Biological responses of two Caribbean reef-building corals to a pier-generated irradiance gradient

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ABSTRACT

Irradiance, sedimentation, and water temperature were studied in a gradient of increased shading when moving towards a pier to determine if changes in these parameters might influence biological characteristics of *Siderastrea siderea*, and *Diploria clivosa*. Forty-six colonies of *S. siderea* were transplanted to four treatment zones: 0 m-under the pier (N=12), 3 m (N=12), 10 m (N=10), and 50 m-control zone (N=12). Eleven controls were randomly selected in the 50 m zone. Nine colonies of *D. clivosa* were studied in the 0 m (N=5) and 50 m (N=4) zone. Irradiance, sedimentation, and hours of shading were measured in all zones; water temperature was monitored in the 0 and 50 m zones. To determine skeletal extension, density, and calcification, *S. siderea* was stained once with alizarin red and sampled after 16 months. The difference in tissue surface area at the beginning and end of the study was used to determine tissue growth rates of *S. siderea*. Zooxanthellae densities, mesenterial fecundity, and oocyte diameter were determined for both species using histological techniques. Recruit (2-40 mm) density of *S. siderea* was assessed by counting recruits along a 50 m transect parallel to the pier at each zone, and monitored for survival from 2000-2002. Irradiance in the 0 and 3 m was significantly lower than the other zones ($p<0.001$-ANOVA). Hours of shading was significantly higher in the 0 and 3 m ($p=<0.001$-ANOVA), but similar in the 10 and 50 m zones ($p>0.05$-Tukey). For *S. siderea*, tissue growth and calcification in the 0 m zone were significantly lower ($p<0.001$-ANOVA) than other zones. In the 0 and 3 m zones, skeletal extension and mesenterial fecundity were significantly lower ($p<0.001$-ANOVA), but oocyte diameter was significantly larger ($p<0.001$-ANOVA) than the other zones. Significant ($p<0.001$) positive correlation were found between irradiance and tissue growth ($r=0.50$), calcification ($r=0.50$), skeletal extension ($r=0.60$), and mesenterial fecundity ($r=0.70$), oocyte diameter correlated negatively ($r=-0.44/p=0.0001$). Juvenile density was significantly lower in the 0 and 3 m zones than the other zones, decreasing gradually during the study ($p<0.0001$-ANOVA). For *D. clivosa*, zooxanthellae densities significantly increased while mesenterial fecundity significantly decreased in the 0 m zone ($p<0.05$-ANOVA).

RESUMEN

La irradiancia, sedimentación y temperatura del agua fueron estudiadas en un gradiente de aumento en sombreo por el muelle para determinar si los cambios en estos parámetros afectan a algunas características de la historia de la vida y densidades de las zooxantelas de *Siderastrea siderea* y *Diploria clivosa*. Cuarenta y seis colonias de *S. siderea* fueron transplantadas a cuatro zonas: 0 m-debajo del muelle (N=12), 3 m (N=12), 10 m (N=10), y 50 m-zona control (N=12). Once colonias fueron seleccionadas al azahar como controles en la zona 50 m. Nueve colonias de *D. clivosa* fueron estudiadas en la zona 0 m (N=5) y 50 m (N=4). La irradiancia, sedimentación y horas de sombra fueron estudiadas en todas las zonas, la temperatura del agua fue monitoreada debajo del muelle y a 50 m. Para determinar extensión lineal del esqueleto, densidad y calcificación, se tiñó *S. siderea* una vez con alizarina roja y se muestreo 16 meses después. Las diferencias en las medidas de área de tejido, hechas al principio y al final del estudio, se utilizaron para determinar crecimiento de tejido vivo de *S. siderea.* Las densidades de zooxantela, fecundidad mesenterial y diámetro del oocito de *S. siderea* y *D. clivosa* fueron determinados mediante técnicas de histología. Para estimar densidad de juveniles (2-40 mm) de *S. siderea*, se realizó un censo utilizando un transecto de 50 m paralelo al muelle en cada zona, y se monitoreo la supervivencia desde el año 2000 hasta el 2002. La irradiancia disminuyó significativamente en las zonas 0 y 3 m ($p<0.001$-ANOVA); mientras que fue similar en la zona 10 y 50 m ($p>0.05$-Dunn's). El número total de horas de sombra fue significativamente más alto en las zonas 0 y 3 m ($p=<0.001$-ANOVA), mientras que fue similar en la zona 10 y 50 m ($p>0.05$-Tukey). Para *S. siderea*, el crecimiento de tejido y la calcificación disminuyeron significativamente en la zona 0 m ($p<0.001$-ANOVA) que en los demás tratamientos. En las zonas 0 y 3 m, la extensión lineal del esqueleto y fecundidad mesenterial disminuyeron significativamente ($p<0.001$-ANOVA), mientras el diámetro del oocito fue significativamente mayor ($p<0.001$-ANOVA) que en las otras zonas. Se encontró una correlación significativa ($p<0.001$) y positiva entre irradiancia y crecimiento de tejido ($r=0.50$), calcificación ($r=0.50$), extensión lineal ($r=0.60$), y fecundidad mesenterial ($r=0.70$), mientras que el diámetro del oocito correlacionó

negativamente (r=-0.44/p=0.0001). Las densidades de los juveniles fueron significativamente más bajas en las zonas 0 y 3 m que en las otras zonas, y disminuyó gradualmente a través del estudio ($p<0.0001$-ANOVA). Para *D. clivosa*, las densidades de las zooxantelas y fecundidad mesenterial disminuyeron significativamente en la zona 0 m ($p<0.05$-ANOVA).

I dedicate this dissertation to my husband *Ivan*.

…thank you for always believing!

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CHAPTER 1. General Introduction

In recent years, there has been an increase in the number of requests for permits to build small docks and piers, and in the numbers of docks constructed and used within the United States coastal zone (Kelty and Bliven, 2003). The rapid development of the coastal zone and increase of docks and pier structures raises concern on the impact it may have on benthic organisms through shading, particularly reef corals and seagrasses. Scientific research documenting the effects of shading by large pier structures (commercial use) or small docks (recreational docks designed for residential use) to phototrophic benthic organisms and to the associated heterotrophic organisms is limited.

The quantity of light reaching the bottom in coastal waters is a critical determinant of the extent and productivity of autotrophic benthic communities like coral reefs (Hatcher, 1990; Muller-Parker and D'Elia, 1996) and seagrass meadows (Onuf, 1994; Gallegos and Kenworthy, 1996; Kraemer and Hanisak, 2000). It has been documented that in multiple coastal areas, anthropogenic impact, and/or natural deterioration of underwater light availability often results in large-scale losses of phototropic benthic organisms like seagrasses (Short and Wylie-Echeverria, 1996). Despite the research done on seagrass responses to light reduction, only a few studies (Shafer, 1999; Shafer and Lundin, 1999; Shafer and Robinson, 2001; Shafer, 2002; Hertler, 2002; Ruiz and Romero, 2003) have assessed the effects of overwater structure (docks, piers) construction on the ecology of seagrasses. These studies found that productivity and abundance are mainly negatively affected by a decrease in light intensity. However, although it is well documented that light is an essential requirement for scleractinian corals because it enables photosynthesis of the zooxanthellae and enhances calcification (Goreau, 1959), reports on the response of reef corals to light reduction due to overwater structures and how this may affect the organisms (i.e., corals) biology and ecology are lacking. Experimentally manipulated light levels in the field or laboratory have documented changes in some life history traits such as growth (Goreau, 1959, 1963; Barnes and Taylor, 1973), settlement (Maida et al., 1994; Babcock and Mundy, 1996; Mundy and Babcock, 1998), tissue regeneration (Nagelkerken et al., 1999), coral cover (Tomascik et al., 1993; Yentsch et al., 2002), and behavior (Lasker, 1977; Levy et al., 2001), among others. However, these

experimental studies alone do not provide a basis for the development of guidelines to reduce dock-shading impacts because they are limited to the study of only one aspect at a time of the life history of the particular coral. Thus, the development and further application of regulatory policy to address any possible impact on coral's life history has been held up by a lack of supporting data that could directly link changes in coral's biology with levels of light reduction associated with overwater structures.

In Guayanilla Bay, the EcoEléctrica Liquefied Natural Gas and Cogeneration Plant (EcoEléctrica LP) was recently built. The US Army Corps of Engineers provided EcoEléctrica LP the permits for the construction of a marine terminal pier. The construction of the terminal pier and installation of the discharge and intake structures took place between July 1998 and November 1999. This terminal is intended for delivery of liquefied natural gas from vessels, for transfer to storage tanks, vaporization systems and a natural gas accumulator pipeline. The construction of the marine terminal section required the installation of pilings into the seafloor along a span of 545 m in a southwest direction within Guayanilla Bay waters. EcoEléctrica LP began discharging cooling seawater into Guayanilla Bay on September 1999 and began commercial operations during March 2000 (Vicente and Associates, 2000).

A gradient of irradiance, due to the shadow of the EcoEléctrica LP pier, provided the best opportunity to conduct an *in situ* study to test the effects of changes in the light regime over the ecology and biological characteristics of *Siderastrea siderea* (Scleractinia: Siderastreidae) and *Diploria clivosa* (Scleractinia: Faviidae), two Caribbean reef-building coral species. *Siderastrea siderea* was selected for this study because it was found to be the most abundant coral species in the area, especially towards the west side of the pier (Vicente and Associates, 2000). Various studies demonstrated that *S. siderea* is a tolerant species capable to adapt to eutrophic environments (Lewis, 1997), extensive coastal development (Debrot et al., 1998), high sedimentation rates (Foster, 1979, 1980), acute temperature fluctuations (Burns, 1985), salinity fluctuations (Muthiga and Szmant, 1987), and oil-spills on coral reef areas (Guzmán et al., 1991; Guzmán and Holst, 1993). However, the number of studies with *S. siderea* is small when compared to other coral species in the Caribbean (i.e. *Montastraea* spp.) and in the Indo-Pacific (i.e., *Pocillopora damicornis*, *Stylophora pistillata*), limiting the potential development of management

plans for this species. A second coral species, *Diploria clivosa*, was selected and studied, although not with the same intensity as *S. siderea*, but as part of a preliminary approach to extend the hypothesis to other scleractinian corals living in similar habitats conditions.

Information on the penetration of the complete range of photosynthetic wavelengths (photosynthetically active radiation = PAR, 400 to 700 nm or visible light) around overwater structures or any other reef setting is of great value because is a broad indication of the availability of light for photosynthesis in an aquatic ecosystem. Thus, the purpose of this study was to examine various biological aspects (growth, reproduction, recruitment and recruit survival, and zooxanthellae densities) of two Caribbean reef-building coral species, *S. siderea* and *D. clivosa*, in relation to a gradient of irradiance due to the pier shadow. Therefore, the main objectives of this investigation were:

1) to asses the effect of changes in irradiance on

    - tissue growth rate
    - skeletal growth (linear extension, skeletal density, calcification)
    - reproduction (mesenterial fecundity, oocyte diameter)
    - recruitment and recruit survival

2) to determine if changes in irradiance affect the concentrations of zooxanthellae,

3) to assess if *S. siderea* is suitable as a mitigating species where man-made structures threatens reef areas.

The main null hypothesis was that growth, reproduction, recruitment and recruit survival of *S. siderea*, reproduction of *D. clivosa*, and zooxanthellae densities of both species will be similar across the irradiance gradient due to the shadow of a pier.

Environmental parameters such as sedimentation, and water temperature were also considered as potential factors affecting biological characteristics of scleractinian corals, therefore, were monitored in this study. As a result, a secondary objective was:

1) to examine if sedimentation and temperature varied with distance from the pier.

Thus, a secondary null hypothesis was that sedimentation and water temperature will not vary with distance from the pier.

The study will provide valuable information for a better comprehension of the biology and ecology of *S. siderea* and *D. clivosa*, which has never been studied before in relation to a gradient of irradiance in the field. This study will also help to understand the importance of monitoring light levels in living coral reefs for management purposes, and for the development and application of regulatory policy to address impacts of dock shading. This study will also examine the possibility of *S. siderea* to become a potential species where colony transplants could be used to restore affected sites.

CHAPTER 2. Environmental characterization of the study area

2.1. ABSTRACT

Few studies have investigated if changes in environmental parameters occur due to large pier structures or small docks. This study was carried out at Guayanilla Bay where a liquefied natural gas power plant was recently built, including a terminal pier. Solar irradiance, sedimentation, and water temperature were studied in relation to increase shading when moving towards the pier. Measurements of irradiance (with a quantum sensor) and collection of sediment (using sediment traps) were done for 14 months in four treatment zones at the pier: at 0 m (under the pier), 3 m, 10 m, and 50 m (control zone) from the pier. Water temperature fluctuations were monitored in the 0 m and 50 m zone with underwater data loggers. To estimate the number of hours of shading by the pier in each treatment zone, observations were done once at the winter and summer solstice, and spring and autumn equinox, from sunrise to sunset. Results indicate that irradiance was significantly lower in the 0 m and 3 m zones ($p<0.001$, ANOVA), but similar in the 10 m and 50 m zone ($p>0.05$, Dunn's Method), implying that the latter zones had similar irradiance at all depths. The total number of hours of shading in the 0 m and 3 m zone was significantly higher ($p=<0.001$, ANOVA) than in the 10 m and 50 m zones. Upper sediment traps collected significantly less sediment than the lower sediment traps ($p=0.001$, ANOVA), implying low resuspension of sediment. Lower sediment traps in the 3 m zone collected significantly less sediment than the 0 m, 10 m and 50 m ($p>0.05$, Tukey Test).

2.2. INTRODUCTION

The behavior of light in aquatic ecosystems has been an important area of scientific study due to the key role that light plays in controlling the productivity, biological composition and distribution of many marine communities. An immediate change in light will occur when it passes from one medium to another, i.e., from air to water, due to reflection and refraction properties of light. Thus, the underwater light environment is by nature a light-reduced environment. The incident light at any given depth can be measured with a submersible quanta meter. The most common and readily measured property of the underwater light field is irradiance. Irradiance (*E*) is defined as the radiant flux per unit area of surface, expressed as W m^{-2}, or quanta (or photons) s^{-1} m^{-2}, or molquanta (or photons) s^{-1} m^{-2}, where 1.0 mol photons is 6.02×10^{23} photons (Avogadro's number) (Kirk, 1994). Radiant flux, Φ, is defined as the time rate of flow of radiant energy, expressed in W (J s^{-1}) or quanta s^{-1}. Downward irradiance (E_d) and upward irradiance (E_u) are the values of the irradiance due to a downwelling and upwelling light stream, respectively.

