Crevices
(n = 354)
% Colonies
60
40
20
0
(a)
Polyp Groups Production
(n = 354)
60
40
20
0
(b)
Ramet Production
(n = 320)
60
40
20
0
(c)
Ramet Release
(n = 320)
% Colonies
80
60
40
20
0
Winter 97
Spring 97
Summer 98
Fall 98
(d)
AUSTRAL SEASON

Fig 7



Ramet Production
80
60
40
20
0
(a)
3
6
9
12
Ramet Release
% Colonies
80
60
40
20
0
3
6
9
12
(b)
Number of Months

Fig 8

	Edge Fission	Pseudo-Colony Lift-Off	Teardrop Formation
Colonies			
Number of colonies exhibiting a given mode of reproduction (n)	247	137	58
Number of colonies exhibiting only this mode	129	48	15
Percent of colonies exhibiting only this mode	52,2%	35,0%	25,9%
Number of colonies reproducing by this plus at least one other mode	118	89	43
Percent of colonies reproducing by this plus at least one other mode	47,8%	65,0%	74,1%
Fission			
Number of colonies exhibiting an increase in crevice length throughout the year	195	102	54
Number of colonies exhibiting an increase in polyp groups throughout the year	209	132	49
Maximum number of group of polyps produced by a single colony within one year			
Ramet			
Maximum number of ramets produced by a single colony within one year	77	18	6
Mean number of ramets produced per colony per year, s.d. and n shown in parentheses	3.8 (6.99; 247)	1.9 (2.04; 137)	1.4 (0.88; 58)
Mean ramet size, in cm^2 (s.d., n)	32.2 (69.31; 276)	43.3 (140.00; 186)	22.4 (36.79; 62)
Range of ramet sizes	0.25 - 725 cm^2	9.0 - 1,518 cm^2	1.5 - 192 cm^2
Area			
Sum of the total area of colonies exhibiting this mode (n = 320)	59.45 m^2	33.22 m^2	28.74 m^2
Sum of the total area of partial colony mortality over one year	2.37 m^2	1.1 m^2	1.53 m^2
Percent of total colony area with partial colony mortality	4,0%	3,3%	5,3%
Estimated cumulative area of ramets produced by each mode	3.05 m^2	1.13 m^2	1.88 m^2
Percent of total colony area released as ramets	5,1%	3,4%	6,5%

Table 2

A. Site		PPo		Total PPo	PR		Total PR
Depth		Shallow n = 80	Deeper n = 81	n= 161	Shallow n = 87	Deeper n = 72	n=159
- Colony size (cm^2)	Mean	2381.3	1691.1	2034.1	2457.3	2509.7	2481.0
	s.d.	3317.4	2256.6	2846.0	3493.4	3431.9	3454.8
- Cumulative length of crevices (cm)	Mean	29.75	24.8	27.3	32.1	43.9	37.4
	s.d.	46.67	33.61	40.5	50.7	53.4	52.1
- Polyp groups per colony	Mean	5.37	7.45	6.42	5.3	8.4	6.7
	s.d.	7.7	18.3	14.0	6.7	9.7	8.3
- Ramet produced per colony	Mean	4.56	4.9	4.73	3.22	4.36	3.74
	s.d.	8.1	11	9.9	3.69	4.4	4.0
- Partial colony mortality (cm^2)	Mean	126.5	96.1	86.45	96.1	65.9	82.4
	s.d.	550.7	184.8	397.6	184.8	117.1	158.06

B. Source	Sum of Squares (SS)	Degrees of Freedom (DF)	Mean Square (MS)	F	P
Mean number of ramet produced per colony					
Site	0.023	1	0.023	0.171	$p > 0.05$
Depth	0.434	1	0.434	3.21	$p > 0.05$
S x D	0.482	1	0.482	3.57	$p > 0.05$
Error	31.86	236	0.135		
Mean cumulative length of crevices					
Site	0.877	1	0.877	1.914	$p > 0.05$
Depth	0.828	1	0.828	1.808	$p > 0.05$
S x D	0.199	1	0.199	0.436	$p > 0.05$
Error	108.14	236	0.458		
Mean number of polyp-groups					
Site	0.259	1	0.259	3.245	$p > 0.05$
Depth	0.185	1	0.185	2.26	$p > 0.05$
S x D	0.115	1	0.115	1.44	$p > 0.05$
Error	18.84	236	0.0798		
Mean area of partial colony mortality					
Site	0.0002	1	0.0002	$2.8\text{x}10^{-4}$	$p > 0.05$
Depth	1.412	1	1.412	2.04	$p > 0.05$
S x D	0.160	1	0.160	0.23	$p > 0.05$
Error	164.03	236	0.6951		

Capítulo III

Bulletin of Marine Science - Submetido para publicação

Asexual Reproduction in a Zoanthid: Fragmentation and Partial Colony Mortality

By

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Running Head: Fragmentation and Partial Mortality in *P. caribaeorum*

Key Words: Asexual reproduction, Fragmentation, Partial Colony Mortality, Storms, Physical disturbance, Ramets, Zoantharia, Zoanthidea, *Palythoa caribaeorum*, Brazil.

ABSTRACT

Fragmentation is an important characteristic of the life history, population dynamics, and genetic structure of at least five Metazoan Phyla. This study represents a first report of modes of fragmentation and their relative importance to population growth in *Palythoa caribaeorum* (Cnidaria, Zoanthidea). Several populations at two coastal sites in São Paulo - Brazil (Praia Portinho, on São Sebastião island, and Ponta Recife, continent) were followed for one year. Fragmentation occurred *via* two modes: 1) partial colony mortality (*i.e.* injury) and 2) physical disturbance (*i.e.* storms, currents, or tides). Both modes involved incidental fragmentation, not actively directed by the parent colony. Only 7.2% of the 579 colonies monitored exhibited at least one mode of fragmentation over the period of one year. These colonies produced 64 new ramets. The frequency of fragmentation or total fragments produced *via* partial mortality was independent of site and season. They were not, however, independent of depth, with significantly higher frequencies occurring in shallow waters. The frequency of colonies fragmenting *via* physical disturbance (storms) was independent of the site and depth, but not of the season. At least 40% of the population exhibited signs of partial colony mortality (lesions), which affected < 5% of the total colony area. The main source of partial colony mortality in *P. caribaeorum* was disease. Partial colony mortality was proportional to colony area. Frequency of partial mortality was independent of depth, but was site-dependent, being higher in the more stressful habitat (Ponta Recife). In contrast with other zoanthids, fragmentation does not appear to play a critical role in ramet production and population growth in *P. caribaeorum*, particularly when compared to the various modes of fission, which exist in this species.

INTRODUCTION

Several modes of asexual reproduction including fragmentation have been reported in the phylum Cnidaria (Vaughan and Wells, 1943; Cairns, 1988). Cairns (1988) divides fragmentation for corals into two categories: 1) Accidental-traumatic (see also Highsmith, 1982), which include partial colony mortality (see Lewis, 1974; Hughes and Jackson, 1980; Highsmith, 1982; Jackson and Hughes, 1985), and 2) Non-accidental, where the corallum is genetically programmed to fracture (see also Lasker, 1984). In some colonial species, fragments may be generated by external forces (Karlson, 1983), while in others it may be facilitated by the degeneration of skeletal or soft-tissue connections (West, 1979; Muirhead and Ryland, 1985; Karlson, 1986). These categories and the lack of clear definitions are some reasons why the term fragmentation is often confused with fission (see Lasker 1984, Karlson 1986, 1988a,b, 1991).

Here, fragmentation is defined as the process by which a live portion of a colony becomes physically separated from the parent colony (following Highsmith, 1982) due to breakage caused by exogenous factors (tissue is not genetically programmed to break at certain places). These factors include: 1) natural physical forces (storms, currents, waves, tides); 2) biological factors (disease, predators, bioeroders); and 3) anthropogenic factors (anchors, boats, diving, fishing and pollution). In contrast with fission (genetically programmed), fragmentation does not require the input of metabolic energy by the parent colony for the production of ramets.

Cloning by fragmentation is a character selected over evolutionary time and has become an important part of the life history of many scleractinian corals (Highsmith, 1982) and of a variety of invertebrate phyla (Hughes, 1989). Fragmentation has been shown to affect the demography, population dynamics, and genetic structure of corals (Higshmith, 1982). It appears to be the predominant mode of reproduction in some major reef-building corals (*e.g. Acropora, Montastrea, Porites, Pocillopora*), which would help to explain their dominance in various reef communities (see review in Highsmith, 1982). In the Zoantharia, two modes of fragmentation have been described thus far: accidental (storm waves), and non-accidental (degeneration of stolons; Karlson, 1983; 1986; Fadlallah et al. 1984). Fragmentation is probably the most important mode of reproduction and dispersal in the zoanthids *Zoanthus sociatus* and *Z. solanderi* (Cooke, 1976; Karlson, 1986). Ryland (1997) stated that in some zoanthids, energy resources are probably dedicated to the production of asexual propagules rather than gametes in order to insure continuity of the genets. The demographic consequences of fragmentation between congeners could be different, as suggested by Karlson (1988a).

The zoanthid *Palythoa caribaeorum* is a common shallow-water species found on corals reefs of the western Atlantic. It is the dominant benthic species in the São Sebastião channel, São Paulo, Brazil. Asexual reproduction *via* fission has been studied in *P. caribaeorum*, as well the importance of its quantitative contribution to population growth (Acosta et al. 1998; Acosta et al. in review – chapter 1 and 2). There are no reports describing fragmentation in this species, nor, of course, its role in population growth. This paper represents a first report of basic information on ramet production by two modes of fragmentation in *P. caribaeorum* - fragmentation *via* partial colony mortality (tissue isolated due to lesions), and *via* physical disturbance (colonies broken into several pieces by catastrophic storms, currents, or tidal currents). The frequency of fragmentation will be compared between sites (representing different levels of environmental stress), between depths (shallow *vs.* deeper), and through time. The relative contribution of fragmentation to population growth, and the effects of partial colony mortality (*i.e.* disease) on fragmentation, will also be considered.

MATERIAL AND METHODS

Study Site. Palythoa caribaeorum populations were studied in southeastern Brazil (23° S.). Sites were located on both sides of the São Sebastião channel on the São Paulo coast: Praia Portinho, located on São Sebastião Island, and Ponta Recife, on the continental coast of São Paulo (Fig. 1). The shores bordering the channel are characterized by alternating sandy and rocky beaches; the sides of the channel itself are steeply inclined. Sand, debris, and boulders of various sizes, create a three-dimensionally complex habitat, which characterizes the bottom. *P. caribaeorum* generally grew as single large colonies over the boulders, and inter-colony contact was common.

This region is under the influence of the south-Atlantic anti-cyclonic weather systems throughout the year, characterized by frequent polar disturbances and associated cold fronts and storms. The local currents are forced mainly by winds (equatorial or poleward) and shelf circulation (Carelli, 1995; Castro Fo, 1990), and are highly variable in space and time (Castro Fo, 1990). Surface seawater temperatures (SST's) and salinities fluctuate widely throughout the year (15 - 31°C; 22 - 36‰; CEBIMar, 1991). The summer (rainy season) is characterized by high mean water temperatures (26.2°C), low salinities, and low currents (< 0.2 ms^{-1}), predominantly SW (Carelli, 1995). The average current velocity during the remaining seasons is generally 0.4 - 0.6 m s^{-1}, predominantly NE (Carelli, 1995). Winter temperatures average 21.3°C, with high wind and waves (Castro Fo, 1990). Tidal currents are 0.03 ms^{-1}

(Carelli, 1995), with a mean tidal range of 0.66m. Turbidity is generally high (visibility <4.3 m, annual mean). The channel receives pollution in the form of sewage from a nearby tourist area (CETESB, 1996) and oil derived from spills from Brazil's largest coastal oil terminal - TEBAR (Zamboni, 1993).

Sampling. Populations were followed at two sites and at two depths in the sub-tidal - 0.5 - 1.5 m, and 2.5 -4.0 m. Three random replicate plots were defined at each depth, with 36-85 colonies in each. *In toto*, 579 colonies, including a wide variety of size classes (range: 2.5 x 10^{-5} m^2 to 2.1 m^2), were monitored for one year (May 1997 to May 1998). Colonies were sampled every three months near the end of each season - August 1997 (end of winter), November 1997 (spring), February 1998 (summer), and May 1998 (fall). Colonies and ramets were mapped using acrylic tables in order to follow changes through time.

The dynamics of fragmentation through time was assessed *via* the following variables: 1) *Colony size* - expressed in area, determined by multiplying maximum colony length by maximum width; (we define a colony as a group of polyps physically independent from other colonies). 2) *Sum of area exhibiting partial mortality.* Partial mortality was considered to be any portion of tissue within the colony exhibiting lesions, skeletal remnants (due to disease), or empty spaces (bare substratum). The area of partial mortality was calculated using the diameter of the affected area; (in some cases, maximum length was multiplied by width). Causes of partial mortality were noted when such could be discerned (*e.g.* disease, predators). To analyze the relationship between frequency of disease and colony size, the colonies were grouped into three size classes: a) small colonies, <0.5 m in diameter; b) medium colonies, 0.5-1.5 m; and c) large colonies, >1.5m. 3) *Position and number of new fragments (ramets) produced per colony* (between samplings). 4) *Type of asexual reproductive mode* from which ramets were derived was recorded wherever such could be discerned: - *via* partial mortality (*i.e.* disease, sedimentation, and human activities), physical factors (*i.e.* storms, currents, or tidal currents), or fission (only if the colony was already associated with a fragmentation event, see Acosta et al. in review – chapter 1 and 2). Details regarding the quantitative contribution of fission to reproduction in this species are presented elsewhere (Acosta et al. in review – chapter 2). 5) *Ramet area* (length x width = area), as a colony character to help differentiate ramets from each other, and to help identify ramets which have been dispersed through time. For the purpose of this study, dispersal was considered to be a ramet moving out of a study plot.

The frequency of colonies exhibiting signs of partial mortality was also quantified during the summer of 1997. 453 colonies were sampled randomly at the two sites, 132 in Praia Portinho, and 321 in Ponta Recife. Data collection was focused on determining the main sources of partial colony mortality.

RESULTS

The two modes of fragmentation occurring in *Palythoa caribaeorum* (Fig. 2) are: 1) Fragmentation as consequence of partial colony mortality, and 2) Fragmentation generated by physical disturbances, associated with storms, currents or tides.

Total fragment production was low (Table 1). Only 7.2 % of the sampled population (n = 579) exhibited at least one mode of fragmentation over the period of a year, contributing 64 new ramets to the population (Table 1). Fission was much more important, 31 of the 42 fragmenting colonies created 307 new ramets *via* fission. Only two colonies in the population (n = 579) exhibited both modes of fragmentation simultaneously.

Fragmentation

Fragmentation by Partial Colony Mortality (lesions). Partial colony mortality (*i.e.* disease) did not generally result in physical isolation of a group of polyps (ramets or fragments) from the parent colony. Only 18 of the 579 sample colonies fragmented this manner within a year, generating 31 new ramets (Table 1). The maximum number of ramets produced *via* partial mortality for a single colony was 6; generally, only one ramet was produced per colony. The mean ramet area for fragments was 30.7 +/- 36.7 cm^2 (n = 19). The maximum ramet size observed was 116 cm^2.

Fragmentation by partial colony mortality does not necessarily result in fragment dispersal; normally, the fragment remained beside the parent colony for three to nine months prior to release. Fusion between the parent colony and the ramet, once formed, was never observed. Colony growth was low, < 3 linear cm per year, and regeneration of lesions was dependent upon the size of the affected area and colony condition. Small injuries, < 25 cm^2, were regenerated within 6 to 12 months.

There was no significant difference in the mean number of fragments produced per colony between the two sites ($p > 0.05$, one-way ANOVA) when depths were pooled. The frequency of colonies exhibiting fragmentation due to partial mortality, and the total number of fragments produced by it were also independent of site ($p > 0.05$; G-test, with William's correction). The frequency of colonies exhibiting fragmentation, and the total fragments produced, however, were dependent upon depth ($p = 0.016$, G-test, with William's correction), being higher in shallow water (Table 1).

The number of colonies exhibiting fragmentation, and the number of fragments dispersed, were independent of time ($p > 0.05$, G-test, with William's correction; Table 2).

Fragmentation due to Physical Forces. Only 24 colonies from 579 sampled broke off into two or more large portions, generally after storms, producing 33 new ramets over the period of a year (Table 1). The maximum number of fragments in which a parent colony was divided was three. The mean area of the fragments produced was 87.5 +/- 276.5 cm^2 ($n = 30$). The maximum ramet size was 1,525 cm^2. These ramets were comparatively larger than those derived from partial mortality.

There was no significant difference between sites or between depths in the mean number of fragments produced per colony by this mode ($p > 0.05$, one-way ANOVA), when depths or sites were pooled, respectively. The frequency of fragmentation, and the number of total fragments produced were also independent of site and depth ($p > 0.05$, G-test, with William's correction; Table 1). The frequency of colonies undergoing fragmentation, however, was found to be dependent on season ($p = 0.01$, G-test, with William's correction), being lower during the winter (Table 2).

Dispersal of fragments was independent of season ($p > 0.05$, G-test, William's correction; Table 2). They were generally carried away within six months of formation. Ramet survival was dependent upon its position with respect to light, and extent of tissue damage incurred during dispersal (*i.e.* rolling).

Total Fragmentation. Pooling data from the two modes of fragmentation, we found no statistical differences between sites in the mean number of fragments produced per colony (p

> 0.05, one-way ANOVA; Table 1). Mean number of fragments per colony does vary significantly, however, between depths ($p < 0.05$, one-way ANOVA), been higher in shallow colonies than deeper ones ($p < 0.05$, Tukey-Kramer Test). The frequency of colonies fragmenting, and the total number of fragments produced were also independent of site ($p > 0.05$, G-test, with William's correction), but not of depth ($p = 0.0074$, G-test; Table 1). These agree with disease frequency, which was dependent of depth ($p = 0.01$, G-test, with William's correction; 55 colonies infected of 293 quantified in shallow water *vs.* 29 colonies infected of 286 quantified in deeper).

Details Regarding Partial Colony Mortality

Sources and Area of Partial Colony Mortality in Palythoa caribaeorum. Sources of partial colony mortality in *P. caribaeorum* included biotic factors: such as disease; abiotic factors: such as high sedimentation, strong currents, storm waves, and low light levels; and anthropogenic factors, such as fishing, diving, and anchoring. The primary source of partial colony mortality in *P. caribaeorum* was a new disease (see chapter 4). Partial mortality was common in colonies of *P. caribaeorum*, occurring in 41 to 50% of the population. Mortality of whole colonies was rare, < 10 colonies per year ($n = 579$) whith area $\leq 100 cm^2$.