Light in the range of 400 to 700 nm of the electromagnetic spectrum, most commonly known as photosynthetic active radiation (PAR) or visible light, is used by autotrophic organisms for photosynthesis. In any aquatic habitat, the photosynthetic photon flux density decreases exponentially with depth and varies temporally (seasonally and diurnally) and spatially, which challenge photosynthetic organisms to develop physiological and morphological adaptations to cope with the varying light regimes. Thus, information of the light quantity available for photosynthesis in the aquatic ecosystem is not only important for phototrophic organisms, but for the coral-zooxanthellae symbiosis (Vandermeulen et al., 1972; Wellington, 1982; Battey and Porter, 1988), for life cycles and life history strategies of seagrasses (Peralta et al., 2002; Backman and Barilotti, 1976), phytoplankton, protozoan (Barcelo and Calkings, 1980), grunts (McFarland et al., 1979), zooplankton and micronekton (Frank and Widder, 2002), sponges (Wilkinson and Trott, 1985), spirorbid polychaetes (Saunders and Connell, 2001), among others.

Light is also an essential requirement for scleractinian corals because it enables photosynthesis of the symbiotic zooxanthellae, which at the same time enhances calcification rates (Goreau, 1959, 1963). It

has been observed that changes in PAR received by coral colonies comprises physiological consequences (Patton et al., 1977, Dustan, 1979, 1982; Titlyanov, 1981; Battey and Porter, 1988; Masuda et al., 1992, 1993; Lesser, 2000; Titlyanov et al., 2001a, b, c) and often require morphological adaptations to maximize light capture (Graus and MacIntyre, 1976, 1982; Barnes, 1973; Dustan, 1975; Vermeij and Bak, 2002). Light affects many aspects of corals life such as coral spawning (Penland et al., 2004), behavior (Lasker, 1977; Levy et al., 2001), regeneration (Nagelkerken et al., 1999), coral cover (Tomascik, et al., 1993; Yentsch et al., 2002), settlement (Maida et al., 1994; Babcock and Mundy, 1996; Mundy and Babcock, 1998), and distribution (Titlyanov and Latypov, 1991).

In addition to light, other physical and chemical environmental parameters have, as well, a significant influence on the ecology, morphology, and physiology of many marine communities. Frequently studied factors include salinity (Ferrier-Pages et al., 1999), temperature (Glynn et al., 1988; Winter et al., 1998; Glynn and D'Croz, 1990), water motion (Geister, 1977; Jokiel, 1978; Dollar, 1982; Oliver et al., 1983; Graus and Mcintyre, 1989; Roberts et al., 1992), sedimentation (Hubbard et al., 1986; Rogers, 1990; Sebens, 1994), and nutrient concentrations (Pastorok and Bilyard, 1985; Szmant, 2002). Although corals respond to the entire set of factors mentioned above, light is widely recognized as a primary limiting factor (Goreau, 1959, 1963; Barnes and Taylor, 1973; Veron, 1995; Vermeij and Bak, 2002) in the growth (Yap et al., 1998) and depth distribution (Titlyanov and Latypov, 1991) of scleractinian corals mainly due to the coral-zooxanthellae symbiosis.

The experimental reduction of incident light by suspended sediments has a greater effect on some coral species than the sediment itself (Loya, 1976; Rogers, 1979). Turbidity and sedimentation decreases net photosynthesis and lead to decline in living coral through secondary effects such as bleaching (Nemeth and Nowlis, 2001), and death (Rogers, 1979, 1983). A reduced amount of light due to turbidity and sedimentation can modify corals energy budget by decreasing photosynthetic production, increasing both relative respiration and carbon-loss through cleaning mechanisms (Abdel-Salam and Porter, 1988; Riegl and Branch, 1995; Telesnicki and Goldbert, 1995). Furthermore, Dodge et al. (1974) and Rogers (1979) found that turbidity decreased light penetration, reduced photosynthesis, and hence, decreased

coral growth rate. Roy and Smith (1971), Loya (1976), and Cortés and Risk (1985) found that population parameters where reduced by half in turbid coral reef waters when compared to clear water reefs.

Although reef corals short-term response to light reduction has been well documented in numerous studies using experimentally manipulated light levels in the field and laboratory, these experimental studies alone do not provide a basis for the development of guidelines to reduce dock-shading impacts. The current information available to address these impacts has been hindered by a lack of supporting data that could directly link changes in coral's life history strategies with levels of light reduction associated with various types of overwater structures. Long-term *in situ* investigation such as this study will be useful on the development and further application of regulatory policy. The purpose of this chapter was to provide a baseline characterization of environmental parameters such as irradiance, sedimentation, and water temperature, with decreasing distance from the pier, and determine if significant differences existed. Therefore, the objectives of this chapter were:

1) to determine if changes in irradiance occur in relation to a pier-shading effect with decreasing distance across four treatment zones to the west side of the pier at:

    - 50 m from the pier - the control zone
    - 10 m from the pier
    - 3 m from the pier
    - 0 m - under the pier

2) to determine if changes in sedimentation occur across the four treatment zones

3) to determine if changes in temperature occur in the 0 m and 50 m zone

The null hypothesis was that irradiance, sedimentation, and water temperature would not change with decreasing distance from the pier.

The results of this chapter were used to correlate environmental variability to changes in biological characteristics of two reef-building corals at Guayanilla Bay, PR (Chapters 3 and 4).

2.3. METHODOLOGY

2.3.1. Study Site

Punta Guayanilla is an extension of land or peninsula at the south coast of Puerto Rico officially belonging to the Municipality of Peñuelas. Although physically connected by currents, Pta. Guayanilla outlines Guayanilla Bay to the west and Tallaboa Bay to the east of the peninsula (Tilly, 1979) (Figure 2.1).

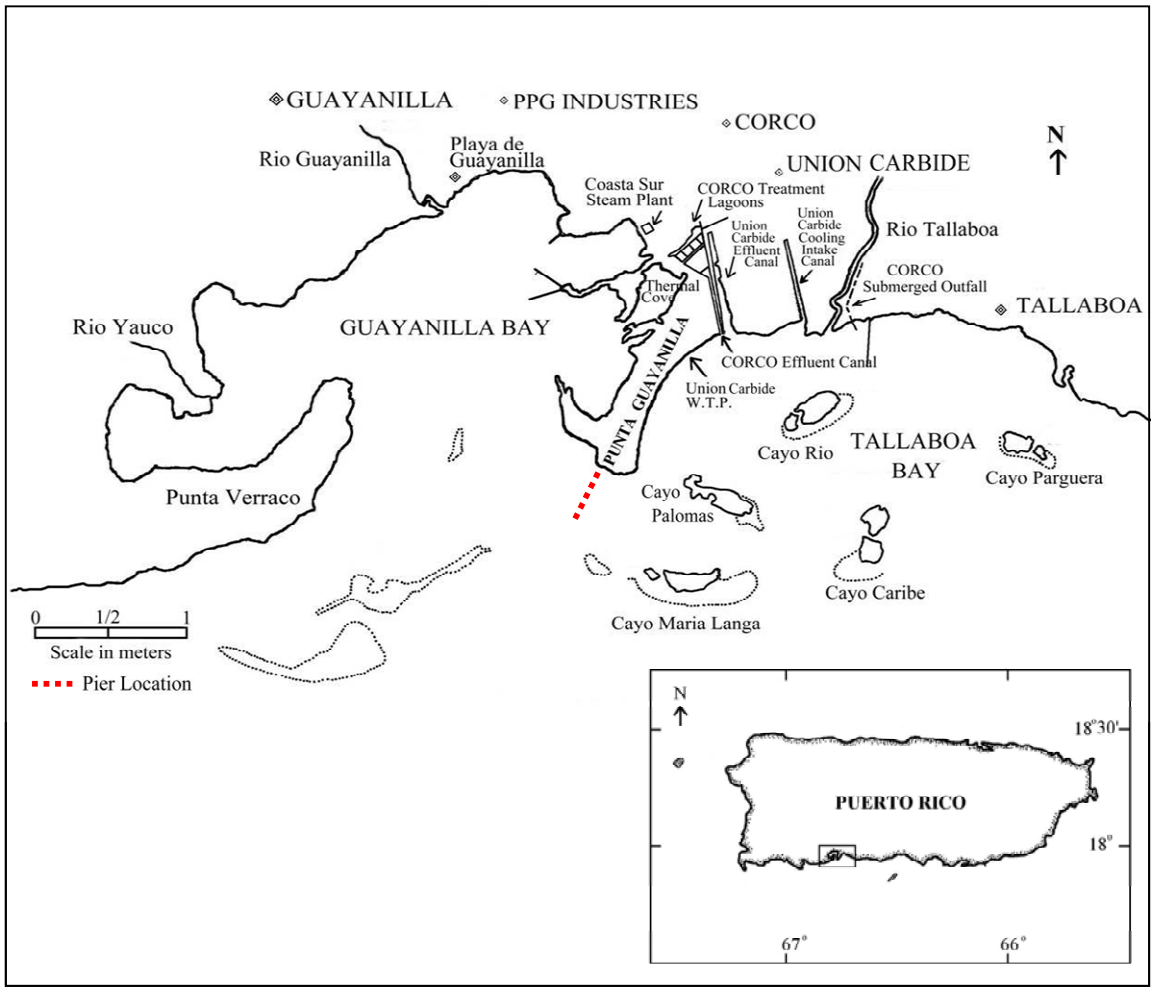

Figure 2.1 Map of the Guayanilla and Tallaboa Bay in the south coast of Puerto Rico showing the industrial development around the area. The EcoEléctrica LP facilities are located in Punta Guayanilla, including the pier (red dotted line). Modified from Tilly (1979).

Even though extensive industrial complexes have been developed at the shores of Guayanilla and Tallaboa Bays, Pta. Guayanilla was not heavily developed. Punta Guayanilla was selected as study site

due to the recent construction of the EcoEléctrica LP, including a terminal pier. The EcoEléctrica LP management supported this study because of their concerned on the possible impact of their recently built pier on marine communities like seagrasses and reef corals in Pta. Guayanilla. The construction of EcoEléctrica LP terminal pier and installation of related structures took place between July 1998 and November 1999. The construction of the marine terminal section (5 m width x 8 m height) required the installation of pilings into the seafloor along an expanse of 545 m, along a northeast-southwest direction within Guayanilla Bay waters. EcoEléctrica LP began discharging seawater, used to cool down turbines, into Guayanilla Bay on September 1999 and began commercial operations on March 2000 (Figure 2.2).

Figure 2.2. Photo showing the EcoEléctrica LP plant and terminal pier in full operations. Courtesy of Vicente and Associates, and Caribbean Engineering and Environmental (2003).

The discharge waters of EcoEléctrica enter the water column through a diffuser system located 513 m southwest from the south shore of Punta Guayanilla. The intake station (Bent 14) is located 354 m northeast (54º) from the discharge (Bent 26) and therefore far enough to become affected by the discharge plume (Figure 2.3). The impact of the pier structure to the coral community nearby and under the pier was unknown. Thus, this was considered and excellent opportunity to explore the potential effects of changes in irradiance produced by the pier shadow over the coral-zooxanthellae symbiotic relation.

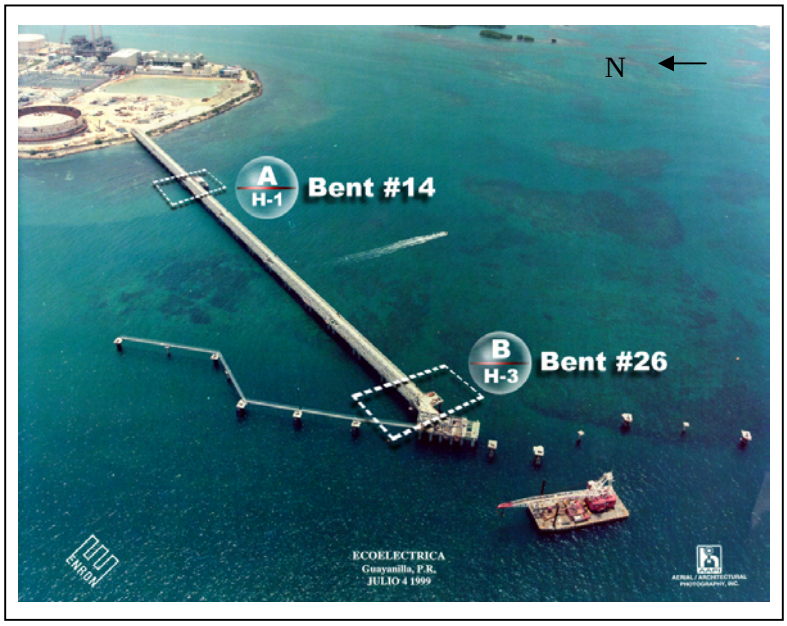

Figure 2.3. Photo showing a construction phase of the EcoEléctrica LP terminal pier and installation of related structures. Pier piling pairs (bents) were numbered and used as reference to locate Bent 14 (study area), Bent 26 was the discharge. Courtesy of Vicente and Associates (2000).

2.3.2. Experimental Design

At the EcoEléctrica pier the piling pairs (bents) were numbered and used as reference to locate the study area, Bent 14 (latitude 17°58'41.32," longitude 66°45'32.42") (Figure 2.3). This bent was selected for several reasons: moving southwest towards bay waters from Bent 14 the substrate changed rapidly to muddy bottom not suitable for transplanting corals, and waters became deeper to the south, moving to the northeast towards the shore from Bent 14, waters became shallower, and changed to sandy bottom with turtlegrass. Thus, after surveying the substrate around the pier, the west side of the pier at Bent 14 was the most adequate site in terms of substrate for the transplants (rocky bottom and outcrops), had little or no seagrass, depth remain constant at 2 m when moving to the west-northwest along a 50 m transect, and most colonies to be transplanted were close to this bent.

A 50 m transect, that ran perpendicular to the pier (from Bent 14 towards the west-northwest), was used to establish three treatment zones along the gradient of irradiance; the fourth zone was under the pier. Previous observation of the shadow movement indicated that the shadow reached 11 m (from the

piling on the west side of Bent 14) around 11am February 2000 (mid-winter when days are shorter, thus, this assured that the shadow of the pier would reach this area the rest of the year), this information was used as reference to establish the treatment zones, characterized by distance from the pier and movement of the shadow (Figure 2.4):

- 0 m, located under the pier where light intensity was minimum throughout the day,
- 3 m, located 3 m from the piling of Bent 14, the zone was covered by the pier shadow approximately until midday (from 4 - 6 hrs during the year, depending on the season),
- 10 m, located 10 m from the piling of Bent 14, the zone was covered by the pier shadow during the first half of the morning (from 2 - 3 hrs during the year, depending on the season),
- 50 m, located 50 m from the piling of Bent 14, the shadow of the pier never reached this zone at any time of the day.

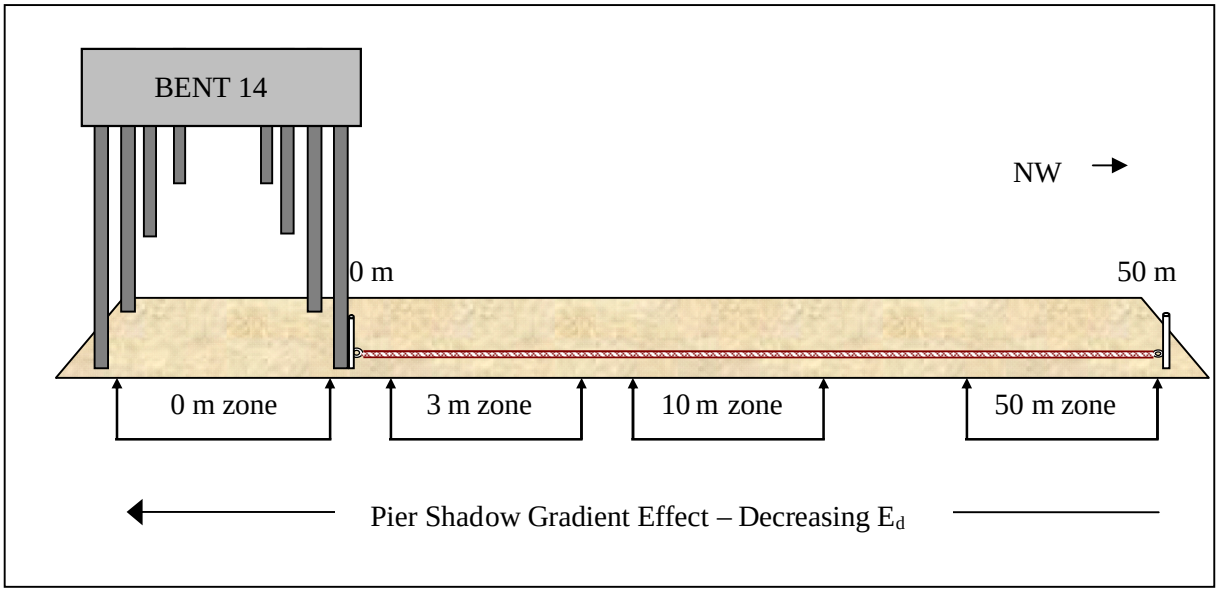

Figure 2.4. Drawing representing the gradient of irradiance (E_d) and the treatment zones of the experimental design at the EcoEléctrica LP terminal pier (Bent 14), Pta. Guayanilla, PR. Modified from Vicente and Associates (2000).

2.3.3. Characterization of environmental parameters near the pier

The most common measurement of the underwater light field is irradiance, *E*, which is defined as the radiant flux per unit area of surface, with units of quanta (or photons) s^{-1} m^{-2} (Kirk, 1994). The local underwater light field, downward irradiance (E_d) in µmol photons s^{-1} m^{-2}, in each treatment zone at the pier was characterized using a LI-1000 Data Logger equipped with a cosine collector LI190SA underwater quantum sensor (LICOR Corp.). The sensor measured the quantum flux in the 400 to 700 nm range. Irradiance readings were taken at each treatment zone, between five to 10 minutes apart. The sensor was lowered from the sunny side of the boat at one-meter intervals, after measuring surface and subsurface E_d (out of the water, and at one cm depth, respectively). Maximum depth of E_d readings was 2 m. An average E_d at each depth was obtained from ten readings per depth.

2.3.3.1. Annual E_d pattern

To characterize E_d in each treatment zone at the pier, measurements were done around midday (when the sun is directly overhead and the penetration of light is maximized and less reflected) every week, from August 2000 to September 2001. Only on two occasions (March 20 and July 31, 2001), E_d readings were not obtained due to bad weather.

2.3.3.2. Seasonal E_d pattern

To assess a seasonal pattern, the number of hours of shading (HS) and E_d was obtained per season in each treatment zone by observations and measurements from sunrise to sunset: one day after winter solstice (December 22, 2000), one week after vernal equinox (March 27, 2001), and during autumn equinox (September 22, 2001) and summer solstice (June 21, 2001). During the equinoxes and solstices, E_d was measured every hour in each treatment zone, following the procedure on section 2.3.3.1. The number of hours of shading caused by the pier in each treatment zone was estimated by analyzing the E_d data and corroborated with field observations.

2.3.3.3. Sedimentation Rates (SR)

To characterize sedimentation rates, two replicate sediment trap units were placed in each treatment zone at the pier (see Figure 2.5). All treatment zones were monitored in a monthly basis from June 2000 to July 2001. A sediment trap unit consisted of two plastic, straight-sided, wide-mouthed jars of 8.9 cm in diameter and 18 cm height (Figure 2.5). The two jars were attached to a 1 m steel rod with duct tape in opposite direction, and driven in the reef framework with a sledgehammer. The jar at the upper end of the steel rod measured variations in resuspension of sediments, while the lower jar measured variations in sediment deposition.

Figure 2.5. Sediment traps positioned at the EcoEléctrica pier, Guayanilla Bay.

After a month, the sediment trap units were capped underwater, collected, and new traps, were setup for sediment collection. The new traps were previously prepared in the lab by attaching clean bottles with duct tape to the steel rod as described above. At the laboratory, small organisms and macroalgae in the jars were carefully removed, when possible. The samples were processed in the laboratory following standard procedures (Goenaga, 1988). Weighting of filters and samples was done with a Mettler Analytical Balance Model H542. The difference between the final and initial filter weight

represents the amount of sediment collected. Sedimentation rates (SR) as mg of sediment per cm^2 per day ($mg/cm^2/d$) was calculated for each treatment zone using the equation (Rogers et al., 1994):

$$\mathbf{SR = sediment\ weight\ /\ (number\ of\ days\ at\ site)\ (\pi r^2)} \qquad \mathbf{(2.1)}$$

where r = radius in cm of the jar opening.

2.3.3.4. Water temperature (WT)

Water temperature fluctuations (^oC) were measured *in situ* with StowAway data loggers for almost nine consecutive months in 2001 (April 2001 to December 2001) for the 0 m and 50 m zones. Each month, data was downloaded in the field and saved to a laptop computer, and the data loggers were placed again in each treatment zone. Additional data on temperature for year 2000 were obtained for the months of July to August and September to October, and for the year of 2002 from April to December.

2.3.4. Statistical Analyses

The homogeneity of variance assumption was tested using the F_{max}-test (Sokal and Rohlf, 1995). E_d data failed the $F_{max(\alpha=0.01)}$-test, even after transformation (log x+1, square root). Therefore, a non-parametric test (Kruskal-Wallis One-Way ANOVA, at $p<0.05$ confidence level) was used to test for significant differences among treatment zones. To identify the group with significantly higher or lower E_d, a multiple comparison test, Dunn's Method (at $p<0.05$ confidence level), was used. The results of the $F_{max(\alpha=0.01)}$-test for the hours of shading, SR, and water temperature indicated no violations of the above assumption. Consequently, a parametric test (One-Way ANOVA for HS and WT, Two-Way ANOVA for SR, both at $p<0.05$ confidence level) was used to test for significant differences among treatment zones. To identify the group with significantly higher or lower values, a multiple comparison test, Tukey Test (at $p<0.05$ confidence level), was used.

2.4. RESULTS

2.4.1. Characterization of environmental parameters near the pier.

2.4.1.1. Annual E_d pattern

A decrease in mean E_d across treatment zones is evident in Figure 2.6 at all depths. The largest decrease in mean yearly E_d occurs in the 0 m zone were the incident solar E_d was blocked almost entirely by the pier structure at all depths (see Appendix I.1 for details). At 2 m depth: the 0 m zone received the least E_d, from approaching 0 to less than 100 µmol photons s^{-1} m^{-2}; the 3 m zone from 20 - 752 µmol photons s^{-1} m^{-2} (had low irradiance for six months October 2000 to March 2001); in the 10 m zone varied from 320 - 776 µmol photons s^{-1} m^{-2}; while in the 50 m zone from 325 - 864 µmol photons s^{-1} m^{-2}.

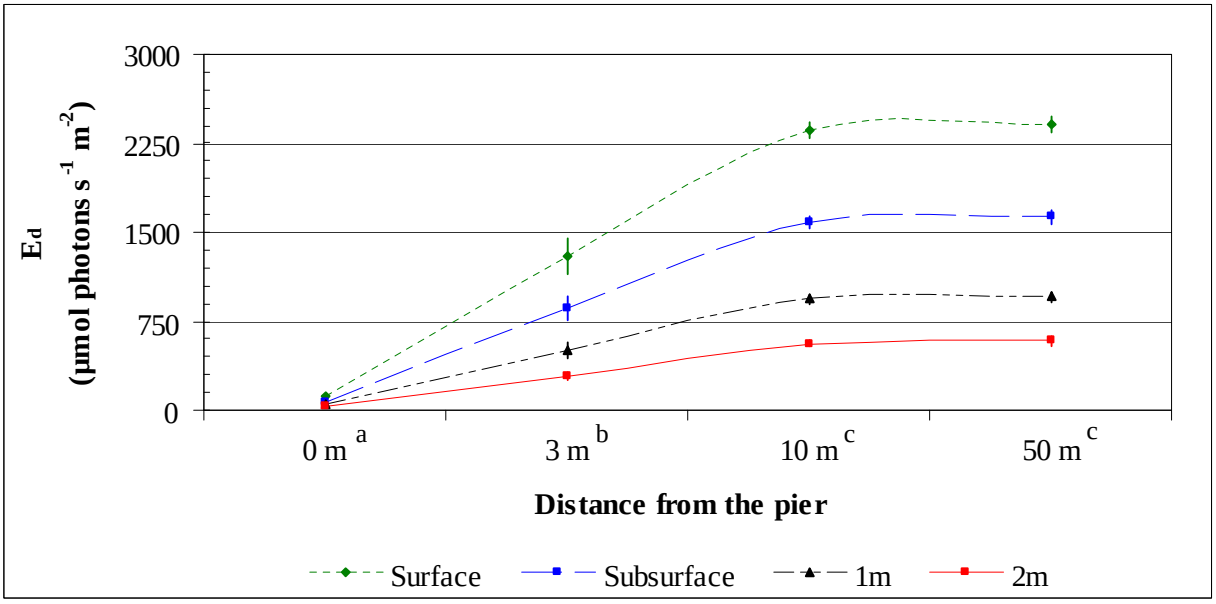

Figure 2.6. Mean yearly E_d (µmol photons s^{-1} m^{-2}) and standard error calculated for each treatment zone in relation to the distance from the pier. Data was pooled and averaged from weekly measures. Treatment zones with different superscript letters were significantly different ($p<0.001$, ANOVA).

Significant differences expected in E_d across treatment zones were confirmed. Mean weekly E_d was significantly low in the 0 m and 3 m zone ($p<0.001$, ANOVA) at all depths (Appendix I.2 to I.5). The 10 m and 50 m zone were similar treatment zones ($p>0.05$, Dunn's Method) at all depths. These results confirmed the existence of a gradient of decreasing E_d with decreasing distance from the pier.

2.4.1.2. Seasonal E_d pattern

Seasonal measurements of E_d at the pier provide insight into the changes across treatment zones and seasons during the year. In Figure 2.7, columns show E_d behavior and the number of hours of shading (HS) for each season in a particular treatment zone, while rows show one season across treatment zones. A decrease in E_d is evident across treatment zones with decreasing distance from the pier, while the opposite is observed for HS.