The mean area of live tissue in parent colonies exhibiting fragmentation *via* partial mortality was 4,997 +/- 4,843 cm^2. For colonies fragmenting *via* physical factors, it was 2,577 +/- 4,226 cm^2, with a range varying from 98 to 20,028 cm^2. The mean area of partial colony mortality was significantly different between the two modes of fragmentation ($p < 0.05$, one-way ANOVA), being higher in colonies affected by partial mortality (294.4 +/- 325.2 cm^2; $n = 18$) rather than by physical disturbance (69.8 +/- 149.0 cm^2; $n = 24$). The range of tissue lost caused by partial colony mortality was between 0 and 857 cm^2. 2.7 to 5.9% of the colony surface was affected by partial colony mortality. Most of the lesions were surrounded by living tissue, and few occurred at the colony edge. Lesions were generally small, with their sizes falling well within the regenerative capabilities of the species.

A regression formula indicated that partial colony mortality was proportional to colony area, assuming that $b = 0.89$ was not different from 1.0 ($p < 0.001$, Kendall's Robust Line and Tau Analysis, Sokal and Rohlf, 1995; Fig. 3).

The mean area of partial colony mortality in the population (from all sources) did not vary significantly with depth ($p > 0.05$, one-way ANOVA). It was, however, significantly different between sites ($p = 0.017$, one-way ANOVA), being lower at Praia Portinho (47.2 +/- 288.40 cm^2, $n = 310$), than in Ponta Recife (52.7 +/- 128.4 cm^2, $n = 269$). The same result was confirmed with data from the summer 1997, where the frequency of partial colony mortality was dependent on site ($p = 0.008$, G-test, with William's correction), being higher in Ponta Recife (46.7%; $n = 321$) than in Praia Portinho (29.6%; $n = 132$).

DISCUSSION

Fragmentation and Life History. The abundance of a number of zoanthid species on tropical shores and shallow reefs may be explained by fragmentation (*e.g. Zoanthus*; Burnett et al. 1995; Karlson, 1986; 1988b; 1991) and recruitment resulting from sexual reproduction. This is despite the high level of sterility found in zoanthid populations (Fadlallah, 1984; Ryland, 1997). In *Palythoa caribaeorum*, however, the low number of ramets produced by fragmentation (64), contrast with the high number of ramets produced *via* fission (1,304) in the same population (Acosta et al. 1998). Colonies undergoing fragmentation in this study were able to produce almost five-times more ramets *via* fission (307) than by fragmentation (64). The genus *Palythoa* is considered to have a high rate of asexual reproduction (Cooke, 1976). Our data confirm this to be true in *P. caribaeorum*, but such is due to fission, not fragmentation. This high rate of asexual reproduction assists in local dispersal, substrate colonization, potential escape from competition for space, reduction of risk from mortality of genets, and enhancement of fitness (Acosta et al. in review – chapter 2). Fragmentation may play a role in population growth of this species, but is probably not a major contributing factor to the broad distribution, abundance, and dominance of this species in the western Atlantic.

As a reproductive strategy, fission has been employed more in the Metazoa (10 phyla) than fragmentation (5 phyla; Hughes, 1989). The relative contribution of fission *vs.* fragmentation in various species may be explained in terms of their respective morphologies, and their particular physiological adaptations for their habitats (Highsmith, 1982). Life history characteristics, habitat conditions, mortality rates, and the importance of asexual reproduction for the most common western Atlantic zoanthids - *P. caribaeorum* and *Zoanthus* spp. - seem to be different. Karlson (1986; 1988a) stated that in a harsh stressful environment, fragmentation is likely to occur in small colonies of *Zoanthus*, reducing costs associated with reproduction and potentially high levels of colony mortality. Other clonal organisms subject to high levels of mortality also exhibit strong abilities to reproduce *via* fragmentation (Highsmith, 1982; Winston, 1983; Karlson, 1986; 1988a). In this way, fitness is increased at small colony size under conditions of physical disturbance (Highsmith, 1982; Stoner, 1986; Wulff, 1991). *P. caribaeorum* have colonies which are on the average larger than those of *Zoanthus* spp. The low-intensity, high frequency disturbance conditions characteristic of our study area may allow *P. caribaeorum* colonies to grow into a "size refuge", which reduce the probability of mortality. Increased colony size in *P. caribaeorum* generally implies increased fitness, since asexual and probably sexual reproduction may be size-dependent (Acosta et al. in progress). A large colony size in *P. caribaeorum* allows colonies in the study area to reproduce by fission instead of fragmentation. In habitats with high-frequency disturbance and higher mortality rates of *P. caribaeorum* colonies, it will be expected more fragmentation, small colony size, and in consequence comparatively less fission.

Palythoa caribaeorum and *Zoanthus* spp. have a number of contrasting life history characteristics. *P. caribaeorum* grows as a carpet in the low intertidal or shallow subtidal (Sebens, 1982). It readily colonizes hard substratum, but rarely sand. It exhibits indeterminate growth and is long-lived. It has a number of polyps and uses inorganic matter as a pseudo-skeleton (Haywick and Muller, 1997). It has low mortality rates and is able to regenerate small lesions to maintain colony area. It has a high rate of asexual reproduction *via* fission (Acosta et al. 1998), and its reproductive effort is higher than *Zoanthus* spp. (see Fadladlallah et al. 1984). On the other hand, *Zoanthus* spp. normally grows as a runner, with few polyps attached to each other aborally by short stolons (Karlson, 1983; 1986, 1988a) above the *Palythoa* zone, for these reasons it is also more exposed to disturbance (waves, storms; Karlson, 1980; Fadlallah et al. 1984), fragmentation, and conditions inducing physiological stress (exposure, osmotic changes; Sebens, 1982) than *P. caribaeorum.* It colonizes unconsolidated or unstable substrate (sand, debris, coral, and rocks), which during storms facilitate fragmentation due breakage of the stoloniferous connections. In consequence *Zoanthus* spp. exhibits low levels of colonial integration (Karlson, 1986) and maintains specific colony sizes through fragmentation (Karlson, 1986; 1988a). Contrasting characters related to mortality, habitat, and colony size may help to explain why these two genera utilize very different asexual reproductive strategies.

Biotic Factors of Influence. Some biotic factors may promote fragmentation, such as bioerosion (Smith and Tyler, 1975), predation, and diseases. A rich fauna of polychaetes and microorganisms live between the base of *Palythoa caribaeorum* colonies and the substratum, and these could affect fragmentation. The recently reported disease in *P. caribaeorum* (Acosta, 1999a,b), which seems to start in this layer, promotes some degree of fragmentation *via* partial colony mortality during summer and fall. Disease is an important source of partial mortality for many invertebrates (Peters, 1993; 1997). This disease seems to be highly species-specific for *P. caribaeorum*, since it does not affect other zoanthids. Predation is known to lead to the production of fragments in sponges and corals (Tunnicliffe, 1981; Highsmith, 1982; Borges et al. 1988). No evidence of intense predation was observed on *P. caribaeorum* in our study area. A. Acosta has noted (pers. obs.), however, a high degree of partial mortality and fragmentation due to predation by the polychaete *Hermodice caruncullata* in Santa Marta, Colombia.

Colonies in shallow water exhibited three times higher fragmentation (total number of fragments) than deeper colonies (Table 1). Physical disturbance associated with storms appeared to have similar low fragmentation effect on shallow colonies as on deeper ones. Thus, the difference in fragmentation rate between depths is better explained by the rate of partial mortality (*e.g.* disease pattern) than physical disturbance. Highest infection rate was observed in shallow-water colonies, which increase fragment production there.

Of the two sites, Ponta Recife (on the continental shore) was characterized by more stressful conditions, in terms of light levels, turbidity, sedimentation rates, and human activities (Acosta et al. in review – chapter 2 and 4). The highest levels of partial colony mortality were observed there, compared to Praia Portinho (off-shore island). Although the mean area of partial colony mortality was significantly higher on the continent, no equivalent increase in number of fragments was observed. It would appear that not all lesions result in fragment formation.

Physical Factors of Influence. Mechanical action generated by hydrodynamic forces is known to favor fragmentation in the alga *Acanthophora* (Kilar and McLachlan, 1986; Walters and Smith, 1994), the seagrass *Zoosteracea* (Cambridge et al. 1983), the sea anemone *Metridium* (Bucklin, 1987), the gorgonian *Plexaura* (Lasker, 1984), and the scleractinian corals *Acropora* and *Porites* (Kojis and Quinn, 1981; Tunnicliffe, 1981). Hydrodynamics do not seem to play an important role in fragmentation in *P. caribaeorum*, although they are important for ramet dispersal. The low fragmentation observed in *P. caribaeorum* probably resulted from a combination of factors such as: large colony size, flat shape (hidrodynamic), high colony thickness, and high colony density, may decrease the chance of colony fragmentation. Similarly, substrate stabilization (colonies covering debris and small boulders), or colonize large-heavy boulders on a low slope decrease the chance partial colony mortality and fragmentation after disturbance (low intensity storms).

Variation in physical factors, such as current velocity, could not explain the temporal pattern in fragmentation observed here. One might expect fragmentation to decrease in the summer when mean current velocity was minimum (Carelli, 1995), but this did not occur. Future studies should focus on the intensity and frequency of major storms to explain temporal variations in fragmentation production.

Colony Size vs. *Partial Mortality.* The area of partial mortality was proportional to colony size in *Palythoa caribaeorum*. The number of lesions has been positively correlated with colony size in other species (Farrant, 1987; Meesters et al. 1996; Lewis, 1997). In contrast, mortality is size-dependent (Connell, 1973; Highsmith, 1982; Karlson, 1986) for some corals and zoanthids (specifically *Zoanthus* spp. and *P. caesia*), with large colonies exhibiting lower levels of mortality (Lasker, 1990; Meesters et al. 1996). Meesters et al. (1996) have shown that small colonies are more vulnerable to partial mortality and eventually death than larger ones, because of their high circumference: surface ratio. They are also more susceptible to colony edge processes (*i.e.* bottom-associated), which cause mortality. Partial mortality in large *P. caribaeorum* colonies are probably the result of: 1) circumference: colony-surface-area ratio; 2) weak or senescent polyps; and 3) a constant disturbance. Low levels of total colony mortality are probably enhanced in *P. caribaeorum* by: 1) colony "size refuge" (see Sammarco, 1982); 2) parent colonies with long polyps ($\leq$ 6cm) overgrowing boulders above the substratum to avoid threatening bottom-associated processes; and 3) the ability to regenerate tissue. *P. caribaeorum* recruits probably experience higher level of mortality than ramets, because they are in direct contact with the bottom, and their single polyp size (< 1.5 cm height) does not represent an escape in size from mortality (Meesters et al. 1996).

Large lesions in a colony of *Palythoa caribaeorum* may also help to increase local benthic species diversity, through the settlement of other epibiota, at least until the colony recovers its space. The tissue lost constitutes a decrease in fitness, in addition to the already high degree of infertility known to occur in this species (Fadlallah et al. 1984).

In summary, we now know that two modes of fragmentation occur in *Palythoa caribaeorum*: Fragmentation by partial colony mortality, and by physical disturbance. This form of asexual reproduction, however, was not as common as fission, which we previously described elsewhere. Although partial colony mortality was common in the population, $\leq 5\%$ of total colony area was affected in this way. Disease seems to be the main source of partial mortality in this species and helps to explain differences found in the frequency of fragmentation *via* partial mortality between shallow and slightly deeper depths. Hydrodynamics (storms) seem to have the same effect on zoanthid populations in the two sites, since similar numbers of fragments were produced *via* physical disturbance. Fragmentation most likely plays a less significant role in population growth in this species than fission.

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FIGURE LEGENDS

Figure 1. Study sites in the São Sebastião channel, São Paulo coast, Brazil. (1) Ponta Recife, on the mainland; (2) Praia Portinho, on offshore island. "T" represents the Terminal Maritimo Almirante Barroso (TEBAR).

Figure 2. *Palythoa caribaeorum.* Schematic illustration of asexual reproduction *via* fragmentation in *P. caribaeorum*. Fragmentation processes proceed from the top to the bottom of the figure. Thick arrows represent principal pathways. (a) Parent colony; (b) Fragmentation by Partial Colony Mortality. Note that a new ramet has been isolated in the middle of the colony after partial colony mortality; (c) Ramet release; (d) Fragmentation by Substrate Instability. Note how the parent colony is being split into two pieces, J′ and J′′; a disturbance such as storm activity might initiate this; (e) Ramet dispersal, usually effected by currents, slope of the bottom, etc.

Figure 3. *Palythoa caribaeorum.* The relationship between partial colony mortality per annum and colony area (cm^2). $\log_{10} (Y + 1) = 0.8946 * \log_{10} (X) - 1.3489$ ($p < 0.001$, Kendall′s Robust Line and Tau Analysis, $n = 330$). Assuming that $b = 0.8946$ was not different from 1.0, then X and Y are proportional, an approximate formula $Y = a * X^b$; $Y = (- 1.3489) * X$

TABLE LEGENDS

Table 1. (A) Frequency of colonies of *Palythoa caribaeorum* reproducing *via* two modes of fragmentation. (B) Total number of fragments produced. Data are organized with respect to site (Praia Portinho *vs*. Ponta Recife), and depth (0.5-1.5m *vs*. 2.5-4.0m). With respect to total fragmentation, frequency of colonies fragmenting (A), and total number of fragments produced (B) were independent of site ($p > 0.05$, G-test, with William's correction), but not depth ($p = 0.0074$, G-test).

Table 2. Temporal variation in the frequency of asexual reproduction using two modes of fragmentation in *Palythoa caribaeorum*. Total number of ramets dispersed in each mode also shown. The number of colonies exhibiting fragmentation, and the number of fragments dispersed, due to partial mortality, were independent of time ($p > 0.05$, G-test, with William's correction). These same characters, when resulting from physical disturbance, varied significantly with respect to seasons ($p = 0.01$, G-test, with William's correction), being lower during the winter. Dispersal of fragments by both biotic and abiotic means was independent of time ($p > 0.05$, G-test, William's correction).

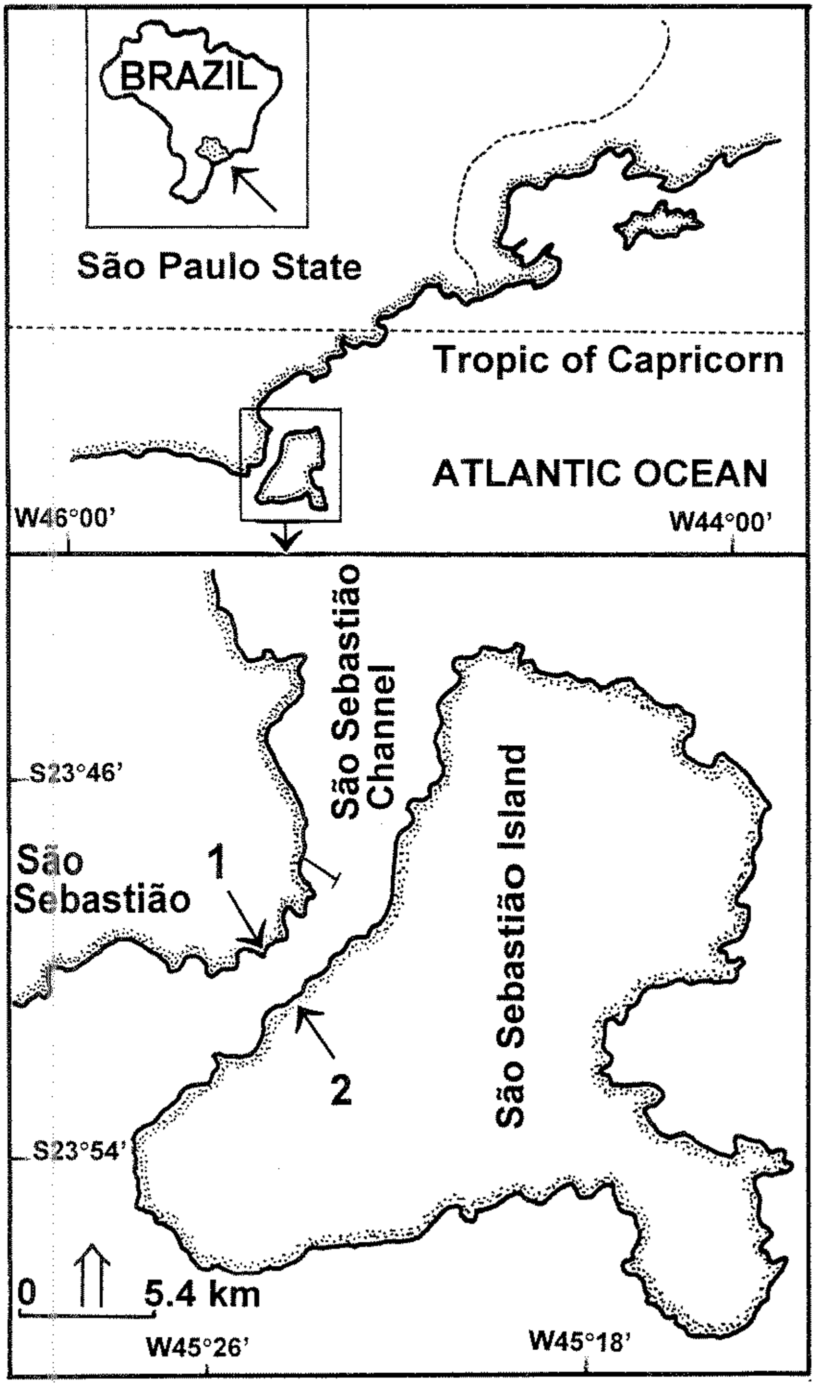
BRAZIL
São Paulo State
Tropic of Capricorn
ATLANTIC OCEAN
W46°00'
W44°00'
São Sebastião Channel
S23°46'
São Sebastião
1
São Sebastião Island
2
S23°54'
0
5.4 km
W45°26'
W45°18'