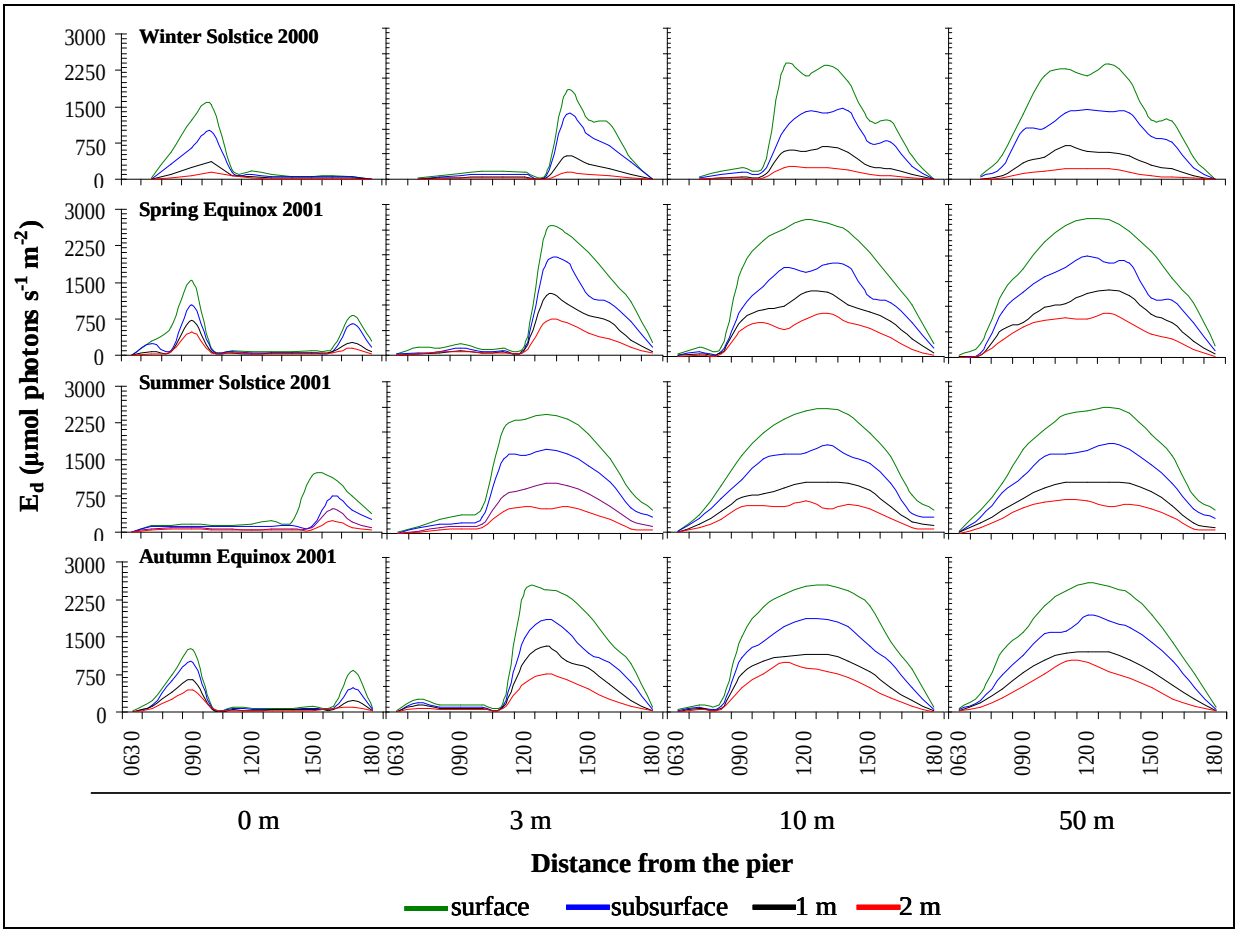

Figure 2.7. Seasonal variation in irradiance (E_d) and hours of shading in each treatment zone. Data was collected during winter and summer solstice (December 22, 2000, June 21, 2001, respectively), and spring and autumn equinox (March 27, 2001, September 22, 2001, respectively).

The number of HS was significantly higher in the 0 m and 3 m zones ($p<0.0001$, One-Way ANOVA, Appendix I.6), while the 10 m and 50 m zone were similar ($p=0.1698$, Tukey Test) (Figure 2.8), which implies that the effect of the shadow increases with decreasing distance from the pier.

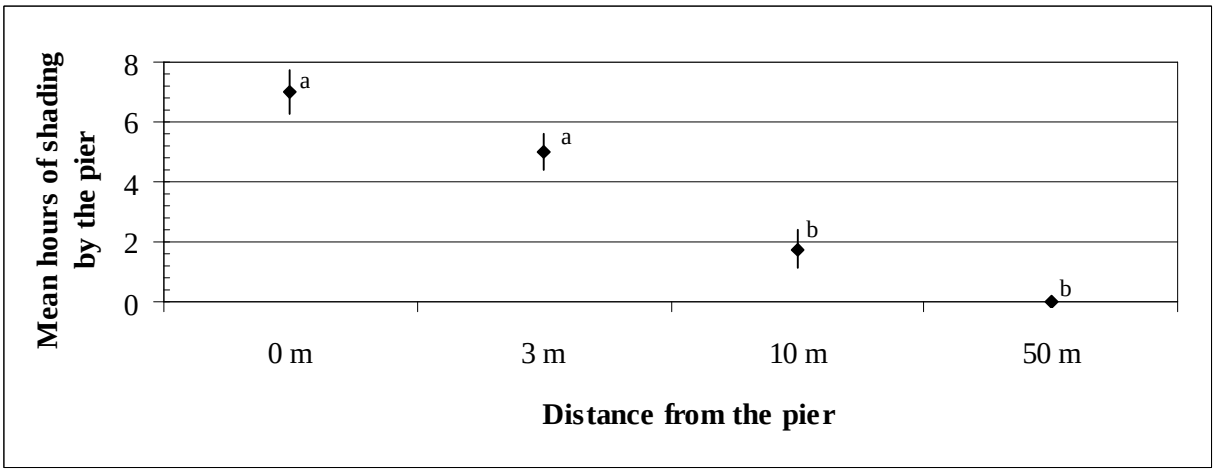

Figure 2.8. Mean hours of shading per treatment zone and standard error calculated from seasonal observations. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

A Pearson Correlation (Figure 2.9) showed a strong inverse correlation between mean HS and mean E_d ($r=-0.9674$, $p=0.02958$, $n=4$).

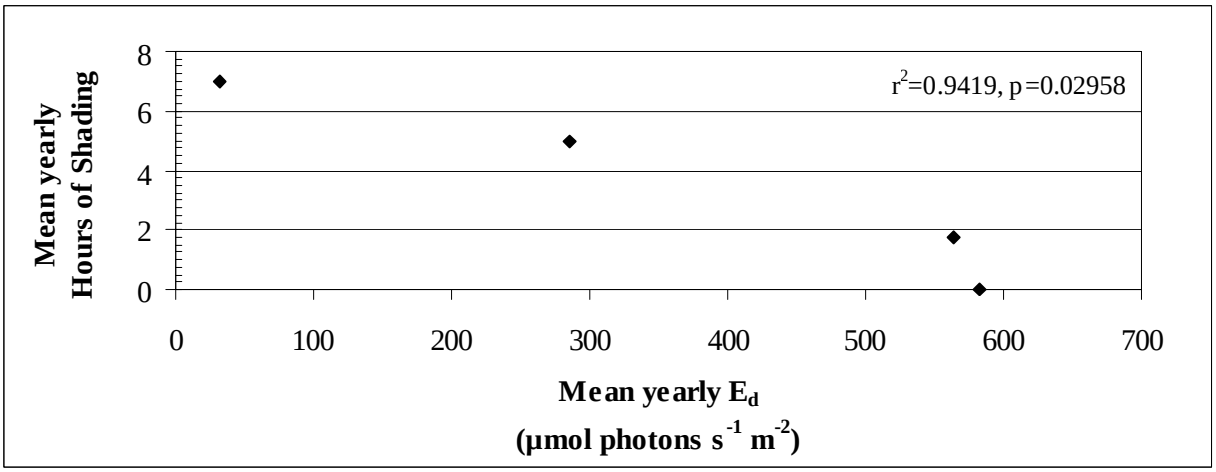

Figure 2.9. Correlation between mean yearly hours of shading and mean yearly irradiance (E_d).

2.4.1.3. Sedimentation Rates (SR)

Mean SR for UST and LST (upper and lower sediment traps, respectively) in each treatment zone at the pier are shown in Figure 2.10. Among treatment zones, the 0 m, 10 m and 50 m zones had significantly high sediment rates ($p<0.001$, Two-Way ANOVA), while among sediment trap position, LST had significantly higher sedimentation rates than UST among all treatment zones ($p=0.001$, Two-Way ANOVA) (Appendix I.7). Mean SR in the UST was comparable among all the treatment zones ($p>0.05$, Tukey Test); however LST collected significantly less sediment in the 3 m zone ($p<0.05$, Tukey Test), but was similar among the 0 m, 10 m and 50 m ($p>0.05$, Tukey Test). Among the possible factors affecting the collection of sediment in the LST in the 3 m zone could be the damselfish *Stegastes fuscus*, which was observed in various occasions disturbing the sediment trap. The results indicate that no distinct trend in sedimentation was found across treatment zones (Figure 2.10).

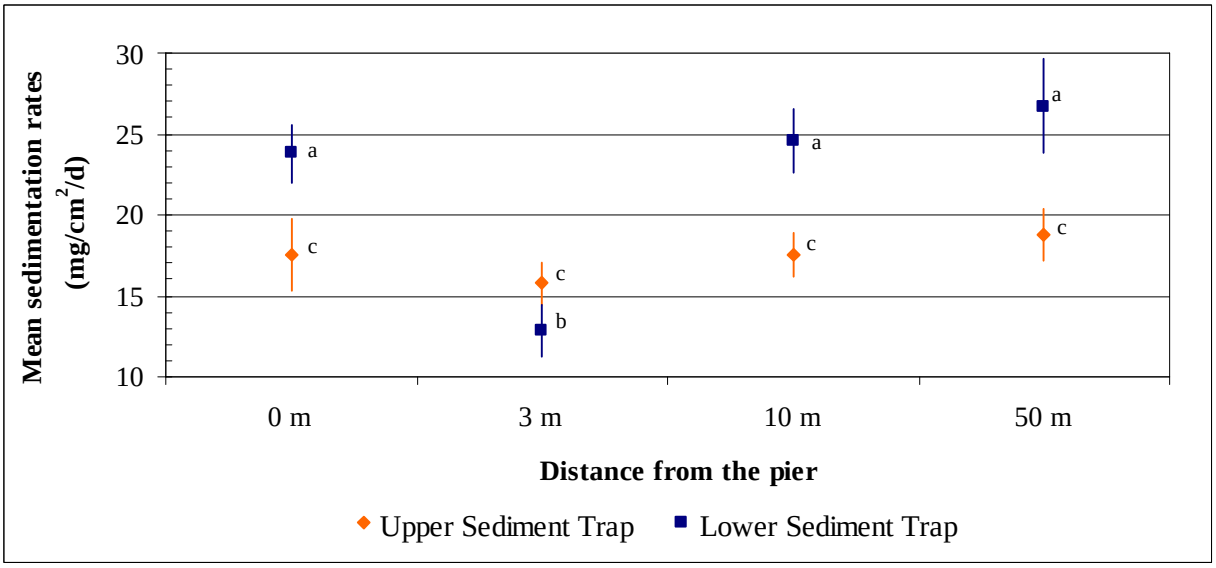

Figure 2.10. Mean yearly sedimentation rates (mg/cm^2/d) and standard error for upper and lower sediment traps in each treatment zone at the pier. Data was averaged from monthly values. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

2.4.1.4. Water Temperature

Mean monthly water temperature (°C) for 0 m and 50 m zones are shown in Figure 2.11. Variations of mean monthly temperature were not significantly different among the treatment zones (p=0.502, One-Way ANOVA, Appendix I.8), which indicated that no changes in temperature occur across treatment zones due to the pier-shading effect.

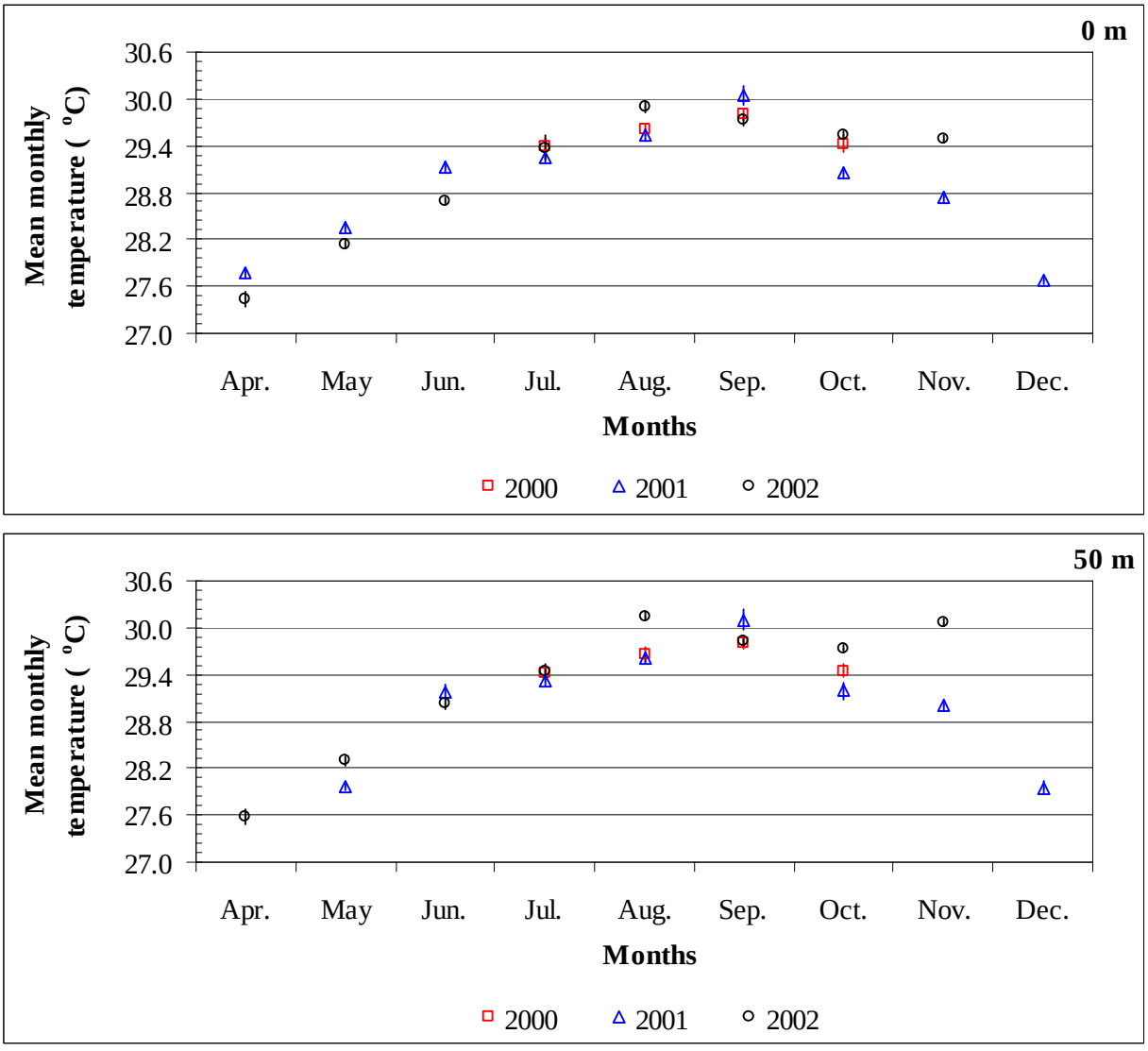

Figure 2.11. Mean monthly water temperature fluctuations (°C) in the 0 m (top) and 50 m (bottom) treatment zones for years 2000, 2001, and 2002. Standard error of the means is shown as vertical lines.