Fig 1

Modes of Fragmentation in *Palythoa caribaeorum*

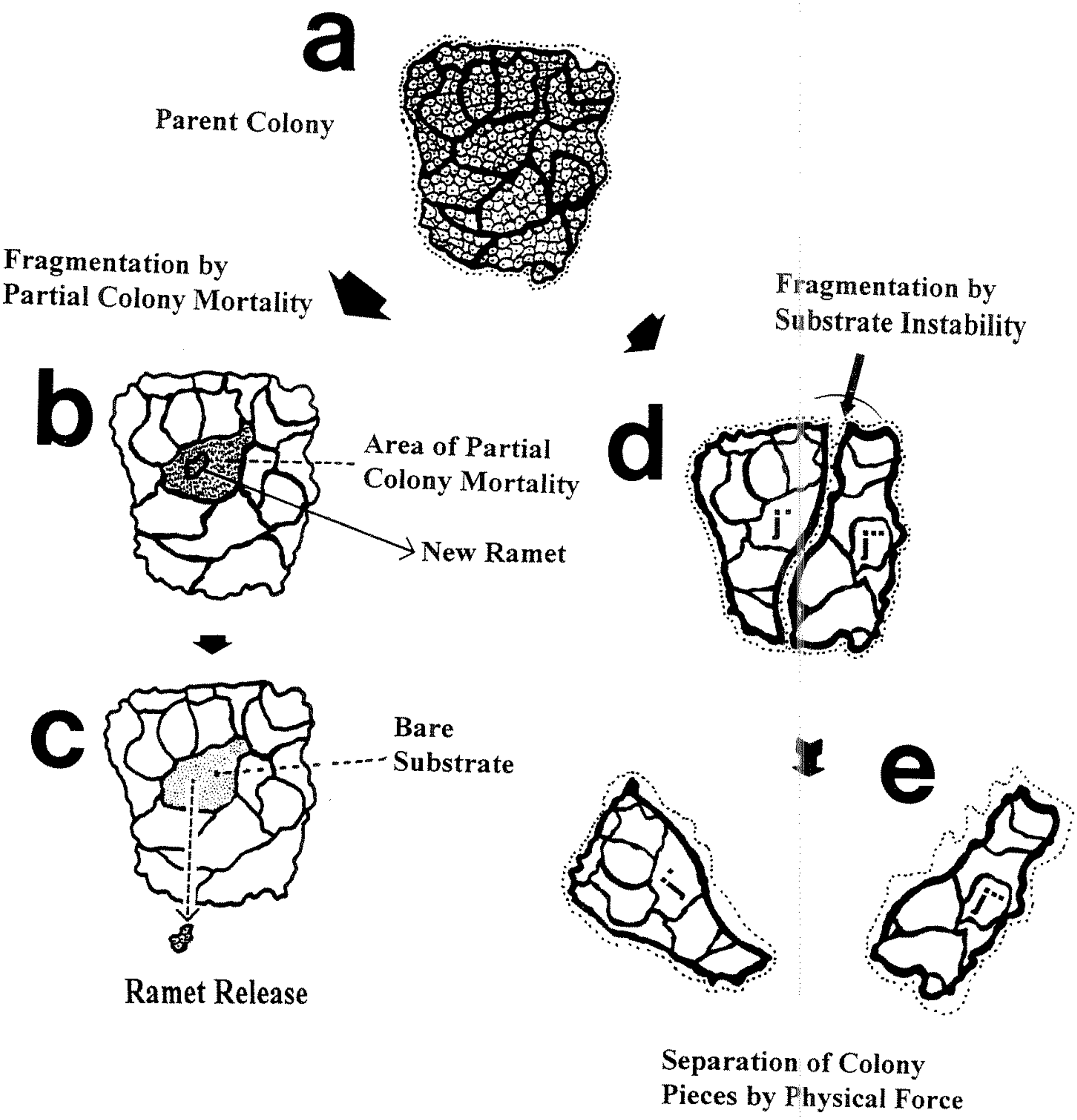

Fig 2

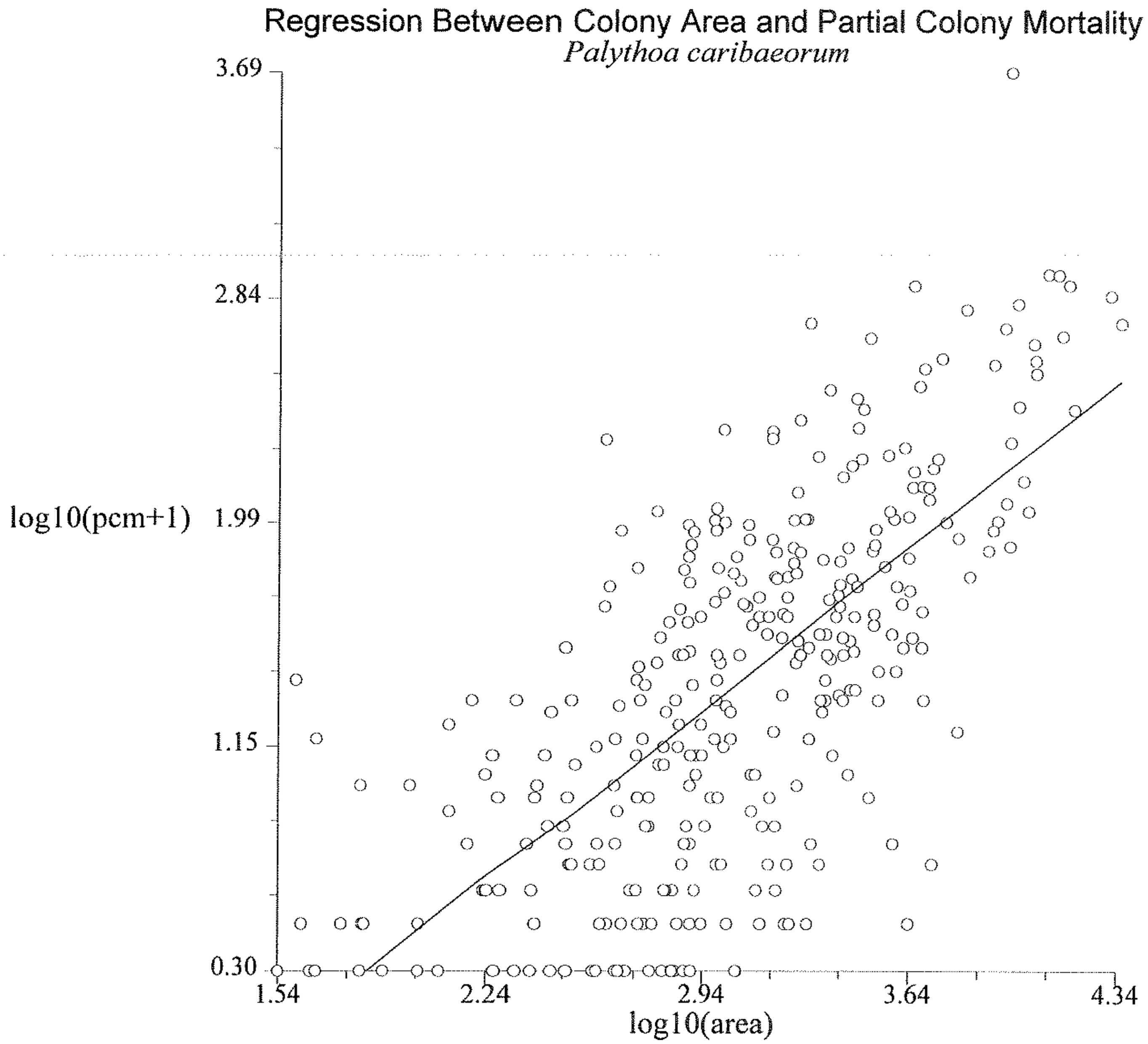
Regression Between Colony Area and Partial Colony Mortality
Palythoa caribaeorum
log10(pcm+1)
3.69
2.84
1.99
1.15
0.30
1.54
2.24
2.94
3.64
4.34
log10(area)

Fig 3

Table 1

A. Frequency of Colonies

	Colonies without fragmentation		Frequency of colonies fragmenting by						
			Partial Colony Mortality		Physical Factors		Total Fragmentation		
	Praia Portinho	Ponta Recife	P. Portinho	P. Recife	P. Portinho	P. Recife	P. Portinho	P. Recife	Total
Shallow	131	132	8	7	2	13	10	20	30
Deep	162	112	3	0	6	3	9	3	12
Total	293	244	11	7	8	16	19	23	42
B. Total Fragments or Ramet Produced									
Shallow			11	14	4	17	15	31	46
Deep			6	0	8	4	14	4	18
Total			17	14	12	21	29	35	64

Table 2

	Winter 97	Spring 97	Summer 98	Fall 98
Number of Colonies Fragmenting *via* Partial Colony Mortality	14	14	15	18
Number of Colonies Fragmenting *via* Physical Factors	3	13	9	13
Total ramets dispersed after Frag. *via* Partial Colony Mortality	3	8	8	4
Total ramets dispersed after Frag. *via* Physical Factors	5	8	5	10

Capítulo IV

Hydrobiologia - Submetido para publicação

Disease in Zoanthids: dynamics in space and time

By

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Key Words: disease, Cnidaria, Zoanthidea, *Palythoa caribaeorum*, spatio-temporal, Brazil, environmental stress.

Abstract

Diseases of benthic marine organisms have increased significantly over the last decade. Here, a new disease (pathogen unknown) is described and quantified in space and time for *Palythoa caribaeorum* (Cnidaria, Zoanthidea) populations on the São Paulo coast, Brazil (23° S). The degree of environmental stress (moderate *vs.* high), depth, and temporal variation (seasons, years) on the frequency of the disease was assessed by monitoring plots at two sites: Ponta Recife (continent) and Praia Portinho (São Sebastião island), and at two depths per site (0.5 - 1.5 m and. 2.5 – 4 m). The disease spread outward from within the colony in a circular pattern. A transverse section extending from normal to diseased tissue showed a progression from normal polyps to pale, swollen polyps, followed by remnant spicule-like structures, and finally fine black matter and bare substratum in the middle of the lesion. The disease occurred in one or more portions of the colony simultaneously. Disease frequency and total area infected increased significantly with colony size. Generally the disease affected $\leq$ 5% of the total colony area, and occurred when gonad development was maximal. 20.5% (n = 306), and 14.6% (n = 578) of the population was infected in two consecutive years respectively. Disease exhibited higher rates during summer (tourist season) and fall, and decreased significantly in the winter with the presence of cool water. Factors associated with the increased instance of disease during the summer were higher temperatures, precipitation, and sewage; the opposite was noted in the winter. Disease frequency varied significantly between years, seasons, sites and depths. Colonies exhibited higher disease frequency in Ponta Recife characterized by high levels of sedimentation, increased turbidity, and low levels of incident light with respect to Praia Portinho. Colonies in shallow-water exhibited greater frequency of disease compared to those in deeper water.

Abiotic and anthropogenic factors (*e.g.* sewage, tourism), which occurs with different intensity and frequency in space and time may explain the differences observed in the frequency of the disease between *P. caribaeorum* populations. Physiological stress, low energy input, energy expenditure, and energy re-allocation may increase the susceptibility of *P. caribaeorum* colonies to disease. It is suggested that this disease may play an important role in the life history of *P. caribaeorum* because of its influence on partial mortality, colony area, population size structure, reproduction, and ultimately fitness. This represents the first report of disease related mortality in zoanthids, for a reef-species in the Southwestern Atlantic.

Introduction

Worldwide, coral reefs ecosystems are now experiencing stress from increased pollution (*e.g.* terrestrial runoff, nutrient rich waters), habitat degradation, and population pressures (Ginsburg, 1994; Leao et al. 1997). This stress can be in the form of exposure to detrimental abiotic factors, physical damage, nutritional depletion, or on interaction of these (Feingold, 1988). Such systems are likely to be more susceptible to diseases and pathogens (Antonius, 1981b; Real, 1996; Bruckner et al. 1997; Peters, 1997), which contribute to coral reef decline (Garrett & Ducklow, 1975; Dustan, 1977; Gladfelter et al. 1977; Rutzler & Santavy, 1983; Brown & Howard, 1985; Brown, 1990; Williams & Bunkley-Williams, 1990; Richardson, 1992; Peters, 1997; Richardson, 1997; 1998; Santavy & Peters; 1997; Antonius & Riegl, 1998; Bruckner & Bruckner, 1998; Hayes & Goreau, 1998; Korrubel & Riegl, 1998; Ritchie & Smith, 1998; Gil & Garzon, 1999).

The causal agent, effect, and relationship between abiotic stressors, anthropogenic influence, and the incidence of disease are little understood (Antonius, 1995; Santavy & Peters, 1997; Richardson, 1998), and remain high priority research areas for effective coral reef management (Antonius, 1995). Likewise, host susceptibility depending on prevailing environmental conditions (*e.g.* space and time) has not been thoroughly investigated for most of the diseases (Anderson, 1986; Antonius, 1995; Bruckner & Bruckner, 1997b; Santavy & Peters, 1997).

Several diseases have been reported to occurs in corals (Antonius, 1995; Peters, 1997; Hayes & Goreau, 1998; Richardson, 1998), alcyonarian corals (Santavy and Peters, 1997), gorgonians (Goldberg & Makemson, 1981; Moorse et al., 1981; Laydoo, 1983; Rutzler et al., 1983; Guzman & Cortes, 1984; Antonius, 1985a; Feingold, 1988; Glynn et al., 1989; Botero, 1990; Santavy & Peters, 1997; Richardson, 1998), and milleporids (Guzman & Cortes, 1984; Feingold, 1988). Nevertheless, only bleaching (Migotto, 1997), and a crustacean parasite belonging to ascothoracid (Grygier, 1985) are known to affect Zoanthidea.

The zoanthid *Palythoa caribaeorum* Duchassaing and Michelotti 1861 is a sessile, colonial organism that grows over hard substrata. It is a common species on shallow-reefs in the western Atlantic. Its vertical range extends from the intertidal to the subtidal maximum to a 12 m depth (Sebens, 1982b), probably because its light dependency (Sebens, 1977; Suchanek & Green, 1981; Steen & Muscatine, 1984; Sorokin, 1991; Mueller & Haywick, 1995). The predominance of this organism may be explained by its high tolerance to environmental variability (Cooke, 1976; Sebens, 1982b; Sorokin, 1991), and reproductive capabilities (Fadlallah et al., 1984; Gleibs, 1994; Acosta et al., 1998; Tanner, 1999). Sub-lethal stressors, however, favored bleaching in *P. caribaeorum* as reported in the Caribbean (Jaap, 1985; Zea & Duque, 1989; Lesser et al., 1990) and on the São Paulo coast of Brazil (Migotto, 1997). Whether *P. caribaeorum* exhibit symptoms of other diseases due stressors is unknown.

Here, a new disease - pathogen unknown - is described for Zoanthidea. It affects *Palythoa caribaeorum* populations on Brazilian coast. Using several populations of *P. caribaeorum,* I determine: 1) if there is significant differences in the frequency of disease between moderately *vs*. highly stressed environment, and 2) whether these differences can be attributed to abiotic factors, and anthropogenic activities. I examined the following hypothesis in space and time: 1) frequency of disease is not different between sites, or between depths; and 2) frequency of disease is not different between seasons, or between years. Here, I will show that in fact disease frequency was significantly different in space and time. Populations of *P. caribaeorum* exhibited a higher disease frequency when subjected to a high stress environment, and appear to be associated with particular environmental conditions during the summer. Disease may play an important role in the life history of *P. caribaeorum*.

Material and methods

Sampling sites

Palythoa caribaeorum populations were studied in Brazil, near the latitudinal limit of its distribution (23° S). Study sites were located on both sides of the São Sebastião channel on the São Paulo coast: Ponta Recife (PR), on the continental coast, and Praia Portinho (PPo), on São Sebastião Island (Figure 1). PR a highly stressed environment in terms of high turbidity, low light levels, and high sedimentation compared with PPo (Acosta, 1999b).

The channel receives pollution in the form of sewage from the continent and the island (CETESB, 1996), oil derived from Brazil's largest coastal oil terminal - TEBAR (Weber & Bicego, 1991; Zamboni, 1993; Ehrhardt et al., 1995; CETESB, 1996), and terrigenous sedimentation due to erosion and dredging (Migotto, 1997). The city of São Sebastião on the continent has approximately 4 times more residents than in the island (31,950 *vs.* 7,240, respectively; FESB - Fomento Estadual de Saneamento Basico-SP, 1971).

This region is subject to frequent polar disturbances and associated cold fronts and storms. The local currents are forced mainly by winds (equatorial or poleward) and shelf circulation (Castro Fo, 1990; Carelli, 1995). The São Sebastião channel is highly hydrodynamic in terms of current energy, velocity and direction (Carelli, 1995). The north continental coast in the channel is characterized by calm water and is considered a zone of deposition of fine sediment. In contrast the island coast is a zone of erosion - high current energy - (Furtado, 1978). Low current velocities (< 0.2 m s^{-1}) predominantly from SW are typical for summer; while, current velocities increases the rest of the year (0.4 - 0.6 m s^{-1}), predominantly from NE (Carelli, 1995). Tidal currents are 0.03 m s^{-1} with a mean tidal flux of 0.66 m (Carelli, 1995). Surface seawater temperatures and salinities in the channel fluctuate widely throughout the year (15 - 31°C and 22 - 36‰ respectively; CEBIMar, 1991), with a mean temperature of 26.2°C in summer versus 21.3°C in winter (CEBIMar, 1991; Migotto, 1997).

First sampling

306 colonies were randomly selected at two fixed sites and depths in São Paulo coast, São Sebastião channel, Brazil. A total of 169 colonies were sampled in Ponta Recife (PR - continent), with 51 colonies located in shallow water (0.5 - 1.5 m), and 118 colonies in a deeper habitat (2.5 – 4 m). Similarly, 137 random colonies were selected in Praia Portinho (PPo – São Sebastião Island), with 91 in shallow water, and 46 in deep water. Sampling was conducted during the summer from 21 December 1996 to 21 March 1997. Colonies ranged widely in sizes, from 23 to 240 cm in diameter (0.0376 m^2 to 4.1 m^2 in area). The frequency of infected colonies was recorded for each of the four habitats. Additionally, were measured 1) colony size: expressed in area, determined by multiplying maximum colony length by maximum width; 2) number of lesions or skeletal remnants, and 3) total area of lesions per colony (disease virulence): measuring the diameter of each lesion to determine area. The infected population was classified into three size classes for statistical comparison, small ($\leq$ 50 cm diameter), medium (>51 to $\leq$100 cm), and large colonies (>101 cm).

Second sampling

12 plots incorporating 578 colonies were monitored repeatedly in order to assess seasonal and spatial variations in disease frequency. Sampling was performed at the two contrasting sites described previously (PR n = 267, and PPo n = 311). Colonies were compared at two depths per site in the subtidal 0.5 - 1.5 m (PR n = 152; PPo n = 141) *vs.* 2.5 – 4 m (PR n = 115; PPo n = 170), never exposed to the air, even during extreme low tides. Three random replicate plots were delineated at each depth (3.2 – 11.6 m^2), with 36 - 85 colonies in each, including a wide variety of colony sizes (range: 2.5 x 10^{-5} m^2 to 2.1 m^2). The positions of the plots were randomly selected using a grid, and the colonies surrounding the random point were mapped using acrylic tables. Mapping assisted in marking and following colonies *in situ* (Acosta et al., in review – chapter 1 and 2). The frequency of disease was determined once every season: August 1997 (end of winter), November 1997 (spring), February 1998 (summer), and May 1998 (fall). It was possible to identify and quantify disease occurrence between sampling periods due the presence of remnant pseudo-skeleton - spicule-like structures in affected colonies (Haywick & Mueller, 1997), as well as the characteristic circular pattern of tissue loss. Variables including colony size, condition, presence/absence of disease, number and area of tissue affected per colony and area of partial colony mortality were assessed as above. Eventual observations were made to determine colony regenerative capabilities, sexual maturity of affected colonies, and geographic extent of disease occurrence. Healthy and infected tissue was collected from several colonies and brought to the laboratory for qualitative comparison under the compound microscope.