These results (Figure 2.11) were comparable with unpublished data from a water quality study at Guayanilla Bay and at the EcoEléctrica LP pier (Vicente and Associates, and Caribbean Engineering and Environmental, 2003). Vicente and Associates, and Caribbean Engineering and Environmental (2003) have collected five years (2000 to 2005) of temperature and salinity data at different locations within Guayanilla Bay, and one of the locations was about 3 m away (to the east) from the zone under the pier of this study. Their data suggests that variations in temperature and salinity at the bay were more related to seasonal patterns than to spatial patterns.

2.5. DISCUSSION

This chapter described the characteristic variations of environmental parameters such as irradiance, sedimentation, and water temperature, across treatment zones at the EcoEléctrica LP pier. Shading by the pier structure had a negative impact on irradiance since a gradient of decreasing irradiance and increasing number of hours of shading was found across treatment zones, although this was not the case for sedimentation and water temperature fluctuations. Thus, shading by overwater structures might change the light regimes that largely determine the habitat characteristics that support phototrophic organisms. Studies have found important ecological implications for various marine and freshwater autotrophic communities. A decrease in irradiance due to shading of overwater structures showed a significant reduction in productivity and abundance of seagrasses like the eelgrass *Zostera marina* (Simenstad et al., 1995; Burdick and Short, 1999; Fresh et al., 2001), the turtlegrass *Thalassia testudinum* (Loflin, 1995; Shafer and Robinson, 2001), and the shoalgrass, *Halodule wrightii* (Shafer, 1999); a summary of existing investigations was compiled by Shaffer (2002) for three species of *Phyllospadix*, and two species of *Zostera*, in the Pacific Northwest; significantly low productivity and abundance were found also for freshwater and upper estuarine (oligohaline) submerged aquatic vegetation (Steinmetz et al., 2003; Garrison et al., 2005). The most common results found on these investigations were very low density or absence of seagrass/aquatic vegetation under the piers (Pentilla and Doty, 1990; Loflin, 1995; Burdick and Short, 1999; Shafer, 1999; Shafer and Robinson, 2001), and an irradiance level under the

piers or docks representing a critical threshold (14 percent of surface irradiance) for most seagrass species survival (Burdick and Short, 1999; Shafer, 1999; Shafer and Robinson, 2001).

Shading by overwater structures might also have significant ecological influence on heterotrophic organisms as well. Able et al. (1998) and Duffy-Anderson and Able (1999) reported a significant reduction of irradiance under and near large piers in the Hudson River and demonstrated that under-pier environments were poor-quality habitats for various fish species. Fish abundance, species richness, and distribution of YOY (young of the year) fishes (Able et al., 1998), and growth rates of juveniles of the winter flounder *Pseudopleuronectes americanus* and the tautog *Tautoga onitis* (Duffy-Anderson and Able, 1999) significantly decreased due to shading of commercial piers in the Hudson River. Duffy-Anderson and Able (1999) experimental design was similar to the one used in this study, they deployed cages with fish along transects that extended from underneath the piers, near and far from the pier. Another study related shading by overwater structures to changes in the behavior of the juvenile Pacific Salmon, causing delays in migration, changes in migratory routes, and loss of schooling shelter (Simenstad et al., 1999). More recently, a comprehensive literature review (Nightingale and Simenstad, 2001) was done on fish and shellfish species with life history strategies strongly related to estuarine and marine nearshore habitats, where piers and pier-related activities occur. They compiled scientific evidence to support the view that overwater structures and associated activities 1) potentially affect habitats and key ecological functions that support recruitment and sustainability of estuarine and marine fauna, 2) can have measurable effects on the distribution and abundance of marine resources, 3) the effects are characterized as alterations to ambient light and alterations to wave energy and substrate regimes, and 4) can impact the ecological functions of habitat through the alteration of those controlling factors that support key ecological functions such as spawning, rearing, and refugia (Nightingale and Simenstad, 2001).

Although it is certain that shading is detrimental for phototrophic benthic organisms and might be unfavorable for some heterotrophic organisms, shading might be beneficial for sessile invertebrates such as subtidal epibiotic assemblages. Epibiotic assemblages underneath overwater structures differ

substantially from those on adjacent natural reefs (Connell and Glasby, 1999; Glasby, 1999b). For instance, a change in community composition, diversity, and abundance was observed when subtidal epibiotic organisms on unshaded pilings were experimentally shaded (Glasby, 1999a). Thus, overwater structures like piers and dock not only provide hard substrata for attachment in the form of pilings, pipelines, and boats, but an appropriate shaded habitat for shade-tolerant species.

Experimental methods to reduce shading impacts have been studied for small docks and piers, including the use of unusual construction materials, such as glass blocks (Steinmetz et al., 2003), grid platforms (Shafer and Lundin, 1999; Shafer and Robinson, 2001), cone-shaped glass prisms built into docks (St. Johns River Water Management District, http://www.sjrwmd.com), light-permeable deck grating on residential floats (Fresh et al., 2001), and the use of three products were tested including a "SunTunnel," deck prisms, and a metal halide light with reflector shield (Blanton et al., 2002). Results of these studies have been used to provide a scientific basis for establishing small dock construction guidelines and regulations for the protection of seagrasses within the U.S., such as structural design specifications like height, width, and sun orientation (Kelty and Bliven, 2003). However, among these structural design specifications, Burdick and Short (1999) reported that height was the primary light determining characteristic of docks.

Ecological implications of a decrease in irradiance due to shading by overwater structures for autotrophic organisms like seagrasses and reef corals could represent the deterioration of important ecological functions like providing habitat, shelter and food to other marine species, filtering nutrients and sediments, stabilizing bottom sediments, and protecting the shore, among others. Shading by overwater structures could also adversely affect the productivity of reef corals (Hatcher, 1990; Muller-Parker and D'Elia, 1996) and seagrass beds (Onuf, 1994; Gallegos and Kenworthy, 1996; Kraemer and Hanisak, 2000, V.P. Vicente unpublished data). Besides providing much of the primary energy, reef-building corals also provide the primary shelter and/or nursery habitat for many organisms associated with the reef such as fish and shellfish, among others (Muscatine, 1980; Crossland et al., 1991). Consequently, reductions in the abundance of reef-building corals are likely to influence the majority of other coral reef

organisms, but might benefit others as well. Shading by pier structures can also reduced the ability or reef corals to grow and calcify, which may also translate into a reduced ability to compete for space with other organisms such as macroalgae. This could eventually reduce the abundance of reef-building corals from particular areas, changing the community structure (Glynn, 1993; Hughes, 1994; Shulman and Robertson, 1996). Thus, the effects of shading on irradiance might be an essential tool for future planning and decision-making processes and forthcoming coastal zone management policies in relation to placement and design of overwater structures.

2.6. CONCLUSIONS

- This chapter presented a baseline characterization of irradiance, and sedimentation across treatment zones, and a description of water temperature variations under the pier and in the control zone.
- A significant decrease in irradiance, and a significant increase in the hours of shading occurred in areas near the pier up to 10 m on the west side of the pier.
- No distinct pattern in sedimentation across treatment zones was found, but resuspension was significantly lower than deposition of sediment at the pier.
- Water temperature fluctuations were similar between the zone under the pier (0 m) and the control zone (50 m) and were more related to seasonal than spatial patterns.

CHAPTER 3. Shading effects on growth, reproduction, and zooxanthellae densities of the reef-building corals *Siderastrea siderea* (Ellis and Solander) and *Diploria clivosa* (Ellis and Solander)

3.1. ABSTRACT

Decreased irradiance caused by shading of overwater structures raises concern about the impact these may have on phototrophic benthic communities like reef corals. This study was conducted in Guayanilla Bay where the EcoEléctrica LP was recently built, including a pier. Changes in irradiance due to shading by the pier were correlated with biological characteristics of two Caribbean reef-building corals, *S. siderea* and *D. clivosa*. Forty-six colonies of *S. siderea* were transplanted from around the pier to four treatment zones: 0 m (under the pier, N=12), 3 m (N=12), 10 m (N=10), and 50 m (N=12) from the pier (control zone-no shading). Eleven colonies of *S. siderea* were selected randomly as controls in the 50 m zone. Nine colonies of *D. clivosa* were studied in the 0 m (N=5) and 50 m zones (N=4). Colonies of *S. siderea* were stained once with alizarin red (8.8 ppm) and sampled after 16 months to determine skeletal extension, density, and calcification. The differences in tissue surface area at the beginning and end of the study was used to determine tissue growth rates of *S. siderea.* Zooxanthellae densities, mesenterial fecundity, and oocyte diameter were studied in both species using standard histological techniques. For *S. siderea*, tissue growth and calcification in the 0 m zone were significantly lower ($p<0.001$, ANOVA) than the other zones. Skeletal extension and mesenterial fecundity in the 0 m and 3 m zones were significantly lower ($p<0.001$, ANOVA), but oocyte diameter was significantly larger ($p<0.001$, ANOVA), than the other zones. A significant ($p<0.001$) positive correlation was found between irradiance and tissue growth ($r=0.50$), calcification ($r=0.50$), skeletal extension ($r=0.60$), and mesenterial fecundity ($r=0.70$), while oocyte diameter correlated negatively ($r=-0.44$, $p=0.0001$). For *D. clivosa*, zooxanthellae increased while mesenterial fecundity significantly decreased in the 0 m zone ($p<0.05$, ANOVA). These results indicate that shading might affect important aspects of growth, reproduction, and zooxanthellae concentrations of corals. This information is important for the decision-making process and future coastal zone management policies in relation to placement and design of overwater structures.

3.2. INTRODUCTION

The importance of light to the coral/zooxanthellae symbiosis has been well-established (Chalker, 1981; Taylor, 1983; Falkowski and Kinzie, 1990), to the extent of considering corals as phototrophic organisms (Wellington, 1982; Battey and Porter, 1988; Muller-Parker and D'Elia, 1996). This symbiotic relationship reflects a high degree of ecological and nutritional integration, which underlines the importance of the surrounding light environment (Dustan, 1982; Dubinsky et al., 1984; Porter et al., 1984; Porter, 1985; Battey and Porter, 1988; Falkowski and Kinzie, 1990). Therefore, light is fundamental for many metabolic functions of the coral/zooxanthellate symbiosis (Chalker, 1981; Taylor, 1983; Falkowski and Kinzie III, 1990), which may affect coral species distribution, and zonation (Jokiel, 1989, Titlyanov and Latypov, 1991), and reef productivity (Hatcher, 1990). Zooxanthellae contribute to coral nutrition (Lewis and Smith, 1971; Muscatine, 1980) recycling limited nutrients back to the coral host, such as nitrogen (Muscatine and Porter, 1977), and translocation of photosynthetic products (Muscatine, 1990) contribute to reproduction (Rinkevich, 1989) and respiration (Muscatine et al., 1981). They also enhance calcification and coral growth (Goreau, 1959, 1963; Barnes and Taylor 1973, Chalker, 1981), and consequently, colony size, which in massive scleractinian corals affect competitive ability (Lang and Chornesky, 1990), and is an important species characteristic which correlates with other life history traits like reproduction (Connell, 1973; Kojis and Quinn, 1985; Szmant-Froelich, 1985; Soong, 1993).

The light environment of the endosymbiotic algae is determined mainly by where the animal host lives. A change on the quantity and/or quality of light received on a reef setting often requires, from the coral colony and the endosymbiotic zooxanthellae algae as well, morphological and perhaps physiological adaptations to maximize light capture. Reaction to low light regimes by some coral species is known as a photoacclimation response, making possible a wide vertical distribution where light intensity spans more than two orders of magnitude (Chalker et al., 1983; Porter et al., 1984; Titlyanov and Latypov, 1991). Photoacclimation to light is a function of compensatory adaptation by both the algae and its coral host to maximize light capture. The coral/zooxanthellae symbiosis could present the following characteristics,

which are not mutually exclusive, as adaptations to cope with the varying light regimes in their environment:

- morphological changes at colony level (Goreau, 1959; Goreau and Wells, 1967; Barnes, 1973; Dustan, 1975, 1979; Porter et al., 1984; Titlyanov, 1987; Titlyanov and Latypov, 1991)
- morphological changes at micro-skeletal level (Foster 1979, 1980)
- changes in the behavior of polyp expansion (Lasker, 1977)
- changes in the production of mycosporine-like aminoacids (MAAs) (Dunlap et al., 1986; Gleason, 1993; Muszynski, 1997)
- changes in zooxanthellae concentrations (Lasker, 1977; Dustan, 1982; Titlyanov, 1981; Titlyanov et al., 1996, 1999)
- changes in the photosynthetic unit (PSU) size (Masuda et al., 1993; Iglesias-Prieto and Trench, 1997a, b)
- changes in the chlorophyll concentrations in zooxanthellae (Titlyanov et al., 2001a, b)
- changes in the 'type' of zooxanthellae (Titlyanov et al, 2001c)

However, light has its own variable factors that can likely exert influence on coral physiology such as: 1) quantitative and qualitative alterations of light within the water column due to absorption and scattering by water constituents (Maritorena and Guillocheau, 1996; Kirk, 1994), 2) latitudinal, daily or seasonal changes in light due to the sun angle, and the consequent alteration of light intensity and spectral composition with depth (Kirk, 1994), and 3) length of day and number of sun hours (Bak, 1974).