Community structure

The community structure and percent cover of *Palythoa caribaeorum* was quantified *via* a random-point technique along a chain transect. 100 points were sampled at each of the two depths: 0.5 - 1.5 m and 2.5 – 4 m, at each of the two sites - PPo and PR - during summer 1997. Density (number of colonies / area) was also quantified in each of the 12 plots. Density was estimated counting the survival colonies at the end of the second sampling period, and measuring the area colonized for them in each plot. Total *P. caribaeorum* cover was also quantified in the plots using 1 m^2 quadrant. A colony was defined as a group of polyps physically independent from other colonies, even if they were separated by only a few millimeters.

Abiotic variables

Measurements were made to explore environmental factors, which could possibly promote stress and disease in the colonies. This included frequent assessment of turbidity (light extinction) using a Secchi disc at the two sites from February 1997 to May 1998 (2 - 7 days per week depending of environmental conditions). Intensity of illumination was also quantified 3 – 5 times per week during fall and winter 1997 using a Rigo-submarine illuminometer at 1.5 and 3 m depth at each site. Sedimentation rates were measured using 12 cylindrical PVC sediment traps per site (35 cm length x 5 cm diameter), 6 at each depth. These were fixed to the bottom, and collected and replaced seasonally. The sediment was oven dried and weighed (units expressed as mg. dry weight cm^{-2} day^{-1}). Sediment traps were sampled from January 1997 to May 1998. Water surface temperature, salinity and precipitation were measured daily (8 am and 4 pm.) at the Centro de Biologia Marinha

(CEBIMar - USP), located on the continent close to PR. Using data from 1991 to 1996 (CEBIMar - USP) I estimated the mean annual temperature and salinity. One thermometer min-max was installed at 1.5 and 3 m depth at both sites for continuous measurement of temperature fluctuation. Abiotic data from summer 1997 and summer 1998 were used for specific comparison. Precipitation data presented here cover the period from January 1997 to March 1998.

Density of *E. coli* (MPN / 100 ml) was used as an indirect indicator of sewage presence, and seawater quality. These data were provided by CETESB (São Sebastião, São Paulo, Brazil), which monitored the density of *E. coli* weekly, all year around, at ≥ 12 stations in the São Sebastião channel. Seasonal comparisons in density of *E. coli* were made using data from 1997 at four stations, PR and Praia Grande on the continent, and Pereque and Itaguacu on the island. Spatial comparison in density of *E. coli* between the continent and the island was made using data at 5 stations in the continent *vs.* 5 stations in the island. They were selected due to proximity to our study sites.

Statistical analysis

Differences between the mean density of *Palythoa caribaeorum* between the four habitats (two sites and two depths) were test *via* multiple pair comparisons using T′, Tukey-Kramer and GT2 methods (Sokal and Rohlf, 1995). Spearman's correlation was used to analyze the relationship between disease frequency and the density of colonies (following Kuta & Richardson, 1996). Data were analyzed using coefficient of dispersion (Sokal & Rohlf, 1995) to determine whether disease incidence was clumped or not (following Edmunds, 1991).

To differentiate if disease was dependent on colony size (during the first sampling), the frequency of colonies infected in each size class was compared using RXC frequency analysis with Yates correction (Sokal & Rohlf, 1995). The total area of tissue affected per colony (disease virulence) was also compared between the three size categories *via* one-way ANOVA, pooling the results of the two samplings periods. Data transformation was applied when necessary (*e.g.* Log_{10} for area of tissue infected per colony). *A posteriori* test T′-Tukey-Kramer and GT2 methods (Sokal & Rohlf, 1995) were performed to know which categories were significantly different.

Disease frequencies of the two samplings were combined to detect general patterns in time (two years) and space (sites and depths). They were compared using RXC frequency analysis with Yates correction. Sampling periods were combined since the higher disease frequency occurred for the two consecutive years during the summer. Nevertheless, the frequencies were also analyzed (as above) in time and space independently for each sampling.

Temporal variations (between seasons or years), and spatial variations (between sites or depths) for temperature, salinity, sedimentation rate, turbidity (light extinction), intensity of illumination, and precipitation were analyzed *via* one-way ANOVA, followed by *a posteriori* test Tukey-Kramer (Sokal & Rohlf, 1995).

Results

Community structure

The vertical range of the distribution of *Palythoa caribaeorum* into the channel was from 0 to 7 m. Study sites were characterized by a three-dimensionally complex hard-bottom habitat, composed of sand, debris, and boulders of various sizes. *P. caribaeorum* was the dominant benthic organism, accounting for 37% cover at depth ≤ 1.5 m, and 50 to 65% cover between 2.5 and 4 m, where the sand bottom started (Table 1). One hundred percent cover of this species was observed between 1.5 and 2.5 m, where inter-colony contact was common. In the plots *P. caribaeorum* accounted for 40 to 95% cover (Table 2), with colonies growing as a single large unit over the boulders. *P. variabilis* was frequent on PPo but rare in PR. Other zoanthids such as *Zoanthus sociatus* and *Z. solanderi* exhibited lower cover (Table 1). Ponta Recife had a higher percentage of free substratum (52%), and the lower cover of zoanthids (43%).

Description of the disease

The disease is perceptible when one or a few polyps and its surrounding coenenchyme, appears swollen - “bumpy” in morphology (Figure 2a), it’s followed by pale, white or translucent polyps from above, while the interior of the polyps appear black (Figure 2b). Usually the diseased polyps were retracted. The consistency of the affected polyps was rigid in initial stages of the disease. Colonies did not appear to produce excessive mucus as a defense mechanism, when compared with normal healthy colonies. The disease spread outward from within the colony in a circular pattern (Figure 2c).

A transverse section extending from normal to diseased tissue was characterized by normal polyps (1 cm diameter; Figure 2c) progressing to pale tissue (discolored polyps or bleached), deformed and smaller polyps, coenenchyme degradation, remnant spicule-like structures or crystal aggregates (preserved upright), and finally fine black matter and bare substratum in the middle of the lesion. Frequently, a thin white layer covered the polyps and the entire area of the lesion (Figure 2c). The fine black matter was also found between the basal portion of the affected polyps and the substratum. Portions of tissue infected were susceptible to loss of attachment to the substratum. Affected tissue removed for microscopic analysis had a strong smell (rotten matter), greater abundance of bacteria (*Vibrio)*, and an identified fungus with respect to controls.

Once the disease exposed part of the internal polyp tissue, a bloom of micro and macro-organisms, probably secondary pathogens, and predators such as copepods, crabs, and fish (*e.g. Abudefduf saxatilis* and *Chaetodon capistratus*) appeared on the colony. They seem to prey upon affected tissue and gonads in *Palythoa caribaeorum* colonies. Mature gonads were observed in February and March, corresponding with the peak of disease; no gonads were present in colonies on 25 April 1997, suggesting spawning. Once the diseased tissue (remnant spicule-like structures and black matter) disappeared due to predation or hydrodynamic forces, the bare substratum remained free of colonization for several months (even by filamentous algae, algal or *Sargassum* sp. blooms). The progression of disease from first development to disappearance (where only bare substratum remained) occurred over a period of weeks. The most rapid tissue loss proceeded at a rate of 57 to 85 cm^2 day^{-1}. The surviving polyps surrounding the affected area developed a cuticle, but the colony did not regenerate or start to recover the lost tissue even after 9 months.

The disease occurred in one or more areas of a colony simultaneously. An individual colony exhibited 1 to 45 different lesions simultaneously, with an of average 2 +/- 3 lesions (n = 130). A single lesion ranged from 1 to 45 cm diameter or 1,600 cm^2. The mean value was 55.49 +/- 151.6 cm^2 (n = 130). Overall, the disease affected a mean of 5% of the total colony area. The maximum percentage of tissue lost due to disease in a single colony was 50%, where its initial surface area was 2 m^2. An entire colony never died due to disease.

Six of the monitored colonies affected during the summer were re-infected during the fall (1998), five of them occurring at the PR site (three in deep-water). *Palythoa caribaeorum* was apparently the only species in the study area affected by disease; it was not observed in the zoanthids *P. variabilis, Zoanthus solanderi,* or *Z. sociatus,* nor in the scleractinian coral *Mussismilia hispida* Verrill 1868. I observed the disease to occur in *P. caribaeorum* elsewhere along the Brazilian coast, e.g. in Rio de Janeiro (Angra dos Reis) and Pernambuco (Recife).

Densities of *Palythoa caribaeorum* differed significantly between the four habitats ($p < 0.05$, T´-Tukey-Kramer-GT2 test; Table 2). Density was higher in PPo and in deeper water (Table 2). Disease prevalence was not correlated with *P. caribaeorum* density (12 plots), indicating density independence ($r = -0.16$, $df = 11$, $p > 0.05$; Spearman's correlation). Indices of dispersion (a measure of distribution) were 2.81, 2.74, and 2.64 during summer, fall, and year round respectively, with values greater than 1 indicating a clumped distribution of diseased colonies.

Colony size

The frequency of the disease was dependent upon, and increased with, colony size ($p < 0.05$, RxC Frequency Analysis with Yates correction; Figure 3). Similarly, the total area of tissue affected per colony, differed significantly among the three size classes ($p < 0.001$, one-way ANOVA, $n = 130$), when the two sampling periods were pooled. Large colonies exhibited a higher mean area of tissue affected (121.5 +/- 235.0 cm^2; $p < 0.05$, Tukey-Kramer Test; $n = 48$), than medium (27.14. +/- 34.0 cm^2; $n = 28$) or small colonies (11.74 +/- 18.45 cm^2; $n = 54$). Similar results were obtained when compared the mean area of tissue affected (or mean number of lesion) in equally surface area of tissue sampled between categories ($p < 0.05$, one-way ANOVA), suggesting that large colonies are more susceptible to disease, not because their higher area exposed to be infected.

Annual variation

The frequency of disease differed significantly between the two years ($p < 0.05$, RxC Frequency Analysis with Yates correction; Figure 4). 20.5% ($n = 306$) of the population was affected in the first sampling period (summer 1997) and 14.6% ($n = 578$) during the second (winter 1997 - fall 1998). The total number of colonies affected during the two sampling periods were 16.6% (147 of $n = 884$), based on pooled data from the two sites and depths.

A comparison of abiotic factors between summer 1997 and summer 1998 showed that the former exhibited lower temperature and higher sedimentation than the latter. The mean water temperature was significantly ($p < 0.001$, one-way ANOVA, $n = 286$) lower in 1997 (24.05 +/- 1.94°C) than 1998 (25.17 +/- 1.85°C; $p < 0.05$, Tukey-Kramer Test). Temperature fluctuation was, however, slightly greater during 1997 (19°C min; 29°C max) than 1998 (20.2 min; 28.9 max). Mean sedimentation rate was significantly different between years ($p < 0.001$, one-way ANOVA, $n = 28$), with higher rates in summer 1997 (28.56 +/- 6.86 mg cm^{-2} day^{-1}) than in summer 1998 (5.93 +/- 2.57 mg cm^{-2} day^{-1}; $p < 0.05$, Tukey-Kramer Test). Precipitation and salinity were not statistically different ($p > 0.05$, one-way ANOVA, $n = 45$), though, total precipitation was 570 mm in the summer of 1997 and 510 mm in the summer of 1998.

Seasonal variation

Frequency of the disease varied significantly between seasons ($p < 0.001$, RxC Frequency Analysis with Yates correction; Figure 5), with a higher number of lesions occurring during the summer, decreasing during fall, and almost disappearing in winter and spring with the presence of cool water. The maximum disease frequency in summer 1997 and 1998 occurred when gonad development was maximal for *Palythoa caribaeorum* in the study area.

In February 1998, there were some days of high water temperatures (29.3°C), precipitation (146 mm), turbidity ($\leq$ 2.5 m, Secchi disc) and sedimentation (13.7 mg cm^{-2} day^{-1}). One week later 28.1% of the population monitored ($n = 578$) exhibited bleaching (de-coloration, and partial bleach); and colonies showed signs of extensive disease.

During the winter, after a period of storms and continuous stress due to turbidity and an extremely high sedimentation rate, 19.7% of the total colonies monitored ($n = 578$) exhibited a thin layer of mucus covering all or part of the colony (mucus layer initially described by Johannes, 1967). Colonies remained retracted, with polyps closed and not feeding. Some of the colonies stayed in this condition for weeks or even months into the winter, appearing to be dead. A reduction in height of the contracted polyps in the whole colony was evident during this stage, suggesting tissue resorption. Weeks later, the colony released this mucus layer, which was sometimes covered by algae and sediment grains, then opened their polyps and started to feed again. A shiny color on the surface characterized the colonies that finished this period of what might be termed "diapause" or "dormancy". No colonies that experienced this stage died.

The mean water temperature was significantly different between seasons ($p < 0.001$, one-way ANOVA, $n = 1317$; Figure 6A), being highest in the summer (26.1 +/- 1.7°C, $n = 423$), followed by fall (25.1 +/- 1.1°C, $n = 280$), spring (22.0 +/- 1.5°C, $n = 341$) and winter (21.5 +/- 1.4°C, $n = 273$; $p < 0.05$, Tukey-Kramer Test). Precipitation also varied seasonally ($p < 0.05$, one-way ANOVA, $n = 66$ days of rain; Figure 6B). The only significant differences, however, between pair comparisons were between spring and fall ($p < 0.05$, T′-Tukey-Kramer Test- GT2 methods). Spring 1997 exhibited higher mean precipitation (38.32 +/- 36.7 mm; total precipitation = 656 mm; number of rainy days $n_r = 17$), than summer (20.35 +/- 14.72 mm; total precipitation = 570 mm; $n_r = 28$), fall (15.04 +/- 17.68 mm; total precipitation = 180.5 mm; $n_r = 12$), or winter (12.94 +/- 19.18 mm; total precipitation = 116.5 mm; $n_r = 9$). Mean differences in sedimentation rate were highly significant between seasons ($p < 0.001$, one-way ANOVA; $n = 126$; Figure 6C). Mean pair comparisons of sedimentation rates indicated that only winter was significantly different from the other seasons ($p < 0.05$, Tukey-Kramer Test). The mean sedimentation rate in winter was higher 124.5 +/- 144.9 mg cm^{-2} day^{-1} ($n = 37$) when compared with other seasons (mean between 15.14 to 16.5 +/- 12.5 mg cm^{-2} day^{-1}). The mean values of salinity (Figure 6D) and light extinction (Figure 6E) were not different between seasons ($p > 0.05$, one-way ANOVA, $n = 1308$ and $n = 129$, respectively). Water turbidity remaining high all year-round (Figure 6E).

Mean values of *E. coli* varied between seasons ($p < 0.01$, one way-ANOVA, $n = 208$; Figure 6F), being highest in fall (3,900 +/- 7,990 MPN / 100 ml; $n = 32$; $p < 0.05$, Tukey-Kramer Test), followed by summer (1,600 +/- 2,685 MPN / 100 ml; $n = 48$), spring (1,216 +/- 3,250 MPN / 100 ml; $n = 60$), and winter (513.7 +/- 1,044 MPN / 100 ml; $n = 68$; $p < 0.01$).

Variation between sites

Disease frequency differed significantly between sites ($p < 0.001$, RxC Frequency Analysis with Yates correction; Figure 7), being higher on the continent than on the island, based on pooled data for depths at each site for the two samplings. Significant differences in disease frequency were also observed between sites for the first sampling ($p < 0.05$, RxC Frequency Analysis with Yates correction), but not for the second sampling ($p > 0.05$). However, for the second sampling the mean area of tissue affected per colony between sites was significantly different ($p < 0.05$, one way ANOVA); colonies in PR showed a higher mean area of diseased tissue (23.27 +/- 43.1; $n = 44$; $p < 0.05$, Tukey-Kramer Test) than PPo (10.1 +/- 16.95; $n = 40$).

The two sites differed in terms of mean sedimentation rate ($p < 0.01$, one-way ANOVA, $n = 134$; Figure 8A), light extinction ($p < 0.05$, one-way ANOVA, $n = 130$; Figure 8B), and intensity of illumination ($p < 0.05$, one-way ANOVA, $n = 100$; Figure 8C). PR exhibited more stressful conditions, with a higher sedimentation rate (62.8 +/- 114 mg cm^{-2} day^{-1} in PR *vs.* 35.1 +/- 70.4 mg cm^{-2} day^{-1} in PPo), a lower level of light (3.5 +/- 1.7 m *vs.* 4.8 +/- 1.8 m, Secchi disc), and low intensity of illumination (1564 +/- 1062 lux *vs.* 1769 +/- 1039 lux) than PPo ($p < 0.05$, T′-Tukey-Kramer- GT2 methods). Mean water temperature 23.0 +/- 2.1°C was the same between sites ($P > 0.05$, one-way ANOVA, $n = 112$), with minimum and maximum values between 15.5 and 29.3°C ($n = 143$). The mean abundance of *E. coli* did not differ significantly between sites ($p > 0.05$, one-way ANOVA, $n = 120$; Figure 8D).

Variation between depths

Significant differences in disease frequency were observed between depths ($p < 0.05$, RxC Frequency Analysis with Yates correction; Figure 9A), when data from the two sites and the two samplings were pooled. Shallow-water colonies exhibited a higher frequency of disease (19.3%, $n = 435$) than deeper ones (14.03%, $n = 449$). Differences in disease frequency were also observed between depths for the second sampling ($p < 0.05$, RxC Frequency Analysis with Yates correction; $n = 578$; Figure 9A); but not for the first one ($p > 0.05$; Figure 9A), when data for the two sites were combined. Significant differences between depths were observed within the same site only for PPo ($p < 0.05$; Figure 9B). Similarly, at PPo the area of tissue affected was different between depths ($p < 0.05$, RxC Frequency Analysis with Yates correction, $n = 311$, second sampling), where shallow colonies lost more tissue due to the disease (17.7%, $n = 141$) than deeper ones (8.82%, $n = 170$).

Intensity of illumination differed between depths ($p < 0.05$, one-way ANOVA), either when sites were pooled or analyzed separately (Figure 10A). Colonies occurring in shallow water received higher mean levels of light (2,043 +/- 1,084 lux, $n = 50$) than deeper ones (1259 +/- 866 lux, $n = 50$, $p < 0.05$, Tukey-Kramer Test). PPo exhibited higher intensity of illumination than PR at both depths. Mean intensity of illumination reaching deeper colonies was significantly higher at the PPo site ($p < 0.05$, Tukey-Kramer Test, $n = 50$), with higher values in PPo colonies. Mean sedimentation rates were not significantly different between depths ($p > 0.05$, one way-ANOVA, $n = 134$), when sites were pooled (Figure 10B).

Discussion

Etiology

The pathogen in the disease affecting *Palythoa caribaeorum* remains unknown at this time, as in most of the reported coral diseases (Richardson, 1998). Bacteria identified as the genus *Vibrio,* were abundant in *P. caribaeorum* tissue with respect to control samples. However, heterotrophic nitrogen-fixing bacteria from the family Vibrionacea (61 strains, 6 types) occur ubiquitously among members of this genus (Shieh & Lin, 1992). Additionally, *Vibrio* have been documented in the channel in several benthic filter-feeders, particularly in the summer during the tourist season (Sanchez et al., 1991; Rivera et al., 1997). Although the pathogen was not isolated, I postulate bacteria as primary pathogen, and fungus and other organisms as secondary invaders.

The pathogen may be species-specific for *Palythoa caribaeorum*, since it did not affect other zoanthids or scleractinian corals at the study sites (Acosta, 1999a). This contradicts observations made in BBD (Black Band Disease) or WBD (White Band Disease), when many anthozoans were infected (Antonius, 1981b; 1985a). Perhaps *P. caribaeorum* may accommodate distinct microbiota lacking in *Zoanthus* and scleractinian corals, as is the case in scleractinian corals (Ritchie & Smith, 1997). The specificity of these microbiotic communities would be maintained by specific carbon sources normally produced by the host species (Ritchie & Smith, 1997).

Geographic distribution

The disease appeared to be widespread along the Brazilian coast, including São Paulo, Rio de Janeiro, and Pernambuco. No evidence has been found for its occurrence in the Santa Marta area, Caribbean coast of Colombia, or from observations made in the Florida Keys. In Panama, Sebens (1982b) reported massive deaths of *Palythoa caribaeorum* during extreme low tides, where "colonies turned black and decomposed"; this brief statement does not appear to fit the disease etiology described here. Other diseases have been found to be widespread (Nagelkerken et al., 1997a; Santavy & Peters, 1997). Further research is needed to show whether: 1) the disease is endemic to *P. caribaeorum* populations in Brazil (see Grosholz & Ruiz, 1997); 2) Brazilian populations are subjected to a more highly stressed environment, or are less resistant; or 3) they carry different bacterial community with respect populations in the Caribbean.

Seasonal differences in frequency of disease

Water-temperature seems to be the primary factor controlling the presence-absence and perhaps the virulence of the pathogen in *Palythoa caribaeorum* populations, as well as the degree of bleaching, which agrees with results from previous studies (Feingold, 1988; Migotto, 1997; Mayal & Pinto, 1999). High water temperature or temperature fluctuation during the summer may directly or indirectly promote pathogen virulence by lowering the resistance of the zoanthid. An increase in the infection rate seems to be common during late summer and fall, when temperatures are higher (Rutzler et al., 1983; Taylor, 1983; Antonius, 1985b; Feingold, 1988; Edmunds, 1991; Peter, 1993; Kuta & Richardson, 1994; 1996; Kushmaro et al., 1996; Korrûbel & Riegl, 1998; Gil & Garzon, 1999). In contrast, cooler water during the winter was associated in this study with a lower frequency of disease. The low virulence in winter may also be explained by the combination of lower precipitation, and low sewage discharges (low tourist season). Cooler water temperatures (below 20°C) also appeared to moderate damage by BBD, WDB, and other diseases in stony corals (Dustan, 1977; Antonius, 1981a; 1985b; Feingold, 1988; Kuta & Richardson, 1996; Bruckner & Bruckner, 1997b), or due cyanobacterial infection in gorgonian corals (Feingold, 1988). The evidence suggested that temperature might be a seasonal trigger for this disease in *P. caribaeorum*.

Spring and summer are characterized by high precipitation, with the accompanying increase in terrigenous input (waste products), sewage (nutrient enrichment), and resuspended sediment. Such inputs represent additional sources of physiological stress for the zoanthid, which may lead to decreased the resistance in the host colonies (physiological stress), and set up the conditions for the development of the pathogen in spring. The disease frequency is, however, not higher in spring perhaps because water temperature remains cold. During the summer the synergistic effect of precipitation, sewage, and increased temperature may exceed the physiological limit of *Palythoa caribaeorum* colonies promoting disease and bleaching. Antonius (1981a; 1995) and Bruckner et al. (1997b) observed an increased incidence of disease associated with high levels of terrestrial runoff, water eutrophication, and high temperature.

In the study area winter seems the most stressful season for *Palythoa caribaeorum* populations in terms of extreme high sedimentation rates, and low temperature. The disease, however, is not present. Thus, the type, frequency, and intensity of abiotic factors acting in a specific season or year are important not only to determine the level of physiological stress experienced by the colonies, but also to fit the biological requirements of the pathogen (see also Antonius, 1981b; Korrûbel & Riegl, 1998).

Annual variation

Disease seems to be a regular process affecting *Palythoa caribaeorum* populations every year. I have observed annual occurrence of the same disease since 1996. Bruckner & Bruckner (1997b) have demonstrated that once BBD invades a reef, it will persist for several years, slowly spreading throughout the population. Also, 41 to 50% of *P. caribaeorum* colonies exhibited bare substratum round-shape, which suggests a history of disease (see also Laydoo, 1998). The low tissue regeneration of *P. caribaeorum* in the study area - less 16 cm^2 $year^{-1}$ (pers. obs.) may help to corroborate evidence of disease persistence in these populations. Portion of bare substratum, however, may also correspond to fission events (Acosta et al., in review – chapter 2).

Climatic and oceanographic conditions differed between the two years compared. Significant differences in water temperature and sedimentation rate were registered. Migotto (1997), reviewing summer data in the channel from 1986 to 1994, found that some years exhibited hot periods - water $\geq$ 27.5°C for more than 5 days (*e.g.* 1992, 1993, 1994) while other years did not. If *Palythoa caribaeorum* populations experience different levels and types of stress each year, then the frequency of disease is expected to be also different, as was the case. Annual variations in coral diseases have been already reported for Florida Keys (Porter et al., 1999), which may be dependent not only on the pathogenicity but also on the interactions between pathogens and other factors such as stress or nutritional status of the colonies. It is not known at this time if the disease is increasing or decreasing in frequency over time in *P. caribaeorum* populations.

During the summer water temperature fluctuation (19 to 32°C) becomes a source of stress for *Palythoa caribaeorum* colonies. The wide fluctuation is in part explained by the South Atlantic Central Water (ACAS) that enters the channel causing temperatures to drop 14 - 15°C (Carelli, 1995). The thermal shock experienced by *P. caribaeorum* colonies may promote zooxanthellae expulsion, as suggested early (Lesser et al., 1990; Migotto, 1997), and may increase the likelihood of infection as suggested for other species (Feingold, 1988; Williams & Bunkley-Williams, 1990). If water temperature controls the expression of the disease in this zoanthid, then cool water may lower disease frequency and virulence within the summer in the study area. If so, could the range of temperature account for differences in disease frequency found between years? Kuta & Richardson (1997) have noted that BBD activity abruptly halts during the warmer months, for unknown reasons. Temperature fluctuation may help to explain this pattern.

Site differences in frequency of disease

Disease frequency differed between sites. PR is a more stressful environment than PPo, evidenced by: 1) a relatively large area of free substratum in the community. This may be explained by the absence of species as the zoanthid *Palythoa variabilis*, higher mortality of benthic organisms, or low recruitment; 2) higher mean area of partial colony mortality respect colonies in PPo (Acosta et al., in review – chapter 3). It has been suggested that injuries may increase the occurrence of disease (Antonius, 1981b; Peters, 1984; Feingold, 1988; Bruckner & Bruckner, 1999); 3) higher frequency of disease; and 4) high probability of colony reinfection (see also Kuta & Richardson, 1996; Peters, 1997). Spatial differences have been documented when comparing BBD between sites in Florida Keys (Antonius, 1981b), or different disease types between the Florida Keys and Dry Tortugas (Santavy et al., 1999).

Several abiotic and anthropogenic factors may contribute to explain differences found between sites. During most of the year, the continental coast exhibits comparatively more turbid water (visibility ≤ 4 m) and a higher sedimentation rate than the island. This is because the fine sediment deposited in the North of the channel is constantly re-suspended and transported by a current parallel to the continental coast in southward direction (Furtado, 1978; Carelly, 1995). This material, including waste products derived from nearby mountains (*e.g.* Atlantic forest), and sewage increased particularly during the summer rainy-tourist season where the population may be twice that which is normal (FESB, 1971). Similarly, increased BBD has been associated with areas impacted by increased sedimentation, terrestrial runoff, and high nutrient loading (Antonius, 1981b; 1985a; Taylor, 1983; Bruckner et al., 1997).

The current pattern helps to explain the chronic water turbidity and accompanying low light levels, as well as the higher sedimentation rate observed in PR with respect to PPo. Low light levels due to turbidity, decrease dramatically the energy input *via* photosynthesis by the symbiotic algae in *Palythoa caribaeorum* (see Suchanek & Green, 1981), *P. variabilis* (see Steen & Muscatine, 1984), and *P. caesia* (Sorokin, 1991). *P. caribaeorum* colonies exposed to low light tend to lose tissue thickness due to resorption - (A. Acosta, unpublished data). Similar responses have been observed in the zoanthid *Zoanthus sociatus* (Karlson, 1983). Reduction in the amount of light available for photosynthesis due to elevated levels of turbidity decrease growth and calcification rates in scleractinian corals (Bak, 1978; Abdel-

Salam & Porter, 1988; Telesnicki & Goldberg, 1995), and may promote disease (Antonius, 1977; 1981a; Dustan, 1977; Peters, 1984). A recent outbreak of coral disease in Puerto Rico has been related to chronic water turbidity (Bruckner & Bruckner, 1997a). Additionally, PR receives low to moderate wave action with respect to PPo (pers. obs.). Low wave energy may also contribute to an increase in the incidence and virulence of the disease in *P. caribaeorum*, as has been suggested for other species (Rutzler et al., 1983; Nagelkerken et al., 1997a).

Current patterns, low light levels, sedimentation, and wave action may be indirectly responsible for the high frequency of the disease in the continent. PR populations appeared to be exposed to a high level of physiological stress, where colonies produce less energy via photosynthesis (less light levels), and expend more energy in sediment rejection and cleaning processes, probably at the expense of vital processes such as defense, and disease resistance (see Dodge & Vaisnys, 1977; Dustan, 1977; Antonius, 1981a; Gladfelter, 1982; Taylor, 1983; Peters, 1984; Antonius, 1988; Williams & Bunkley-Williams, 1990; Slattery, 1999). *P. caribaeorum* and other zoanthids are relatively tolerant to stressful conditions (Cooke, 1976; Sebens, 1982a,b; Karlson, 1983; Sorokin, 1991). However, a combination of factors acting synergistically can decrease their tolerance, making them weak or vulnerable to disease or bleaching.

Water temperature appeared to be the same for the two sites and the two depths, and could not explain spatial differences. This variable, however, is important in explaining temporal variation, or when comparing sites on a large geographical scale (*e.g.* populations exposed to different oceanographic and climatic regimes).

Depth variation

Shallow water populations of *Palythoa caribaeorum* showed a higher frequency of disease when compared with deeper ones, in agreement with previous reports in other species (see Michell & Chet, 1975; Antonius, 1981a; 1988; Kushmaro et al., 1996). These differences were not explained in terms of colony size or to levels of partial colony mortality. Shallow-water colonies, however, seems to be subjected to higher environmental fluctuation (stressors of greater intensity) and physiological stress (sub-optimal conditions) than deeper ones.

Light levels were significant different between depths (0.5 – 1.5 *vs.* 2.5 – 4 m), and could be related directly or indirectly to the presence of the pathogen in shallow-water. Feingold (1988) suggested that high light levels could enhance growth of the photosynthetically active cyanobacterium pathogen; although exposure to UV could also increase the susceptibility to disease (see also Jokiel, 1980; Lesser et al., 1990). BBD is highly dependent on light, shutting down completely at night and occurring at a higher rate in shallow water (Antonius, 1985a). The last statement, however, contrast with Richardson's (1992) findings. Other diseases are also found more frequently in shallow-water (Lauckner, 1980; Feingold, 1988; Bruckner & Bruckner, 1997b; Gil & Garzon, 1999), and can be enhanced by light (Antonius, 1985a). Nagelkerken et al. (1997a) indicated that depending on the bathymetric range of the host species and its associated pathogen, the disease incidence could be positively correlated with depth.

The question remains: why did deeper-water colonies not show a higher frequency of disease if they received less light than shallow ones? Some of the possible explanations to be tested are: 1) The pathogen is in some way light dependent; 2) the pathogen has vertical limitations in distribution; 3) Deeper water colonies have a better defense system, or more efficiently utilize light; and 4) shallow-water colonies are exposed to more sources of stress, and as a consequence they spend comparatively more energy on other vital process at the expense of defense.

Precipitation could have a significant impact on shallow-water populations, particularly when combined with different sewage sources coming from submarine pipes (CETESB, 1996). This less dense water (low salinity) remains in the surface for a variable period of time, where it may negatively impact shallow-water colonies, particularly in calm water. Stressful condition could affect the defense mechanisms of *Palythoa caribaeorum* colonies (see also Taylor, 1983), and may decrease mucus or palytoxin production (see Attaway & Ciereszko, 1974; Gleibs, et al., 1995; Haywick & Mueller, 1997; Peters, 1997). Although the stress is insufficient to kill the zoanthid directly, it can enhance partial colony mortality indirectly by stimulating harmful microbial processes (see Michell & Chet, 1975; Dustan, 1977; Ducklow & Michell, 1979).

Clumped distribution

Diseased colonies of *Palythoa caribaeorum* exhibited a clumped distribution, suggesting that this disease could be highly infective. Similarly, the spread of some diseases has resulted in a clumped distribution (Rutzlet et al., 1983; Antonius, 1985a; Bruckner & Bruckner, 1997b). Nevertheless, some diseases may show a random distribution, or be density independent (see Edmunds, 1991; Kuta & Richardson, 1996; Grosholz & Ruiz, 1997; Nagelkerken, 1997a). Diseased colonies were not correlated with *P. caribaeorum* density. In contrast, the scleractinian coral *Dichocoenia stokesii* has been found strongly correlated with density (Richardson et al., 1998a). For species as *P. caribaeorum* that colonize large areas, cover and not density seems to be more important to understand disease distribution and virulence, due to the inverse relationship between colony size and density. A high percentage cover leads directly to increased disease due to increased transmission rates. Here *Palythoa caribaeorum* exhibited a high percent cover (37 - 65%) when compared with other areas in the Caribbean as Florida Keys - 18.6 +/- 19% (Mueller & Haywick, 1995), Virgin Islands - 10.2 +/- 16.6% (Suchanek & Green, 1981), and Colombia - 16.7 to 19% (Gleibs, 1994; A. Acosta pers. obs.).

Effects of disease at population level

The higher incidence of disease found in the populations studied (14.5 to 20.5%) was similar to that reported in the scleractinian coral *Dichocoenia stokesii* (8.7 to 20%) in Florida Keys (Richardson et al., 1998a,b; Feingold & Richardson, 1999), or due to WBD in *Acropora* (2 – 42%; Peters et al., 1983). However, it was much higher with respect to other diseases affecting the Caribbean sea-plume *Pseudopterogorgia acerosa* (8%; Feingold, 1988), or several scleractinian corals (0.2 to 6%; Edmunds, 1991; Kuta & Richardson, 1996; Bruckner & Bruckner, 1997a; Grosholz & Ruiz, 1997).

This high occurrence of disease may have a great impact in terms of cover, population size structure, population growth, reproduction, and fitness of *Palythoa caribaeorum*. Disease seems to be an annual process, which can infect high percentage of the population, particularly large colonies, especially during the peak of gonadal maturation and sexual reproduction.

Field observations suggest that disease is a major source of partial colony mortality in *P. caribaeorum* population, accounting for 10% of the total partial mortality found in the populations. Disease could be one of the factors that control the high cover of this species. On average less than 5% of the total colony area is lost to a single disease event in *Palythoa caribaeorum*. Similar results were observed in *Diploria strigosa* after BBD 3.9% (Edmunds, 1991).

Colonies of *Palythoa caribaeorum* can be severely affected by a highly virulent disease episode, or be re-infected in the same or in different years, as its known to occur in stony corals (see Feingold, 1988; Kuta & Richardson, 1994; Bruckner & Bruckner, 1997a). *P. caribaeorum* exhibited a positive relationship between area of tissue affected per colony (virulence) and colony size (*i.e.* age, larger colonies 50 - 100 years old). Similarly, in some gorgonian and scleractinian corals the incidence of the disease was higher in the larger colonies, and even polyp size seems to be correlated with the degree of resistance (Antonius, 1988; Nagelkerken et al., 1997b). Due to limited tissue regeneration following the disease and continuously stressful conditions it is expected that *P. caribaeorum* colonies could make the transition to a previous size class, affecting long-term populations size structure. Feingold & Richardson (1999) indicated that population structure of *Dichocoenia stokesii* may become skewed to smaller size classes reducing survivorship and fecundity since large colonies are affected more than smaller colonies by Plague type II disease (see also Szmant-Froelich, 1985).

Tanner (1999) documented for *Palythoa caesia* that small changes in adults colonies may produce a disproportionately large change in the population growth rate; as well as exert effects on size structure. The effects of the disease in terms of population growth are unknown, however, large single colonies, which were heavily infected, were divided into several remnant colonies, promoting fragmentation and population growth (Acosta et al, in review – chapter 3). Bruckner & Bruckner (1997b) also observed fragmentation following disease in scleractinian corals.

Additionally, in large colonies of *Palythoa caribaeorum* the pathogen reduces the number of polyps, affecting gonad maturation and production of gametes (potential new recruits), with negative implications for sexual reproduction and fitness in the species. It has been suggested that diseases affecting gonads, sexual maturation, associated tissues, and spawning behavior may also lead to reduced fecundity of individuals, with subsequent reductions in population size (Peters et al., 1983; Edmunds, 1991; Kuta & Richardson, 1997; Peters, 1997). The disease also reduces the area of polyps for feeding and photosynthesis, thus affecting energy input. Energy remaining may thus be re-allocated to maintenance, tissue regeneration, and disease fighting, at the expense of sexual reproduction (see also Hall, 1997). Large colonies of *P. caribaeorum* also produced more number of asexual propagules (Acosta et al., 1998). Disease may affect not only sexual reproduction, but also asexual reproduction through a decrease in colony area.