A decrease in irradiance can be caused by high turbidity and/or sedimentation, acting like a light filter of varying density, and decreasing coral growth rates (Rogers, 1979). Reductions in live coral cover due to high sedimentation and consequently, decrease in light intensity, are frequently reported along with low coral growth rates (Chansang et al., 1981; Cortés and Risk, 1984, 1985; Acevedo et al., 1989; Debrot et al., 1998; Torres and Morelock, 2002). Roy and Smith (1971), Loya (1976), and Titlyanov and Latypov (1991) found that while very turbid water (i.e., low light intensity) did not inhibit the presence of corals, coral coverage was decreased in comparison with clear water reefs. Acevedo et al. (1989) observed shift of zonations, changes in dominant coral species, and upward migration of zone depth on coral reefs with low light intensities due to high terrigenous input when compared to coral reefs with clear waters. Sublethal effects (i.e., on reproduction, photosynthesis) resulting from the cited stresses above,

may perhaps have long-term consequences and most likely exceed that of the initial environmental disturbance (Bak, 1978). Noticeably, one of the major drawbacks in reef monitoring programs that relate the effects of abiotic factors to coral communities is that some of these studies seem to be short-term assessments; moreover, qualitative rather than quantitative methods were used on most of these studies for evaluation of disturbances on coral reef communities (Bak, 1978). Long-term assessments of the effects of disturbances on the coral reef community are necessary. Along with the need of long-term assessments, Rogers (1990) emphasizes the need for measurements of physical and chemical processes to correlate organism and ecosystem responses and for adequate long-term data sets.

Light availability seems to play a significant role in coral tissue regeneration (Bak, 1983; Meesters et al., 1992; Meesters and Bak, 1995; Meesters et al., 1996). Nagelkerken et al. (1999) found that the recovery of artificial lesions in *Porites astreoides* and *Stephanocoenia michelinii* were negatively correlated with water depth, or decreased light intensity, during the initial phase of the regeneration process. Similarly, Bak (1983) found the percentage of recovered lesions to be higher in shallow water than in deep water colonies of *Porites astreoides*, which also suggests the influence of light on coral regeneration. Muscatine et al. (1984); Spencer-Davies (1984), Edmunds and Davies (1986) found shallow water coral colonies to be metabolically supersaturated with light leading to storage of surplus energy. This argument was used by Nagelkerken et al. (1999) to explain the high efficiency of tissue regeneration of shallow water coral colonies.

Reproduction of scleractinian corals have been a subject of intense study and great interest to coral reef scientists, reviews are available from Fadlallah (1983), Harrison and Wallace (1990), Richmond and Hunter (1990) and more recently by Fautin (2002). Studies on coral reproduction have concentrated mostly on different aspects such as sexual patterns and mode of development, gametogenic cycles, reproductive effort, fecundity, spawning and brooding behavior, timing, planula development and recruitment, among others (Harrison and Wallace, 1990). Few studies have reported any short or long-term effect of variation of light regimes on coral reproduction. Kojis and Quinn (1984) related high sedimentation rates and poor water transparency to reduced fecundity of *Acropora palifera* (Australia),

which also limited their depth distribution, and reduced the abundance of this species. Several studies have suggested that photoperiod provided a more consistent annual pattern for regulating reproduction in shallow reef-flat environments for *Acropora palifera* (Kojis, 1986), for regulating spawning periodicity for both *Montipora verrucosa* and *M. dilatata,* but for *M. verrucosa* day length was the environmental cue that triggered mass spawning on Hawaiian reefs (Hunter, 1988), and influenced spawning synchronicity between temperate and tropical reefs of Western Australia (Babcock et al., 1994). However, three years of data confirmed that a difference in depth seemed to affect mass spawning synchronicity on two coral reefs at the Great Barrier Reef (Willis et al., 1985), suggesting a role of decrease light intensity. Mass spawning events occur exactly one lunar month later on a deep offshore reef when compared to a shallower inshore reef at the same latitude (Willis et al, 1985). More recently, Penland et al. (2004) related onset of gametogenesis and spawning synchronicity more to solar irradiance than to sea surface temperatures; the latter being a delayed consequence of the former.

In recent years, there has been an increase for requests of permits to build small docks, and in the number of docks constructed within the United States coastal zone (Kelty and Bliven, 2003). This rapid development of the coastal zone and increase of piers raises concern about the impact that shading may have on benthic communities, particularly reef corals. Scientific research documenting the effects of shading by large pier structures (commercial use) or small docks (recreational docks designed for residential use) to phototrophic benthic organisms and how this reduced light regime affects different aspects of their biology are scarce for seagrasses (Shafer, 1999; Shafer and Lundin, 1999; Shafer and Robinson, 2001; Shafer, 2002; Hertler, 2002; Ruiz and Romero, 2003), and lacking for corals. Information on the penetration of the photosynthetic waveband (400 to 700 nm) is of great ecological value as a broad indication of the availability of light for photosynthesis in an aquatic ecosystem. Thus, the purpose of this chapter was to assess if changes in irradiance due to the EcoEléctrica pier shadow affect coral growth of *S. siderea,* and reproduction and zooxanthellae densities of *S. siderea* and *D. clivosa.* The objectives of this investigation were:

1) to determine if changes in irradiance with distance from the pier could affect coral growth:
    - tissue growth rate,
    - skeletal extension rates,
    - skeletal density,
    - calcification
2) to determine if changes in irradiance with distance from the pier could affect mesenterial fecundity and oocyte diameter
3) to determine if changes in irradiance with distance from the pier alter concentrations of zooxanthellae/polyp.

The null hypothesis was that changes in irradiance do not affect coral growth of *S. siderea*, or reproduction and zooxanthellae densities of *S. siderea* and *D. clivosa.*

3.3. METHODOLOGY

3.3.1. Experimental Design

Forty-six colonies of *S. siderea* were selected near the EcoEléctrica LP pier, most of them from Bent 14, for the transplanting experiment, and 11 additional 'healthy' colonies were selected as controls in a nearby site. Transplanted and control colonies (not transplanted) were within the same depth (2 m); control colonies were located in the control zone, at 50 m from the pier, with no shadow interference. Colony selection for transplant and controls of *S. siderea* was made according to size so that all the experimental colonies had similar dimensions and shape; only colonies with 'healthy-looking' tissue were selected. The main species selected was *S. siderea* because this species was dominant within the pier domain (Vicente and Associates, 2000). A second coral species also common within in the area, *Diploria clivosa*, was studied as part of a preliminary approach to extend the hypothesis to other scleractinian corals. The 46 colonies of *S. siderea* were transplanted and distributed (Figure 3.1) into four treatment zones (see section 2.3.2) at Bent 14. All colonies selected for the study were tagged in the field with a number.

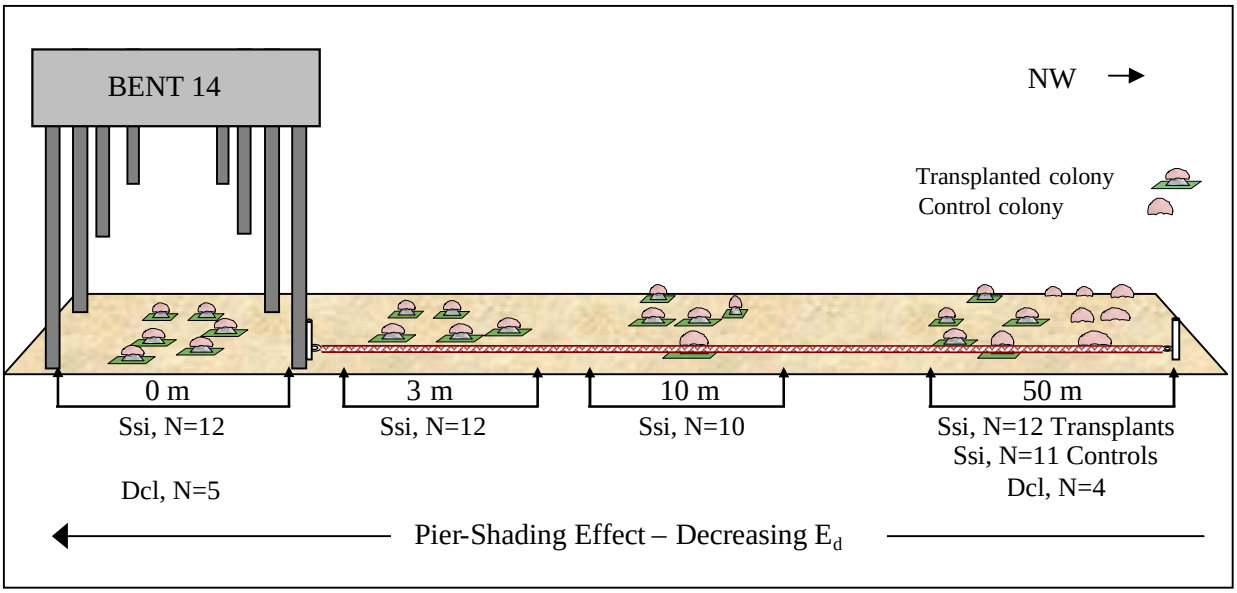

Figure 3.1. Drawing representing the gradient of irradiance (E_d) and transplanted and control colonies of the experimental design at the EcoEléctrica LP pier. Ssi = *S. siderea,* Dcl = *D. clivosa,* N = number of colonies. Modified from Vicente and Associates (2000).

3.3.2. Transplanting Procedures

The majority of the colonies found during a previous inspection were nearly convex on the underside; therefore, a cement base was used for proper coral-substrate attachment (Figure 3.2). Coral colonies were attached to the cement base with ultrabond (underwater epoxy). To assure adherence between the ultrabond and the calcareous skeleton, the undersurface of the colonies to be transplanted (devoid of tissue) was carefully cleaned with a wire brush from deposited silt, algal overgrowth and from biofouling organisms. The coral-base unit was attached to a plastic lattice with screws and expansion and this new unit was attached to the substrate with more screws and expansions to assure the physical stability of the transplanting unit (Figure 3.2). All coral-transplanting units were fixed at the same depth (2 m), in the same orientation, and were approximately 4 cm above the substrate. EcoEléctrica LP facilitated all the field logistics.

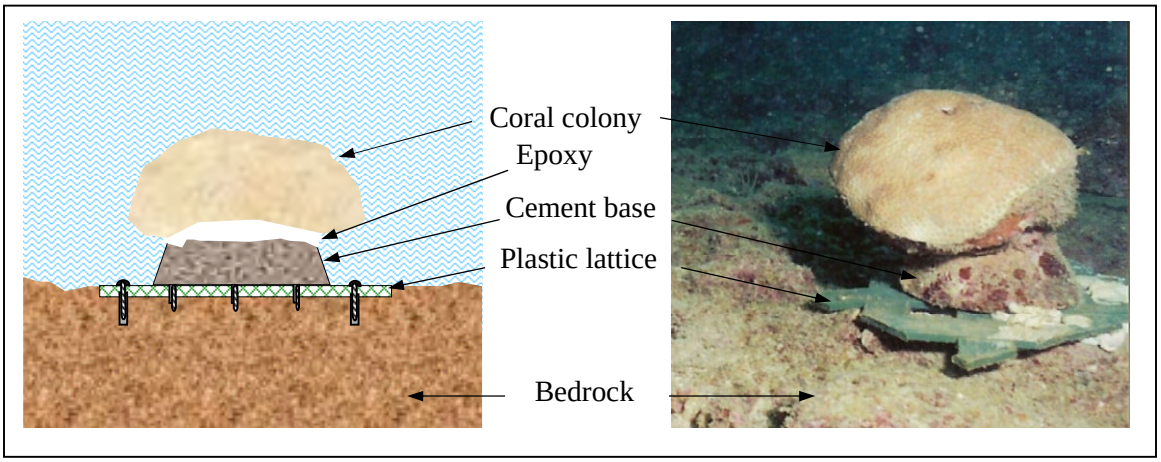

Figure 3.2. Drawing showing details of the materials and arrangement of the coral-transplanting unit, and photo of a *S. siderea* transplanted colony in the 50 m zone (control zone) (April 2000). Modified from Vicente and Associates (2000).

Diploria clivosa was selected two months prior to sampling date. Thus, colonies of *D. clivosa* were not transplanted but studied *in situ* for reproduction and zooxanthellae densities. Colonies of *D. clivosa* were not found under the pier at Bent 14, therefore, samples were obtained from colonies under the pier at Bent 23 (N=5) at 4 m depth, and at Bent 14 (N=4) at 2 m depth in the 50 m zone.

3.3.2.1. Staining coral colonies

After transplanting, colonies of *S. siderea* were allowed to acclimatize for two weeks before staining with one gram of sodium alizarin sulphonate [$C_6H_4COC_6HOH_2(SO_3Na)CO$], also known commercially as Alizarin Red S (Lamberts, 1974, 1978), to estimate linear skeletal extension rates. The dye was weighed at the lab, packed in a piece of wax paper (5 cm x 5 cm), wrapped with a rubber band, and sealed up safely into one of the corners of a transparent plastic bag (114 liters or 30 gallons) with another rubber band (Goenaga, 1988). In the field, the plastic bag was tied securely around the base of each transplanted and control colonies of *S. siderea* in all treatment zones (Figure 3.3) during the morning.

Figure 3.3. Photo of a colony of *S. siderea* during the staining process (April 2000) with Alizarin Red S.

After releasing the dye, the amount used yielded an approximate final concentration of 8.68 mg/liter (8.8 ppm). The bag was removed after 24 hrs. Although Lamberts (1978) and Rogers et al. (1994) recommended using a concentration of 10 ppm and 10 to 15 ppm, respectively, Durant (1995) used this method previously with *M. annularis* using a lower concentration (6 ppm) with success.

Transplanted and control colonies of *S. siderea* were stained once and allowed to grow for 16 months. Staining dates per treatment zone were on April 6, 2000 in the 0 m zone, April 7, 2000 in the 3 m and 10 m zones, April 10, 2000 and May 10, 2000 for control and transplanted colonies in the 50m zone, respectively.

3.3.2.2. Sampling

On July 10, 2001, two random colonies of *S. siderea*, not previously selected for this study, were chosen in the 50 m zone to check for presence of mature gametes. These two colonies were bearing spermatocytes at stage V *sensu* Szmant-Froelich et al. (1985), probably ready to spawn due to the proximity of the spermatocytes bundles to the oral end of the polyp. Therefore, colonies were sampled during the first two weeks of August 2001, a month before the September 2001 full moon, when mass spawning is expected to occur for *S. siderea* and other massive coral species in the Caribbean and Florida (Soong, 1991; Guzmán and Holst, 1993). The colonies had one reproductive event before sampling (sampling was done at the second reproductive event after transplantation).

Two cores (approximately 2.5 cm in diameter and 2 to 3 cm height) were obtained from each transplanted and control colony of *S. siderea*, and one core from colonies of *D. clivosa*, using a pneumatic hand drill connected to a scuba tank (Figure 3.4), 16 months after staining. One core was cleaned of tissue with tap water and the remaining skeleton was used for the growth study, second core was decalcified and used for the reproductive study. All core samples were collected from the top surface of the colony; marginal infertile areas and vertical surfaces of the colonies were avoided using Guzmán and Holst (1993) recommendations.

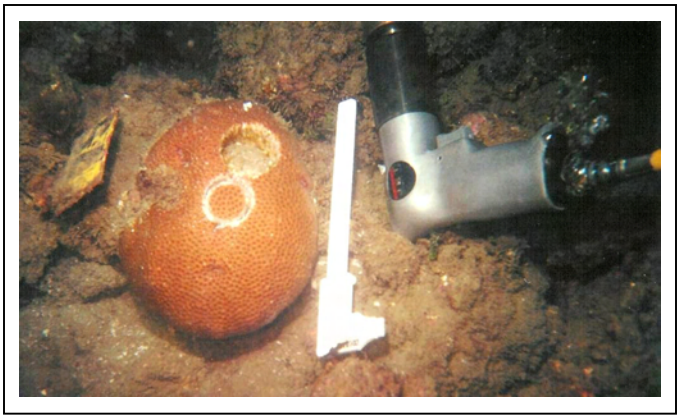

Figure 3.4. Photo of a control colony (# 75) of *S. siderea* at the 50 m zone showing two cores made at the top of the colony during sampling in August 2001.

The holes (two on each *S. siderea* and one on each *D. clivosa*) were filled out with cement plugs previously submerged at the site or with epoxy (Figure 3.5). Filling holes with epoxy was an alternative method when we ran short of cement plugs during sampling.

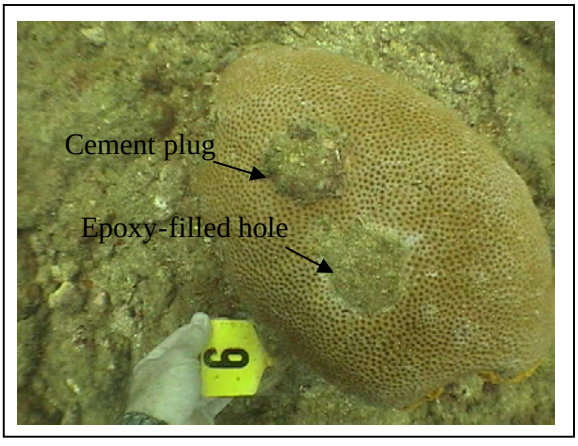

Figure 3.5. Photo of a transplanted colony of *S. siderea* showing the filling of two holes made at the top of the colony during sampling in August 2001.

Core samples used for the reproductive study were fixed in Zenker Formalin (Helly's solution); decalcification, dehydration, embedding, sectioning and subsequent tissue staining process (with Heidenhain's Aniline-Blue method) were done following standard histological procedures from Coolidge and Howard (1979) (Appendix III).

3.3.3. Coral Growth

3.3.3.1. Live coral tissue (LCT, cm^2) and Tissue Growth Rate (TGR, cm^2/yr)

Colony size in corals is an important characteristic related to most life history traits. Live coral tissue (LCT) measurements to estimate area (cm^2) of LCT can be equivalent to an estimate of colony size. Measurements were done with a flexible measuring tape to account for the contour of the colony. LCT was estimated by measuring (to the nearest 0.5 cm) along the maximum perceived diameter (L), and across (W) - along the second longest perceived diameter (to the nearest 0.5 cm), perpendicular to L. Area of surface tissue (cm^2) was calculated by multiplying L by W. LCT for March 2000 and July 2001 were calculated, and pooled to obtain mean LCT per treatment zone. LCT was estimated for colonies of *D. clivosa* for July 2001, since this species was included during the late stages of this study.

Tissue growth rate (TRG) might be an important biological assessment tool of shading by the pier. Thus, to determine TGR (cm^2/yr) of live coral tissue in time for all transplanted and control colonies of *S. siderea* across treatment zones, the following equation was used:

$$\mathbf{TGR\ (cm^2/yr) = (LCT_1 - LCT_0) / t,} \qquad \mathbf{(3.1)}$$

where LCT_1 and LCT_0 were the data of live coral tissue (cm^2) measured on July 2001 and March 2000, respectively, and t was time of growth in years (16 months = 1.33 years). Negative results from Eq. 3.1 (some colonies lost tissue), were substituted for zero, meaning no tissue growth.

3.3.3.2. Skeletal growth

For a comprehensive description of coral growth and the potential effect of shading, three parameters were evaluated and described in this study: linear skeletal extension, bulk density (measures distribution of calcium carbonate) and calcification rate (mass of calcium carbonate deposited over time)

(Dodge and Brass, 1984). If any two of such parameters are known, the third can be calculated. Dustan (1975) suggested that the amount of calcium carbonate deposited in the skeleton over a known period is proportional to its extension rate. Taking this assumption as correct, the calcification value obtained from the product of skeletal extension rate (SER) times skeletal density (SkD) was used as an estimate of calcification or relative calcification rate (RCR) (Dodge and Brass, 1984).

3.3.3.2.1. Skeletal Extension Rate (SER, cm/yr)

A high-speed rotary tool (Dremel MultiPro, Model 396T6, 5000 - 35,000 RPM) equipped with cutting discs (Dremel item #540) was used to section the coral core in the laboratory. Various longitudinal slabs of 4 to 5 mm thick were made, through the plane of maximum growth, parallel to the direction of corallites. The distance between the upper limit of the stain line and the periphery of the colony (border of corallite's septa) was measured to determine linear extension (mm) of new skeleton (Figure 3.6).

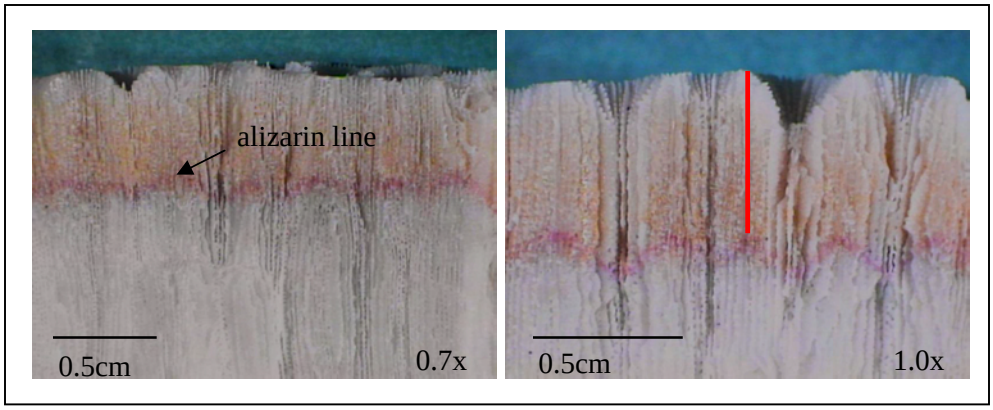

Figure 3.6. Photo of a longitudinal section of a core from *S. siderea* (# 67) with the alizarin red s line (horizontal line). Linear extension of new skeleton (red vertical line) was determined by measuring the distance between the upper limit of the stain line and the periphery of the colony.

A dissecting microscope (Olympus Stereomicroscope Model SZH10) with a color video camera was used to make photos of each section to be measured. Ten measures per colony were made from the photos using a computer program (Sigma Scan Pro 5). Skeletal extension rate (cm/yr) was calculated from the measures obtained on the longitudinal section and the time the colonies were allowed to grow after staining (16 months = 1.33 yrs).

3.3.3.2.2. Skeletal density (SkD, g/cm^3)

To determine SkD (g/cm^3) of *S. siderea*, two small pieces of coral skeleton from above the staining line were obtained from all colonies with a well-defined stain line using a high-speed rotary tool (see Section 3.3.3.5). Pieces obtained were as thin as possible (1 to 2 mm) to facilitate water going through the skeleton's open spaces. Volume and weight of each piece were obtained with an Ohaus Explorer Analytical Balance (Model E11140) modified with a Density Determination Kit (Model P/N 470007010). The balance was calibrated, prepared with the density determination kit, and the weight of the sample and the volume was determined and recorded. A detailed description of the procedures and calculations can be found in Appendix II. The proportion of weight/volume is the skeletal density expressed in grams per cubic centimeters.

3.3.3.2.3. Relative Calcification Rate (RCR, g/cm^2/yr)

Relative calcification rate (RCR) was calculated for transplanted and control colonies of *S. siderea*, which had both SER and SkD. The following equation was used:

$$\textbf{RCR (g/cm}^2\textbf{/yr) = SER (cm}^2\textbf{/yr) x SkD (g/cm}^3\textbf{)} \qquad \textbf{(3.2)}$$

where SER was skeletal extension rate, and SkD the skeletal density of the same colony.

3.3.4. Reproduction

3.3.4.1. Gender

Siderastrea siderea is a gonochoric species. The gender was determined examining histology slides. Colonies with spermaries were designated as M (male), with oocytes as F (female), and without spermaries or oocytes as I (immature).

3.3.4.2. Mesenterial Fecundity (MF)

A light microscope equipped with a digital camera was used to digitize images from histology slides of *S. siderea* and *D. clivosa*. Digitized images of longitudinal sections (40x total magnification) of polyps with 12 consecutive mesenteries were used to compose and print a photograph of a complete polyp (Figure 3.7). To determine mesenterial fecundity (oocytes per mesentery), oocytes were counted from the

photographs, and crosschecked with histology slides. Various composite photographs of the same polyp were used to account for all oocytes in the mesentery. For *S. siderea*, 12 consecutive mesenteries per polyp within a colony (N=36) were used to estimate mesenterial fecundity. For *D. clivosa*, 12 consecutive mesenteries per polyp within a colony (N=24) were used, following the protocol describe by Vargas-Toledo (2002).

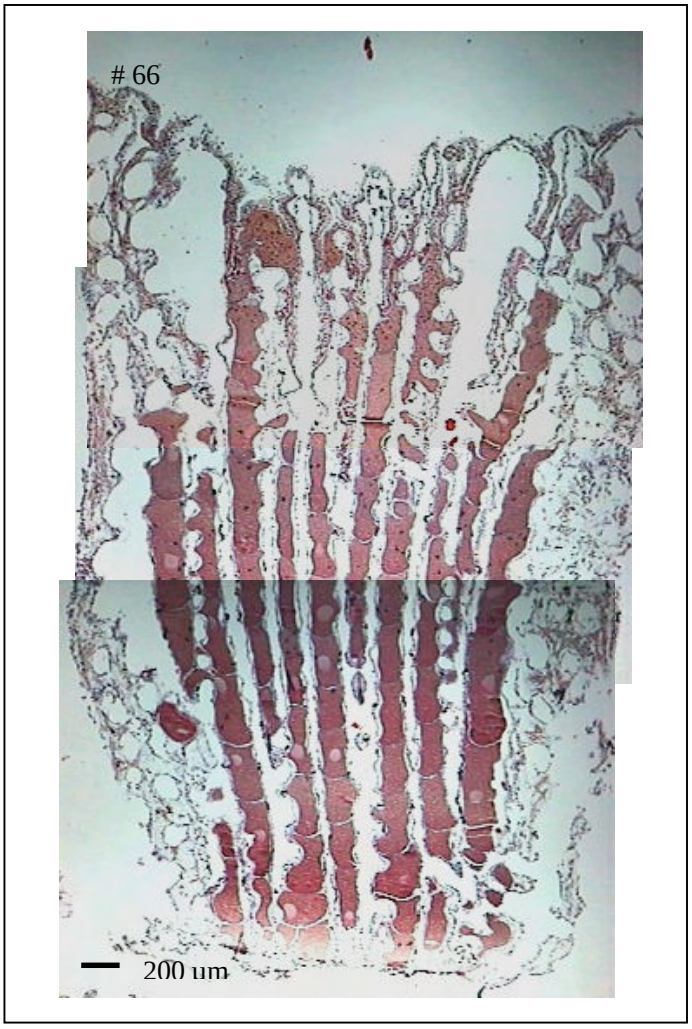

Figure 3.7. Composite photograph of longitudinal sections (40x) of a polyp from colony # 66 in the 50 m zone used to estimate mesenterial fecundity of *S. siderea*.

3.3.4.3. Oocyte Diameter (OD, µm)

A light microscope equipped with a digital camera was used to digitize oocyte images from histology slides of *S. siderea* and *D. clivosa* (Figure 3.8). Digitized images of longitudinal sections of

polyps with oocytes (100x total magnification) were used to measure maximum perceived oocyte diameter (OD, µm) using Sigma Scan Pro 5.0. To determine mean OD, 60 oocytes were used per colony for each species.