Sexual and asexual reproduction appears to be primarily responsible for population growth and for the successful persistence and monopolization of space in zoanthids (Karlson, 1983; Tanner, 1997; 1999; Acosta et al., 1998). Since *Palythoa caribaeorum* populations in PR are more exposed to stressful conditions and disease than PPo, we may expect a relative reduction in their reproductive effort and fitness, although this remains to be demonstrated. This disease may play an important role in the life history of *P. caribaeorum* because of its influence on partial colony mortality, colony area, reproduction, population growth, and ultimately, fitness.

For epidemic bacterial infections there is clear evidence that the proportion of resistant hosts tend to increase following an epidemic (Bailey, 1973). In ecological time, recurrent disease may induce a selective pressure and may therefore help to maintain genetic heterogeneity in the host population (Anderson, 1986; Price et al., 1986; Lively, 1996; Simms, 1996; Grosholz & Ruiz, 1997). If this is the case in *P. caribaeorum*, disease may potentially favor the production of genetically variable progeny. Increased local genetic diversity in this species its important, considering the high level of disturbance, the high number of clones produced, the low recruitment due to sexual larvae, and the low immigration rate exhibited by the population (Acosta et al., in prep.).

Effects of disease at community level

The disease may enhance diversity of the local community by opening up new spaces. Diseases represent important factors in changing the composition, structure and function of coral-reef communities, through opening substratum for colonization (Gladfelter, 1982; Scott, 1988; Edmunds, 1991; Aronson & Petcht, 1997; Kuta & Richardson, 1997; Peters, 1997; Aronson et al., 1998). Colonization of free space may take time, or be prevented, particularly if it occurs within a *Palythoa caribaeorum* colony. Field data indicate almost no colonization of areas, even after 9 months of infection. Some explanations to be explored include 1) active and passive competition for space of *P. caribaeorum* (Suchanek & Green, 1981; Gleibs, 1994), 2) chemical alteration of the substratum by the pathogen or persistence, and 3) the free area may act as a sediment trap limiting settlement. Edmunds (1991) noted that areas of corals killed by BBD did not show any scleractinian recruits after 2 years. In the long term, however, the disease may increase local diversity in the channel.

Palythoa caribaeorum is known to accumulate as 3 - 4 kg of fine sediment m^{-2} of tissue area (Mueller & Haywick, 1995). Once the tissue is destroyed by the pathogen this material is released and re-suspended into the environment, increasing turbidity, sedimentation, and decreasing light levels for autotrophic species (see also Kuta & Richardson, 1996).

Adaptation?

Whether *Palythoa caribaeorum* colonies have developed direct or indirect strategies to fight the disease is unknown. Division of the colony into several groups of polyps connected by a thin basal coenenchyme is a normal process during fission in *P. caribaeorum* (Acosta et al., 1998). Isolation of the infected tissue, whether physical (breakage of basal connections) or physiological (no communication between basal coenenchyme; Figure 2b) may prevent spreading of the pathogen. These hypotheses however will need to be demonstrated experimentally.

In conclusion there is sufficient evidence to suggest that sub-optimal conditions resulting from both abiotic and anthropogenic influence the presence and intensity of disease in *Palythoa caribaeorum* both spatially and temporally. Further studies should focus on the etiologic agent of the disease, its biological requirements, and how interactions between environment factors influence the pathogen-host relationship.

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Figure Legends

Figure 1. Study sites located on the São Paulo coast, Brazil. 1. Ponta Recife, located on the mainland. 2. Praia Portinho, on an offshore island (São Sebastião). T = represents the Terminal Maritimo Almirante Barroso (TEBAR).

Figure 2. Disease in *Palythoa caribaeorum.* A. Initial stages of the disease. Few polyps appear swollen - "bumpy" in morphology. B. Polyps infected appears retracted, pale, white or translucent from above. Note empty polyps and remnant spicule-like structures preserved upright in portions of the tissue affected (arrow). Also noted how the spreading of the pathogen throughout the colony was limited for connecting basal coenenchyme between pseudo-colonies, basal coenenchyme is produced during fission process. C. A transverse section extending from normal to diseased tissue is characterized by normal polyps (1 cm diameter) progressing to deformed and smaller polyps (≤ 0.5 cm), and bare substratum. Note a thin white layer covering the polyps in the area of lesion.

Figure 3. Percentage of *Palythoa caribaeorum* population exhibiting disease respect colony size. Results correspond to sampling made during the summer 1997, n = 124 for small, n = 97 medium, and n = 85 for large colonies respectively. Error bars represent 95% confidence limits.

Figure 4. Temporal variation. The frequency of disease is shown for two samplings periods, n = 306 and n = 578, respectively. Error bars represent 95% confidence limits.

Percentage of *Palythoa caribaeorum* population exhibiting disease (filled bars) *vs.* healthy colonies (unfilled bars).

Figure 5. Temporal variation. Seasonal percentage of *Palythoa caribaeorum* population exhibiting disease (n = 578). Error bars represent 95% confidence limits.

Figure 6. Mean comparison of abiotic factors between seasons: A. Temperature, data from 1991 to 1996, n = 1,317; B. Precipitation, data from January to December 1997, n = 66; C. Sedimentation rates, data from January 1997 to May 1998, n = 126; D. Salinity, data from 1991 to 1996, n = 1308; E. Light extinction (Secchi-disc), data from February 1997 to May 1998, n = 158; and F. Abundance of *E. coli* (MPN), data from January to December 1996, n = 356. Bars represent standard deviation. Source of temperature, salinity and precipitation CEBIMar (1991), and CETESB (1996) for abundance of *E. coli*.

Figure 7. Percentage of *Palythoa caribaeorum* population exhibiting disease between sites, Ponta Recife (unfilled bars) *vs.* Praia Portinho (filled bars). The results are shown for sampling made in summer 1997 (n = 306), sampling from August 1997 to May 1998 (n = 578), and total combining the two years (n = 884). The frequencies of disease were respectively: PR = 47 of 169, PPo = 16 of 137; PR = 44 of 267, PPo = 40 of 311; and PR = 91 of 436, and PPo = 56 of 448, when depths per site were pooled. Error bars represent 95% confidence limits.

Figure 8. Mean comparison of abiotic variables between sites: Ponta Recife (unfilled bars) *vs.* Praia Portinho (Filled bars). A. Sedimentation (n = 59 PR; n = 60 PPo); B. Mean light levels, using Secchi disc (n = 69 PR; n = 61 PPo); C. Intensity of illumination (n = 58 PR; n = 42 PPo); and D. Abundance of *E. coli* (MPN; n = 1004). Data of the last variable correspond to mean values of 5 stations in the continent *vs.* 5 in the island from January to December 1996 (source CETESB, 1996). Bars represent standard deviation.

Figure 9. Percentage of *Palythoa caribaeorum* population exhibiting disease between depths. A. Frequency of disease for two sampling periods (pooling sites); they were also combined to explore the general pattern between depths (n = 884; pooling years). B. Depth comparison per site, sampling from August 1997 to May 1998; shallow 0.5 - 1.5m (n = 152 PR; n = 141 PPo) *vs.* deeper 2.5 - 4m (n = 115 PR; n = 170 PPo); and C. Depth comparison per site, sampling made during the summer 1997 (n = 306). Error bars represent 95% confidence limits.

Figure 10. Mean comparison of abiotic variables between depths (1.5 *vs.* 3 m): A. Intensity of illumination for each site, and for the total, where sites are pooled. (n = 29 for 1.5 and 3 m at PR; n = 21 for 1.5 and 3 m at PPo); and B. Sedimentation rate for each site, and for the total (n = 31 for 1.5 m at PR, n = 28 for 3 m at PR; n = 27 for 1.5 m at PPo, n = 33 for 3 m at PPo). Bars represent standard deviation.

Table Legends

Table 1. Benthic community structure and percent cover of *Palythoa caribaeorum* quantified at two sites: Ponta Recife (PR), and Praia Portinho (PPo), and at two depths: shallow 0.5 -1.5 m and deeper water 2.5 – 4 m. Values means percent cover for each group.

Table 2. Density of *Palythoa caribaeorum* populations at two sites: Ponta Recife, and Praia Portinho, and at two depths: shallow 0.5 - 1.5 m and deeper water 2.5 – 4 m. The range is showed for several variables. Values summarized the results of three plot quantified per depth.

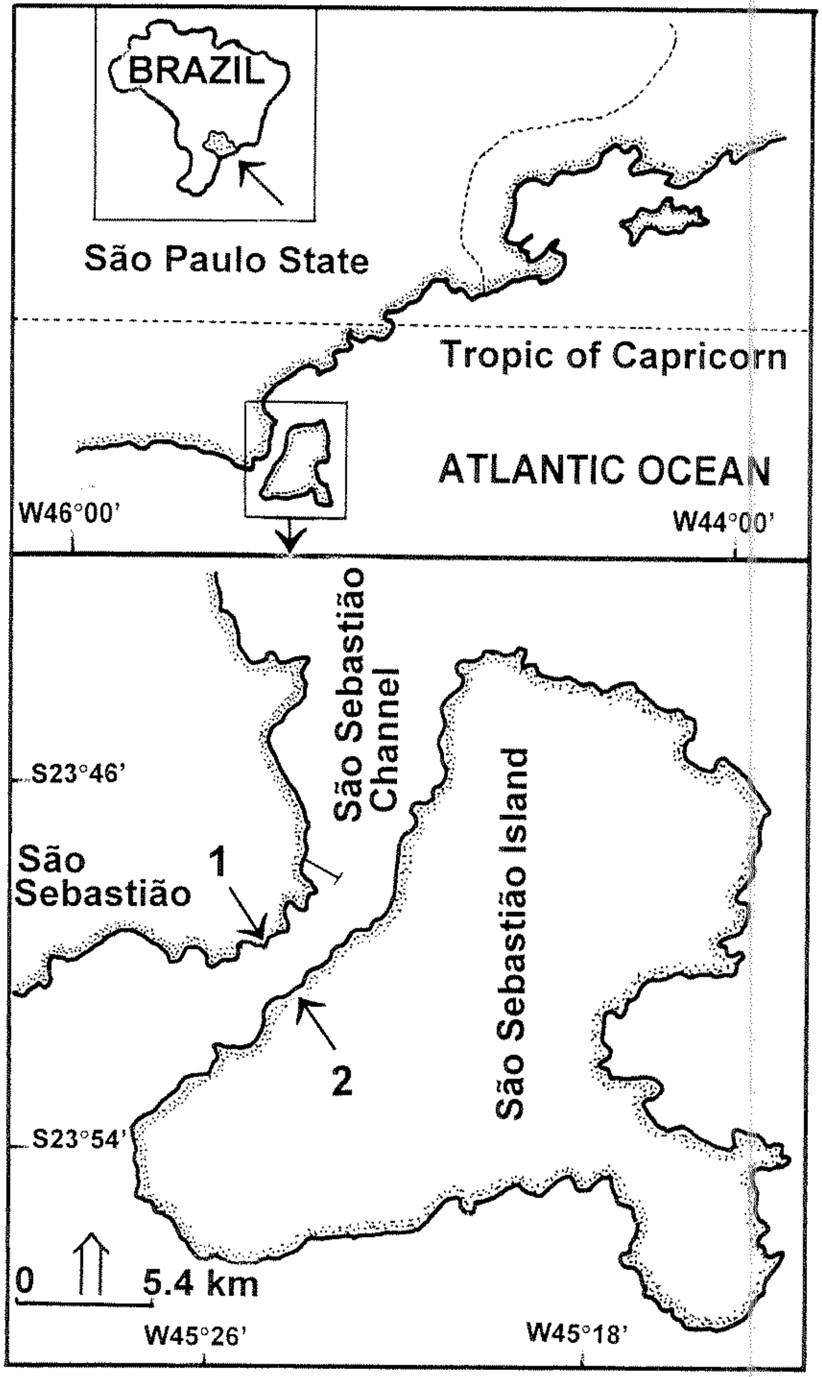

BRAZIL
São Paulo State
Tropic of Capricorn
ATLANTIC OCEAN
W46°00'
W44°00'
São Sebastião Channel
S23°46'
São Sebastião
1
São Sebastião Island
2
S23°54'
0
5.4 km
W45°26'
W45°18'

Fig 1

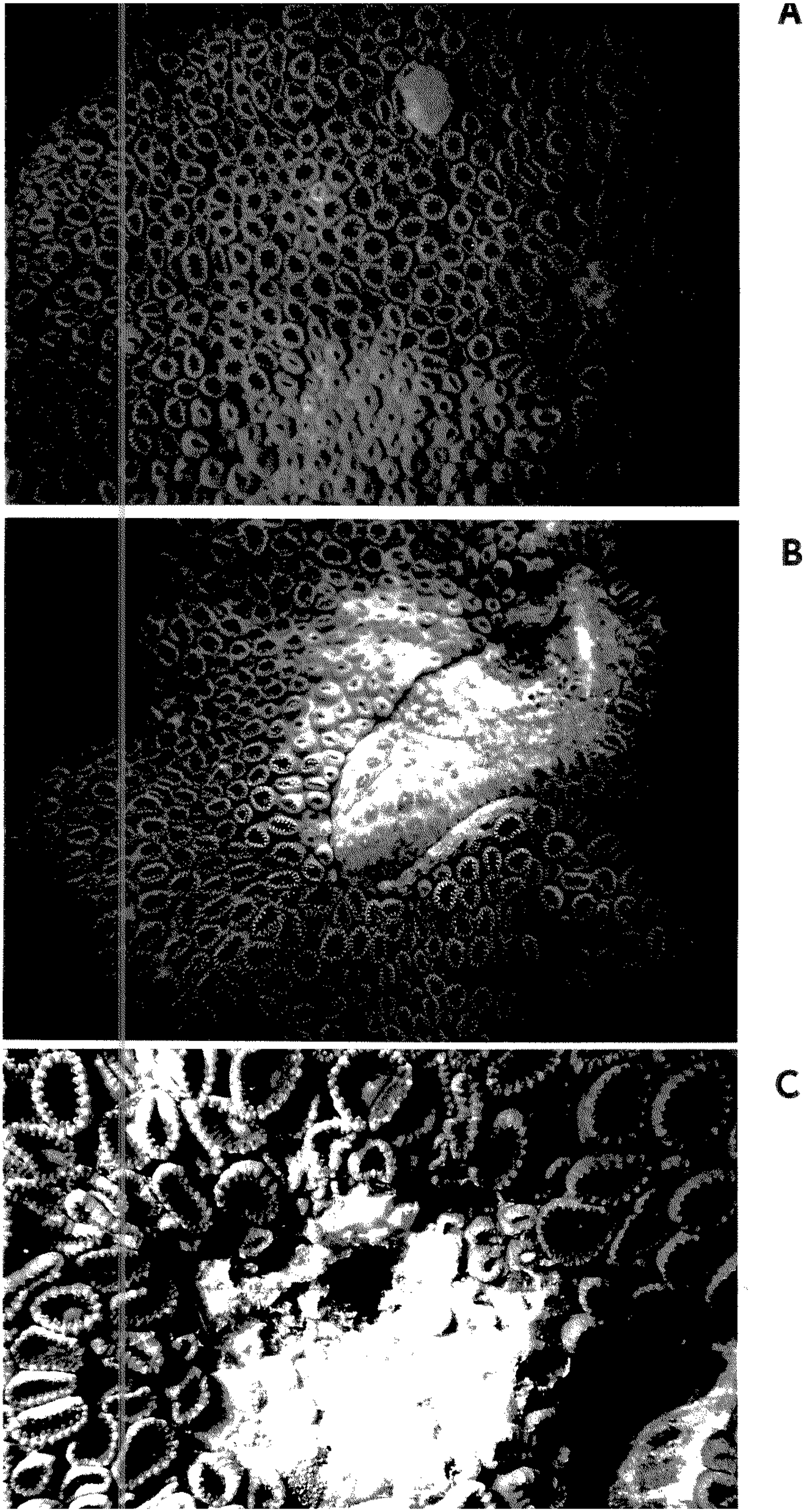


Fig 2

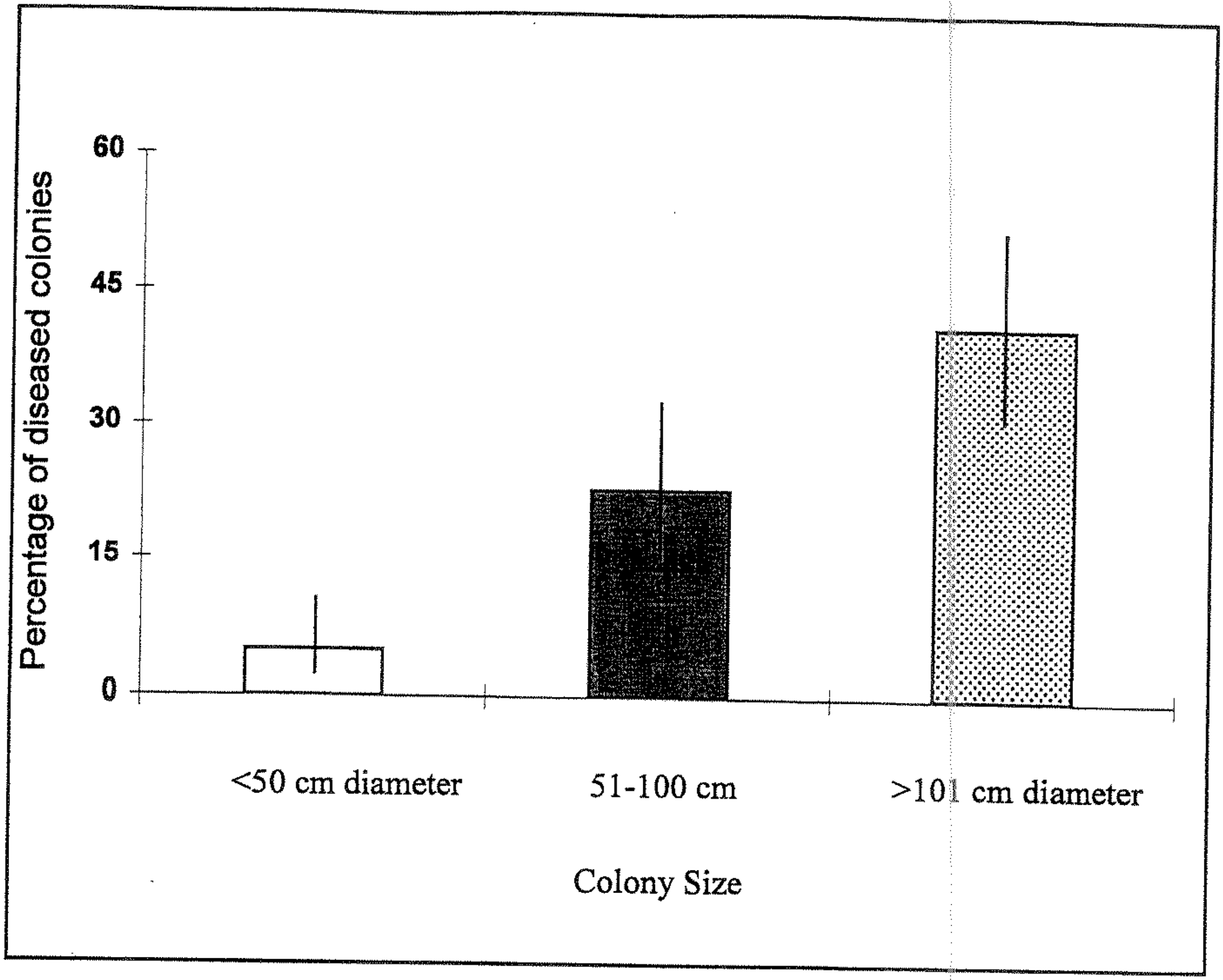

60
45
30
15
0
Percentage of diseased colonies
<50 cm diameter
51-100 cm
>101 cm diameter
Colony Size

Fig 3

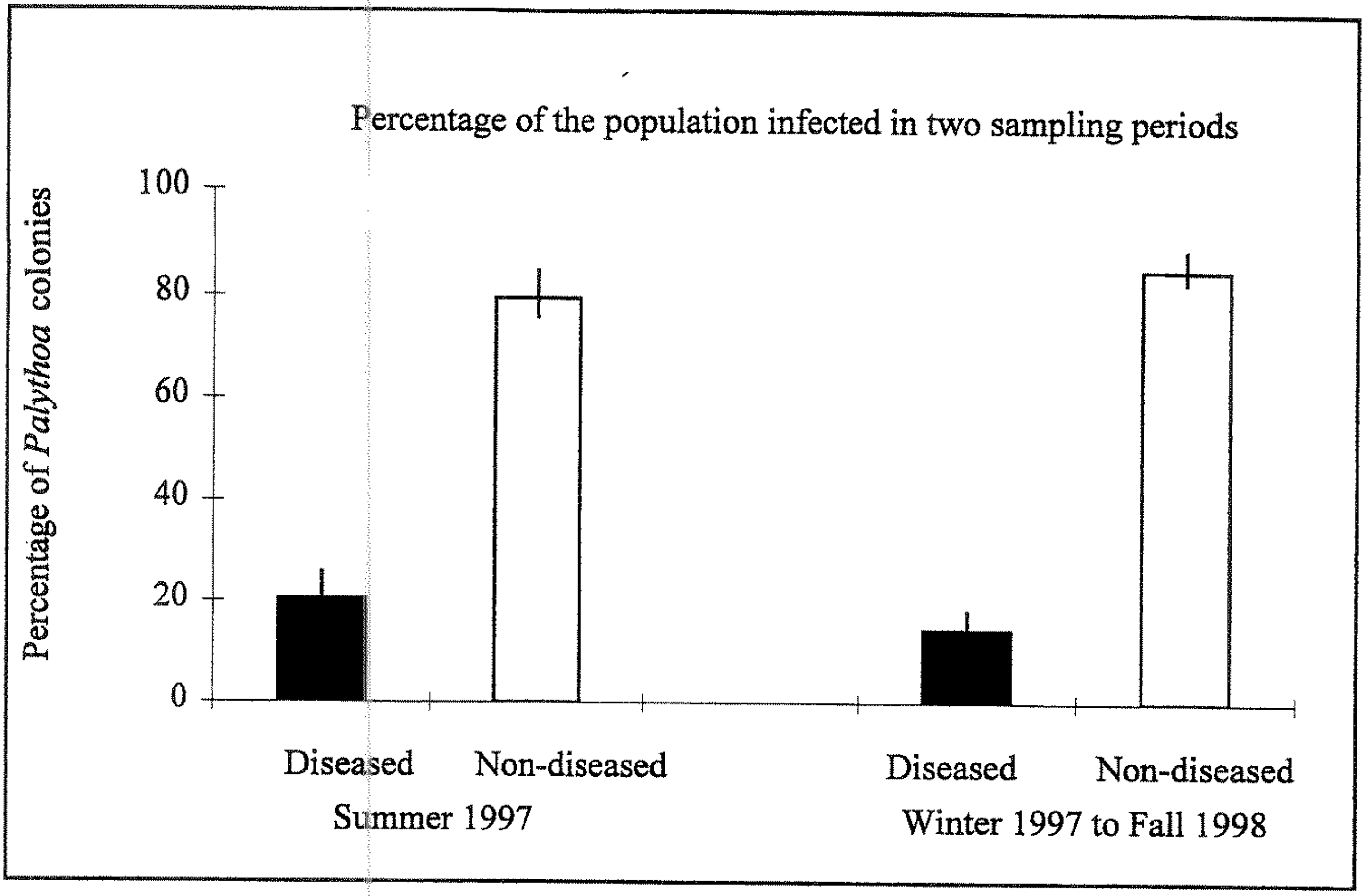
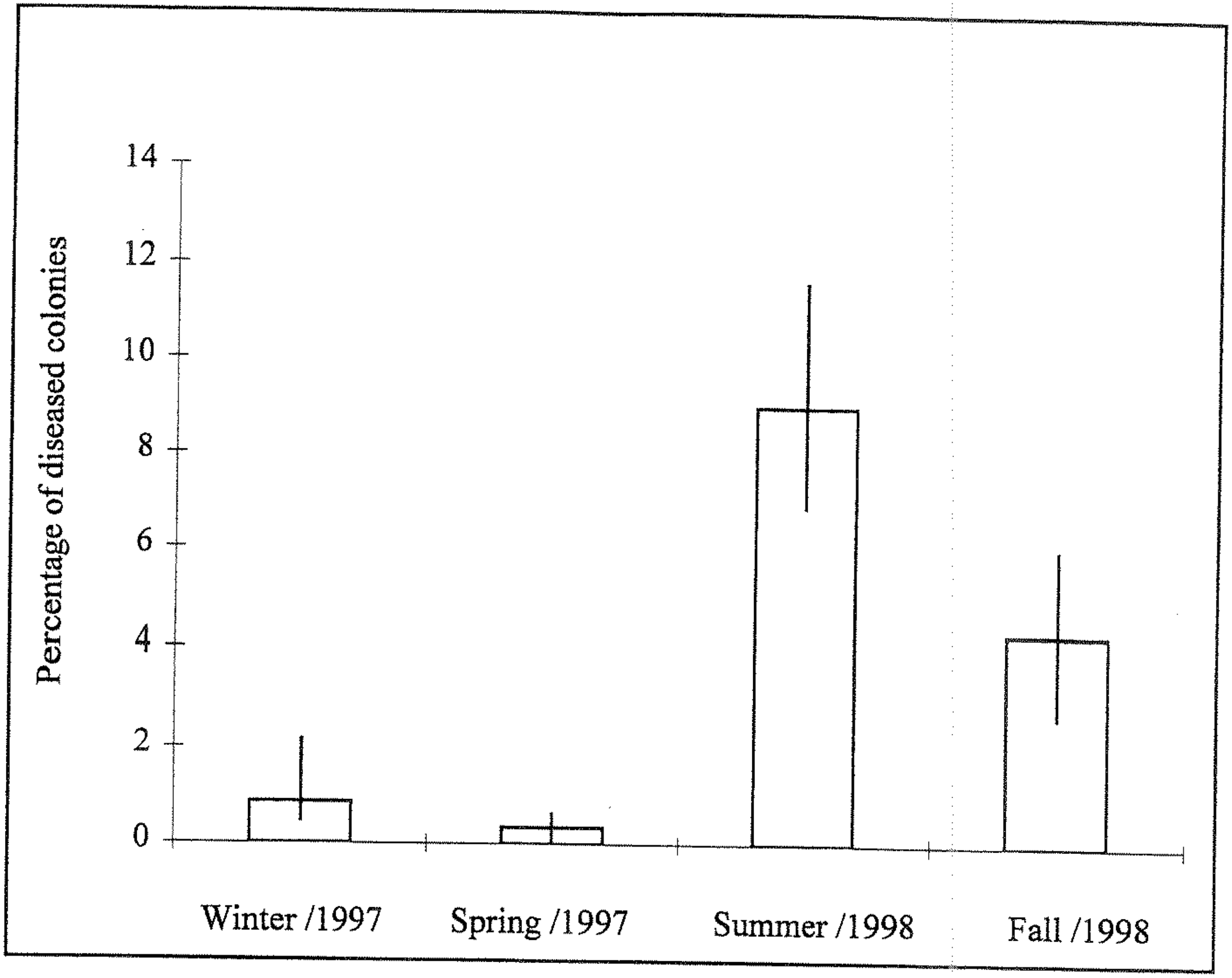

Percentage of the population infected in two sampling periods
Percentage of *Palythoa* colonies
100
80
60
40
20
0
Diseased
Non-diseased
Summer 1997
Diseased
Non-diseased
Winter 1997 to Fall 1998

Fig 4



Percentage of diseased colonies
14
12
10
8
6
4
2
0
Winter /1997
Spring /1997
Summer /1998
Fall /1998

Fig 5

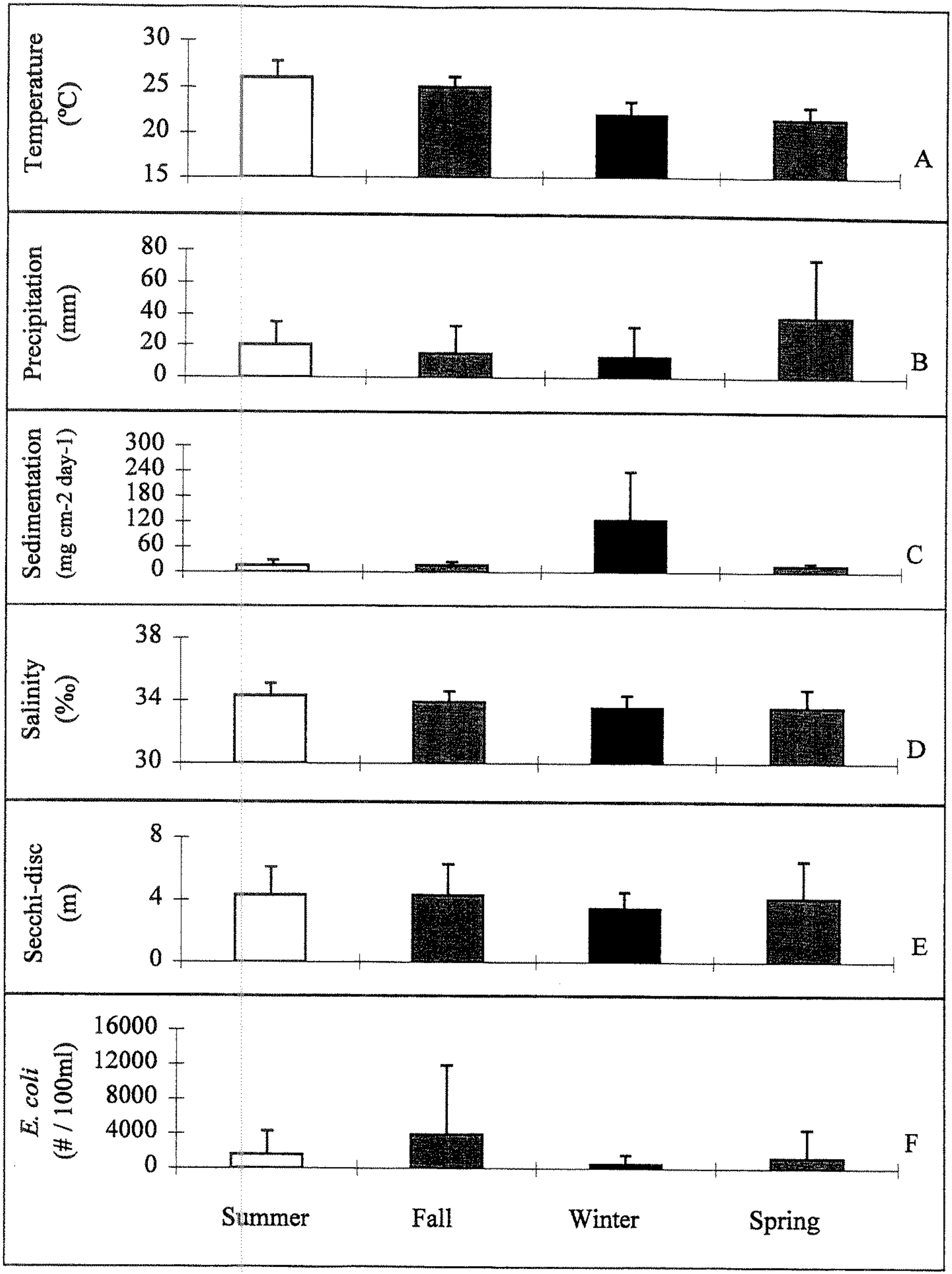

Temperature (°C)
30
25
20
15
A
Precipitation (mm)
80
60
40
20
0
B
Sedimentation (mg cm-2 day-1)
300
240
180
120
60
0
C
Salinity (‰)
38
34
30
D
Secchi-disc (m)
8
4
0
E
E. coli (# / 100ml)
16000
12000
8000
4000
0
F
Summer
Fall
Winter
Spring

Fig 6

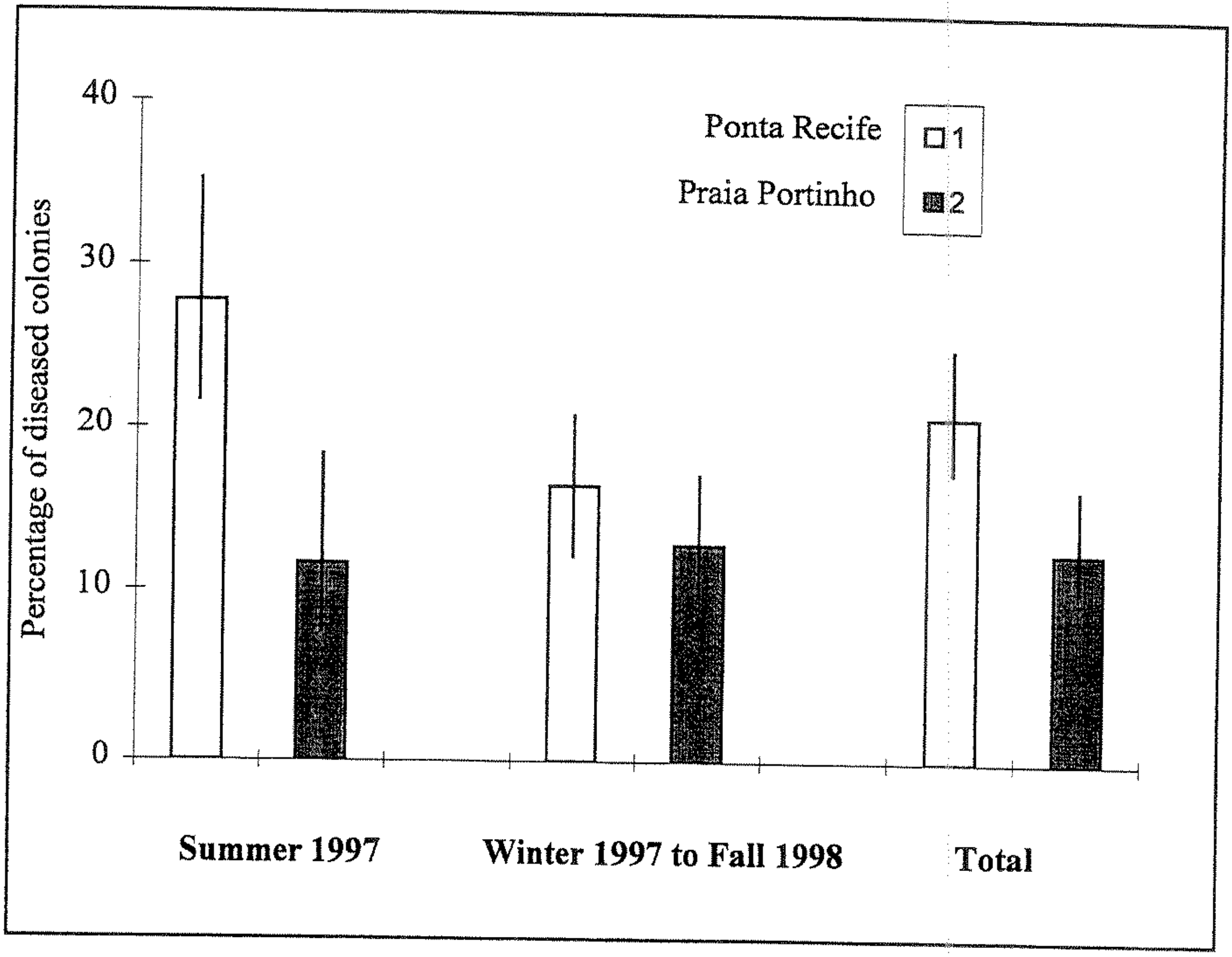

40
30
20
10
0
Percentage of diseased colonies
Ponta Recife
Praia Portinho
1
2
Summer 1997
Winter 1997 to Fall 1998
Total

Fig 7

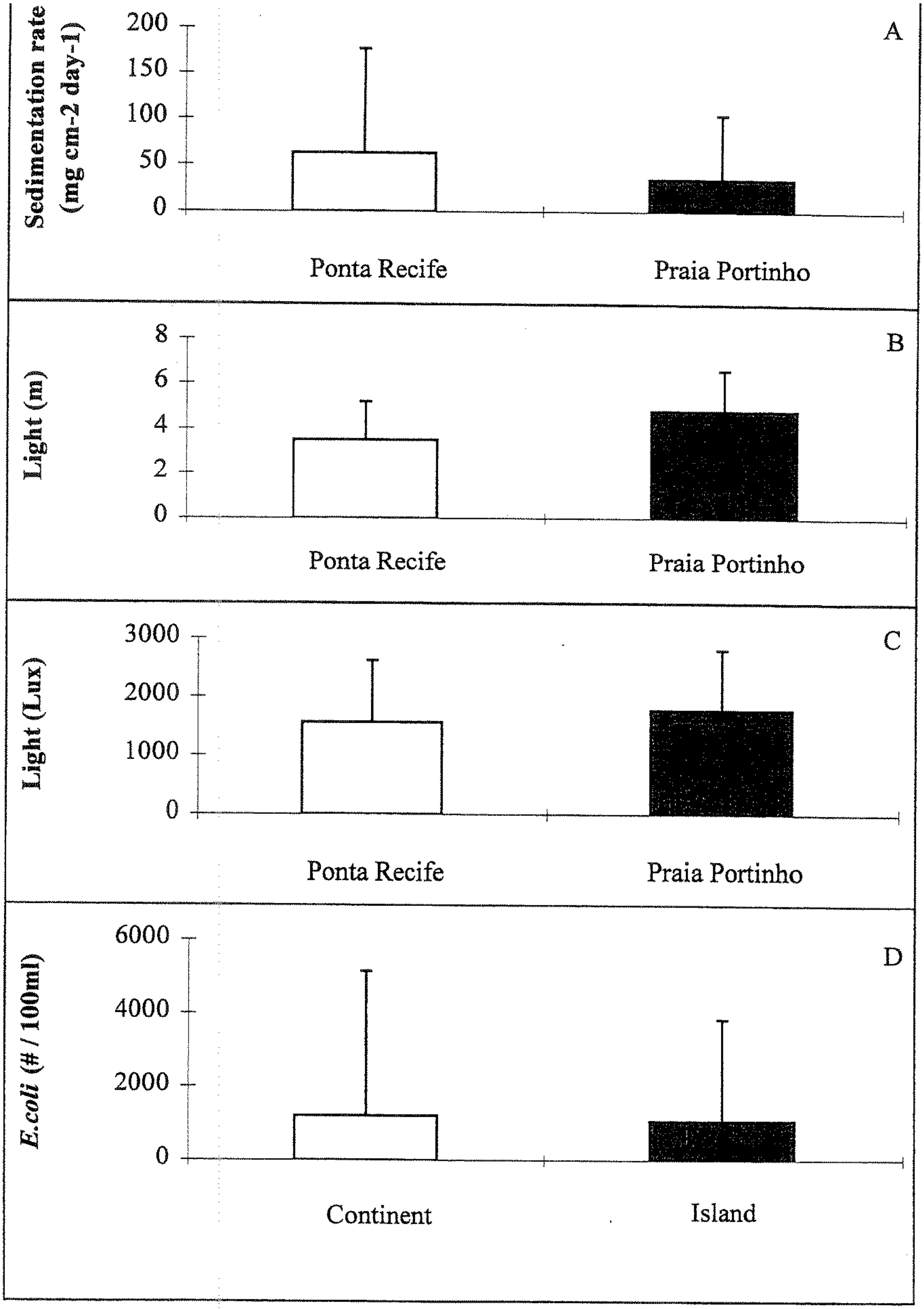

A
Sedimentation rate (mg cm-2 day-1)
200
150
100
50
0
Ponta Recife
Praia Portinho
B
Light (m)
8
6
4
2
0
Ponta Recife
Praia Portinho
C
Light (Lux)
3000
2000
1000
0
Ponta Recife
Praia Portinho
D
E.coli (# / 100ml)
6000
4000
2000
0
Continent
Island

Fig 8

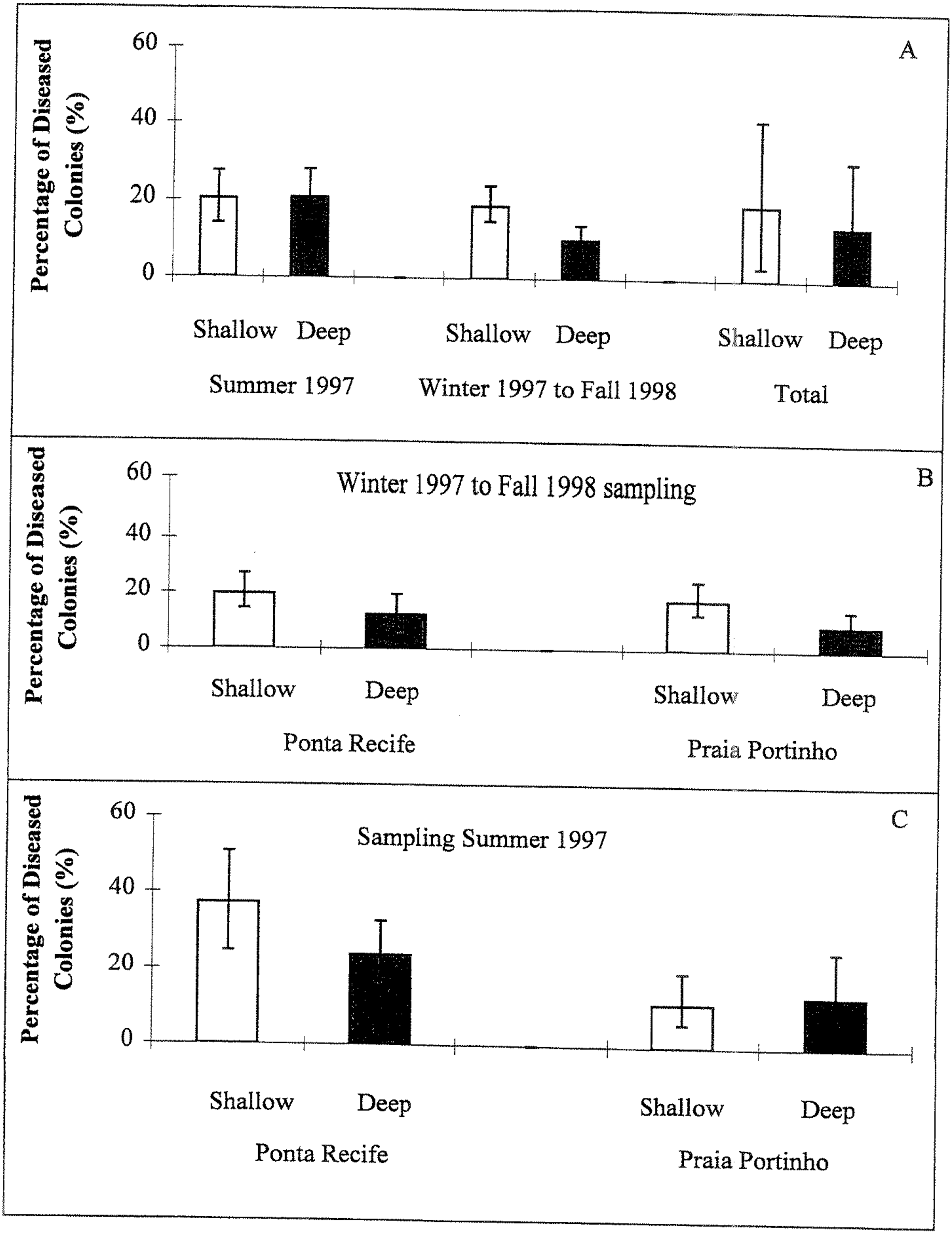

A
Percentage of Diseased Colonies (%)
60
40
20
0
Shallow
Deep
Shallow
Deep
Shallow
Deep
Summer 1997
Winter 1997 to Fall 1998
Total
B
Winter 1997 to Fall 1998 sampling
Percentage of Diseased Colonies (%)
60
40
20
0
Shallow
Deep
Shallow
Deep
Ponta Recife
Praia Portinho
C
Sampling Summer 1997
Percentage of Diseased Colonies (%)
60
40
20
0
Shallow
Deep
Shallow
Deep
Ponta Recife
Praia Portinho

Fig 9

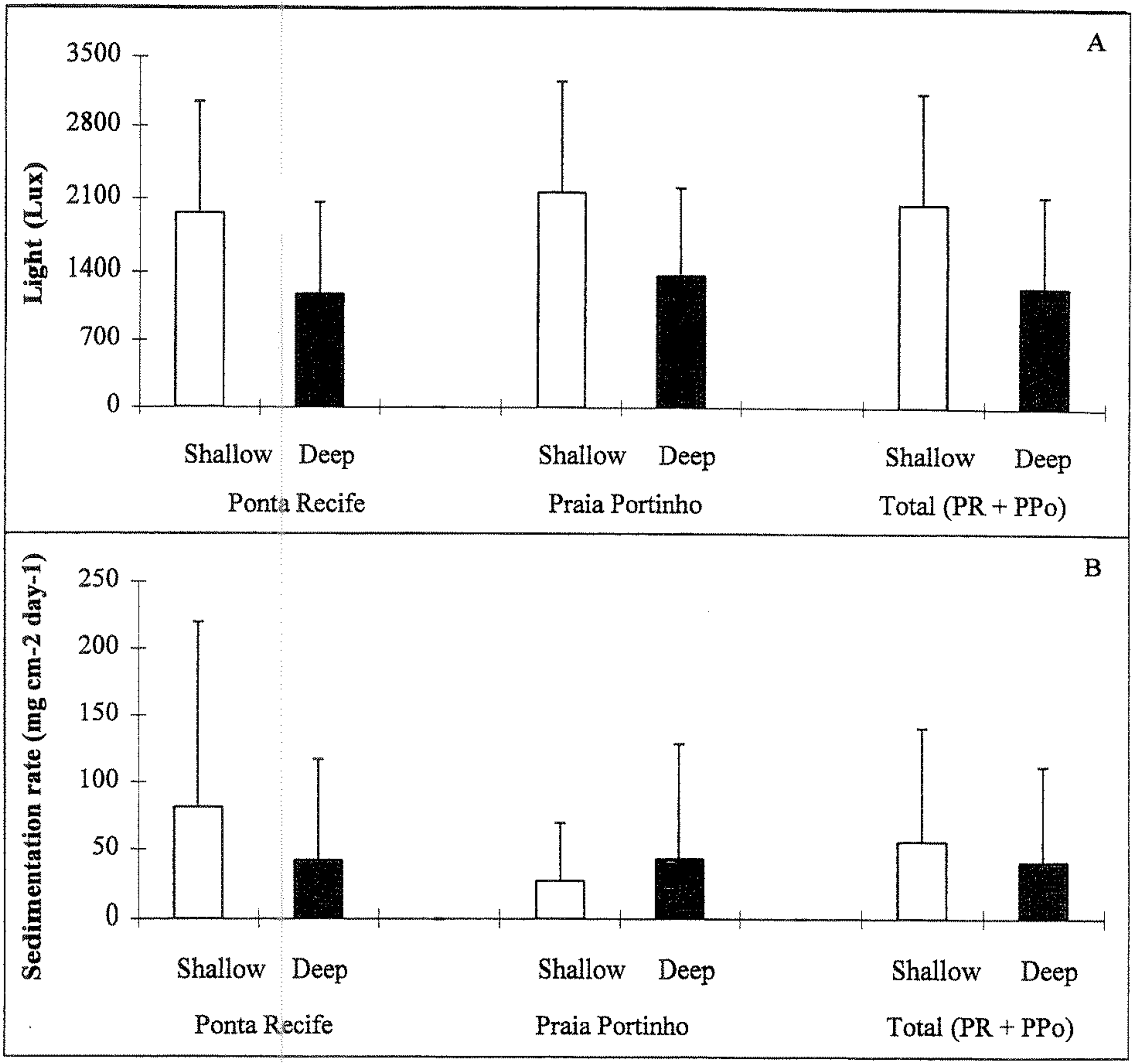

A
Light (Lux)
3500
2800
2100
1400
700
0
Shallow
Deep
Ponta Recife
Shallow
Deep
Praia Portinho
Shallow
Deep
Total (PR + PPo)
B
Sedimentation rate (mg cm-2 day-1)
250
200
150
100
50
0
Shallow
Deep
Ponta Recife
Shallow
Deep
Praia Portinho
Shallow
Deep
Total (PR + PPo)

Fig 10

Table 1

	Ponta Recife		Praia Portinho	
	Shallow 0.5 - 1.5	Deep 2.5 - 4	Shallow 0.5 - 1.5	Deep 2.5 - 4
Palythoa caribaeorum	37	50	37	65
Palythoa variabilis	0	0	25	0
Zoanthus sociatus	6	5	6	2
Sargassum sp.	0	0	11	0
Algae	3	4	2	0
Sponge	0	0	1	0
Rock plus Filamentous algae	52	39	15	30
Sand + Debris	2	2	3	3
Total cover (%)	100	100	100	100

Table 2

	Ponta Recife		Praia Portinho	
	Shallow 0.5 - 1.5	Deep 2.5 - 4	Shallow 0.5 - 1.5	Deep 2.5 - 4
Total colonies sampled	152	115	141	170
Plot number	3	3	3	3
# colonies / plot (range)	43 - 63	38 - 39	43 - 54	39 - 90
Plots area (range in m^2)	3.8 - 8.5	4.0 - 5.6	5.5 - 11.6	3.2 - 5.8
Density # col / m^2 (+/- SD)	9 (3)	8 (2)	6 (1)	14 (8)
Density range	5 - 11	6 - 10	5 - 7	7 - 22
Palythoa caribaeorum % cover	45 - 90	90 - 95	40 - 95	60 - 90

Capítulo I.

1) O zoantídeo *Palythoa caribaeorum* se reproduz assexuadamente no Canal de São Sebastião, S.P., Brasil, através de quatro variantes da fissão incluídas em dois processos.

2) O primeiro processo é fissão direta e o segundo requer a produção prévia de grupos de pólipos. Cada processo incluiu duas variantes ou modos de fissão. O primeiro contém os tipos de fissão denominados "Teardrop Formation" e "Polyp Ball Production". O segundo inclui "Edge Fission" e "Pseudo-Colony Lift Off". Três das quatro variantes de fissão (exceto Edge Fission) constituem novos registros para o gênero; "Polyp Ball Production" é um novo tipo de fissão para Zoanthidea e "Pseudo-Colony Lift Off" parece ser um novo modo de fissão para o filo Cnidaria. O processo de fissão parece ser controlado pela colônia (geneticamente), porém, sua expressão pode mudar dependendo de fatores extrínsecos (ex. densidade). A diversidade de táticas reprodutivas usadas por *Palythoa caribaeorum* via fissão, sugere alta plasticidade fenotípica e alta capacidade das colônias para responder a diferentes condições e limitações do habitat durante seu crescimento.

Capítulo II.

1) O maior número de ramets foi gerado por "Edge Fission" seguido por "Pseudo-Colony Lift Off", "Teardrop Formation" e finalmente por "Polyp Ball Production". "Edge Fission" foi o modo de reprodução assexuada predominante em *Palythoa caribaeorum*.

2) Foram gerados durante um ano 1304 ramets e 762 grupos de pólipos, sendo eqüivalente a um crescimento populacional potencial máximo anual de 225% via fissão.

3) A taxa de fissão não foi diferente entre os dois locais contrastantes comparados (Praia Portinho PPo e Ponta Recife PR), isto é, a fissão não aumenta em populações expostas a maior estresse (por turbidez, sedimento e luminosidade).

4) A taxa de fissão não foi diferente entre profundidades (0,5 – 1,5m *vs.* 2,5 – 4,0m), nem sazonalmente, sugerindo que a freqüência de fissão não é afetada por fatores abióticos como intensidade de luz e temperatura, respectivamente.

5) Cerca de 74% da população apresentou sinais de fissão em progresso.

6) A fissão ocorreu em colônias de qualquer tamanho ($\geq$ 5cm^2 de área) com taxa constante e uniforme durante o ano todo. A contínua produção de ramets poderia garantir o recrutamento, manutenção e aumento da população.

7) As colônias podem gerar ramets em 3, 6, 9, e 12 meses com igual probabilidade, ainda que o processo de fissão possa levar possivelmente anos para algumas colônias. A liberação dos ramets aconteceu três meses após sua formação (ex. Edge Fission). Isto sugere formação destes em qualquer tempo e rápida dispersão.

8) A dispersão dos ramets ocorreu o ano todo, facilitada pelas correntezas.

9) O tamanho dos ramets gerados pelas colônias variou entre 0,25 e 36 cm^2 de área; um menor número delas chegou a ter área de 1518 cm^2. Isto pode implicar em alta mortalidade e pequena contribuição ao crescimento populacional de *Palythoa caribaeorum*.

Capítulo III.

1) Além das variantes de fissão, *Palythoa caribaeorum* apresentou dois modos de fragmentação. Eles foram chamados: fragmentação causada por mortalidade parcial da colônia (ex. doenças), e fragmentação causada por distúrbios físicos (ex. tormentas). A

fragmentação se diferenciou da fissão por não ser endógeno, sendo um evento acidental (extrínseco). Neste caso a fragmentação foi registrada pela primeira vez para a espécie.

2) Cerca de 7,2% da população exibiu fragmentação num ano (n = 579); as 42 colônias fragmentadas contribuíram com 64 novos ramets à população. Assim a contribuição potencial máxima da fragmentação ao crescimento populacional de *Palythoa caribaeorum* foi de 11%, sendo consideravelmente menor ao registrado para a fissão.

3) A fragmentação via mortalidade parcial foi independente do local e da estação do ano. Porém, foi dependente da profundidade, com maior probabilidade de ocorrência em locais rasos, onde também há maior frequência da doença e maior hidrodinamismo. A fragmentação via distúrbios físicos foi independente do local e da profundidade, mas dependente da estação do ano, sendo menor no inverno. Isto sugere que os distúrbios físicos (ex. tormentas) geram taxas similares de fragmentação porque ocorrem com igual probabilidade ou similar intensidade entre locais e profundidades. A intensidade dos distúrbios físicos porém muda com as estações do ano, o que altera a freqüência de fragmentação no tempo.

4) Aproximadamente 40% da população foi afetada por mortalidade parcial. As colônias perderam menos de 5% da área ao longo de um ano, sendo uma nova doença a sua principal fonte. A freqüência de mortalidade parcial das colônias foi independente da profundidade, mas dependente do local, tendo um maior efeito nas populações expostas a maior nível de estresse (PR). Assim, a mortalidade parcial das colônias refletiu o nível de estresse a que estiveram submetidas. Ainda que a mortalidade parcial seja comum nas populações, não necessariamente leva à reprodução assexuada (através de fragmentação ou indução de fissão) e, portanto, à formação de ramets.

5) A fragmentação teve menor importância que a fissão na produção de ramets e no crescimento populacional de *Palythoa caribaeorum*, em contraste com o observado para outros zoantídeos.

Capítulo IV.

1) Uma doença é registrada pela primeira vez na Ordem Zoanthidea e no Atlântico Sul. A doença, de patógeno desconhecido, atinge *Palythoa caribaeorum*. Esta apresenta um padrão circular e aparece em uma ou mais porções da colônia simultaneamente. O patógeno parece ser controlado pela temperatura da água e ser limitado pela profundidade. Esta doença foi uma das principais causas de mortalidade parcial, afetando 14 a 20% da população, podendo ser um agente regulador do tamanho populacional. Afeta principalmente colônias de maior tamanho e próximas ao pico da reprodução sexuada da espécie. Como a reprodução aumenta com o tamanho da colônia em *P. caribaeorum*, a presença da doença (influindo na perda de tecido, de gônadas, de área de alimentação, e em gasto energético), poderia diminuir a aptidão desta espécie.

2) A taxa de infestação mudou entre os anos, as estações do ano, os locais e a profundidade. A maior freqüência da doença ocorreu no local com maior distúrbio (PR raso), explicando possivelmente a maior taxa de mortalidade parcial observada nas colônias deste local.

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