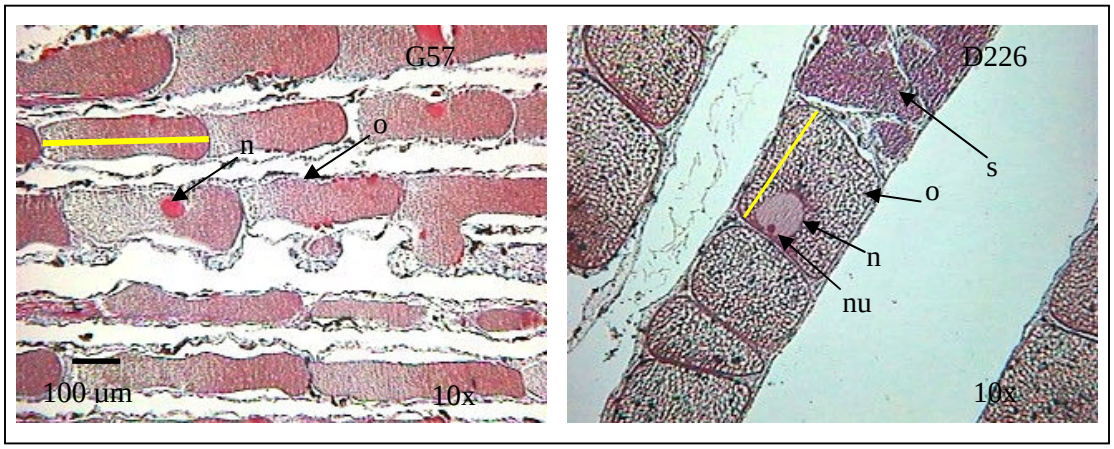

Figure 3.8. Histological samples of colony # 57 of *S. siderea* and # 226 of *D. clivosa*. Oocytes (o), nucleous (n), spermary (s), nucleolus (nu) are shown. Yellow line represents maximum length (diameter) of the oocyte.

3.3.5. Zooxanthellae Population Density

Zooxanthellae population densities (ZD) of *S. siderea* and *D. clivosa* were examined from the same colony tissue sample used for the reproduction study. For both species, zooxanthellae slides were made from the oral end of the polyp without affecting the rest of the polyp bearing oocytes and/or spermaries. Zooxanthellae cells were counted from polyps' cross-sections. Six different pictures (replicates) from each colony were taken with a light microscope equipped with a digital camera. Microscope objective magnification was 100x, total magnification in all pictures was 1000x. On each of the six replicates, the same area was examined using Power Point computer program as follows: a rectangle was outlined in an empty slide in Power Point, then copied and pasted to each replicate image in the same position (Figure 3.9). All zooxanthellae within the established area were counted, including those touching the rectangle borders. The rectangle area (mm^2) was determined with Sigma Scan Pro computer software to be 0.004961 mm^2; zooxanthellae densities were calculated as number of zooxanthellae cells/mm^2.

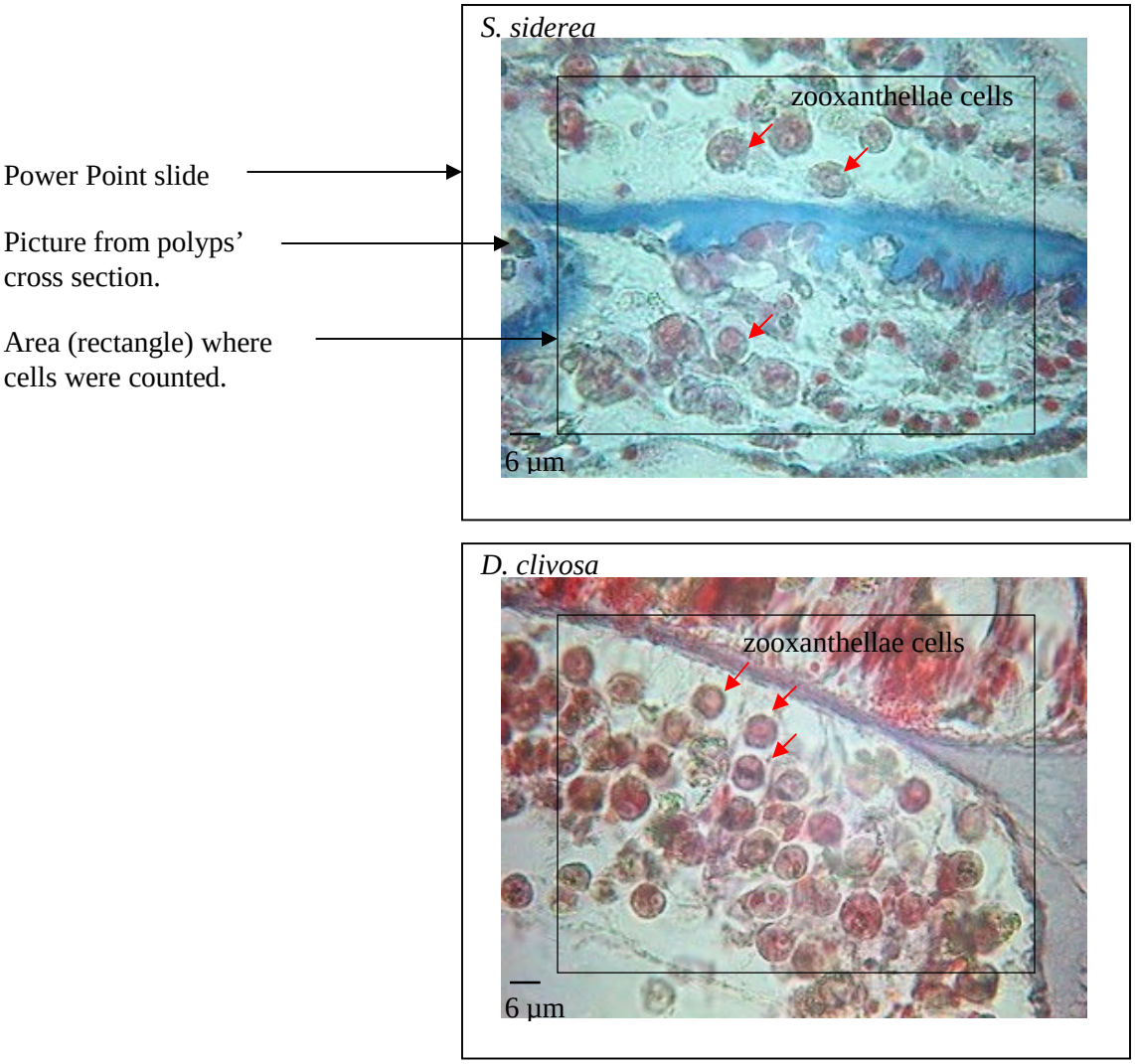

Figure 3.9. Photo of a cross-section (100x) of the oral end of a polyp of *S. siderea* (top) and *D. clivosa* (bottom) showing the area (inside rectangle) used to count zooxanthellae (red arrows) *in hospite*.

3.3.6. Statistical Analyses

In this study, no data passed ($p<0.001$) the Kolmogorov-Smirnov Normality test. Therefore, the homogeneity of variance assumption was tested using the F_{max}-test (Sokal and Rohlf, 1995). The results of the $F_{max\ (\alpha=0.01)}$-test for SER, SkD, RCR, ZD of *S. siderea*, and MF (for both species) indicated no major violations of the above assumption. TGR, ZD of *D. clivosa* and OD of *S. siderea* complied with the assumption of homogeneity of variance after being transformed (log x+1). Consequently, for all the biological parameters of *S. siderea* and *D. clivosa* mentioned above, a parametric test (One-Way ANOVA,

at $p<0.05$ confidence level) was used to test for significant differences among treatment zones. To identify the group with significantly higher or lower values, a multiple comparison test, Tukey Test (at $p<0.05$ confidence level), was used. A Pearson Correlation (r) was used to explore the relationship between *S. siderea* biological characteristics and irradiance. Only OD of *D. clivosa* failed the homogeneity of variance assumption even after transforming the data (log x+1, square root), thus a non-parametric test (Mann-Whitney Rank Sum Test, at $p<0.05$ confidence level)) was used to test for significant differences between two treatment zones. A Pearson Correlation was used to explore the relationship among biological characteristics of *S. siderea* and *D. clivosa* in each treatment zone.

3.4. RESULTS

3.4.1. *S. siderea*

3.4.1.1. Live coral tissue growth (LCT, cm^2) and Tissue Growth Rates (cm^2/yr)

Variations in colony size (LCT, cm^2) across treatment zones are shown on Table 3.1 for *S. siderea.* Colonies of *S. siderea* were over 100 cm^2 at the beginning of the study, but some transplanted colonies lost tissue by the end of the study.

Table 3.1. Mean (±standard deviations) colony size measured as live coral surface tissue (LCT - cm^2) of *S. siderea* at transplantation (March 2000) and before sampling (July 2001).

Distance from the pier	LCT (cm^2) March 2000	LCT (cm^2) July 2001
0 m	226.06 (124.92)	181.50 (89.13)
3 m	317.27 (215.54)	376.40 (254.20)
10 m	290.55 (97.92)	392.65 (160.07)
50 m	288.00 (180.48)	427.13 (222.99)
50 m*	347.98 (193.11)	323.39 (117.64)

50 m* = control colonies in the 50 m zone.

A decrease in mean TGR with decreasing irradiance across treatment zones is evident in Figure 3.10. Fourteen (25%) of all *S. siderea* transplanted and controls colonies at the pier showed tissue loss during the study period; however, forty-three (75%) showed tissue growth. Sixty-seven percent of colonies in the 0m zone lost tissue (8 out of 12), followed by colonies at 3 m and 50 m zone with 17%

each (2 out of 12). Only 18% of control colonies in the 50 m zone lost tissue (2 out of 11). At 10 m, all transplanted corals gain tissue during the study.

Mean TGR of *S. siderea* was significantly higher in transplanted colonies in the 50 m zone (p=0.0004, One-Way ANOVA, Appendix IV.1.1), while transplanted colonies in the 0 m, 3 m, 10 m and control colonies in the 50 m zones were similar (p>0.05, Tukey Test, Figure 3.10). There was a significant positive correlation (Figure 3.11) between TGR and irradiance (r=0.4519, p=0.0006031, n=57), thus, a significant lost of tissue occurred with a decrease in irradiance across treatment zones.

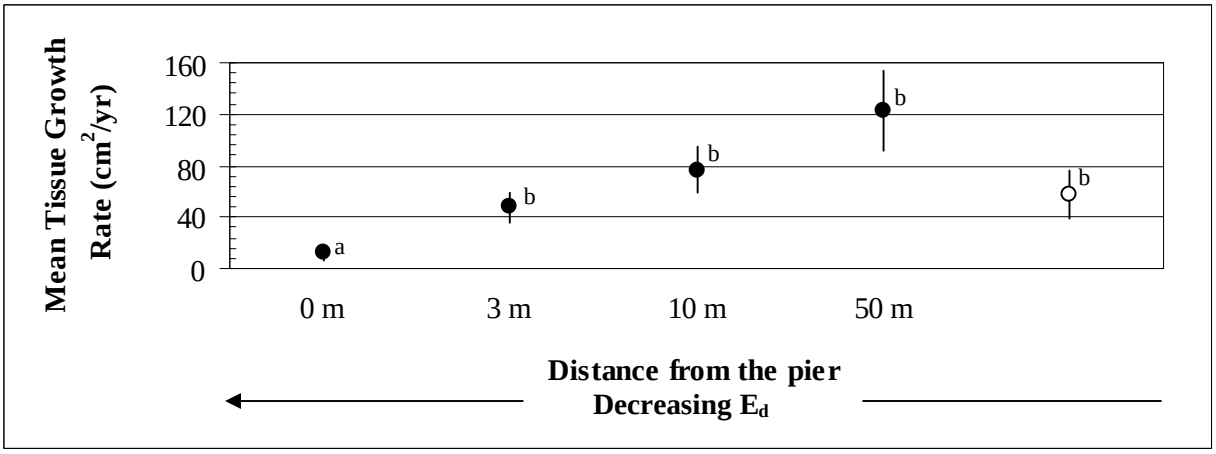

Figure 3.10. Mean tissue growth rate (cm^2/yr) and standard error of *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different (p<0.05, Tukey Test).

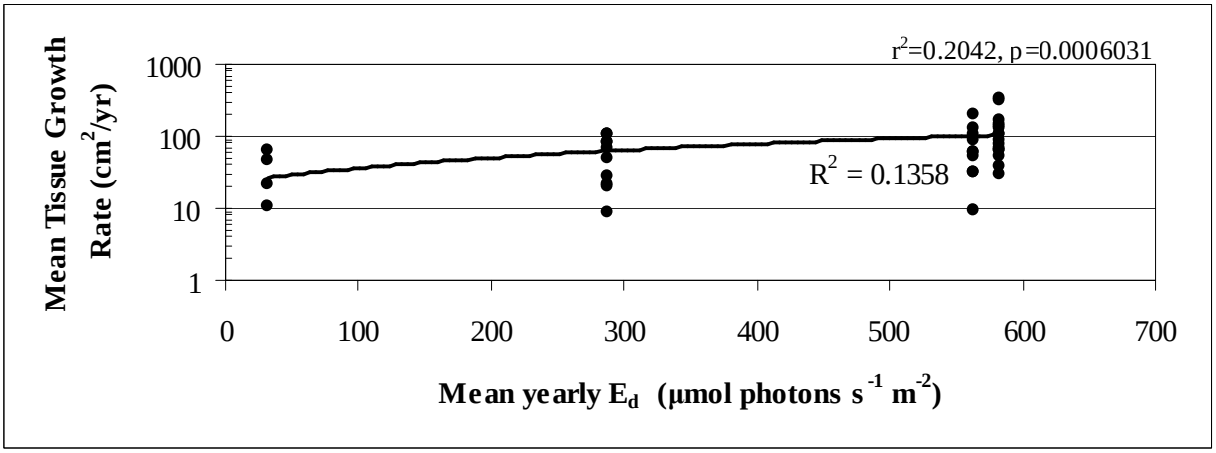

Figure 3.11. Correlation between mean tissue growth rate of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d) calculated for each treatment zone.

3.4.1.2. Skeletal Extension Rate (SER, cm/yr)

A decrease in SER (cm/yr) with decreasing irradiance across treatment zones is evident in Figure 3.12 from longitudinal sections of the skeleton of transplanted and control colonies of *S. siderea*. Mean SER was significantly lower for transplanted colonies in the 0 m and 3m zone ($p<0.0001$, One-Way ANOVA, Appendix IV.1.2) than for transplanted and control colonies in the 10 m and 50 m zones (Figure 3.13). Transplanted colonies in the 10 m zone, and transplanted and control colonies in the 50 m zone had similar SER throughout the study ($p>0.05$, Tukey Test). There was a significant positive correlation (Figure 3.14) between SER and irradiance ($r=0.5637$, $p=1.2541E-023$, $n=280$), thus, a significant reduction in linear skeletal extension occurred along with a decrease in irradiance across treatment zones.

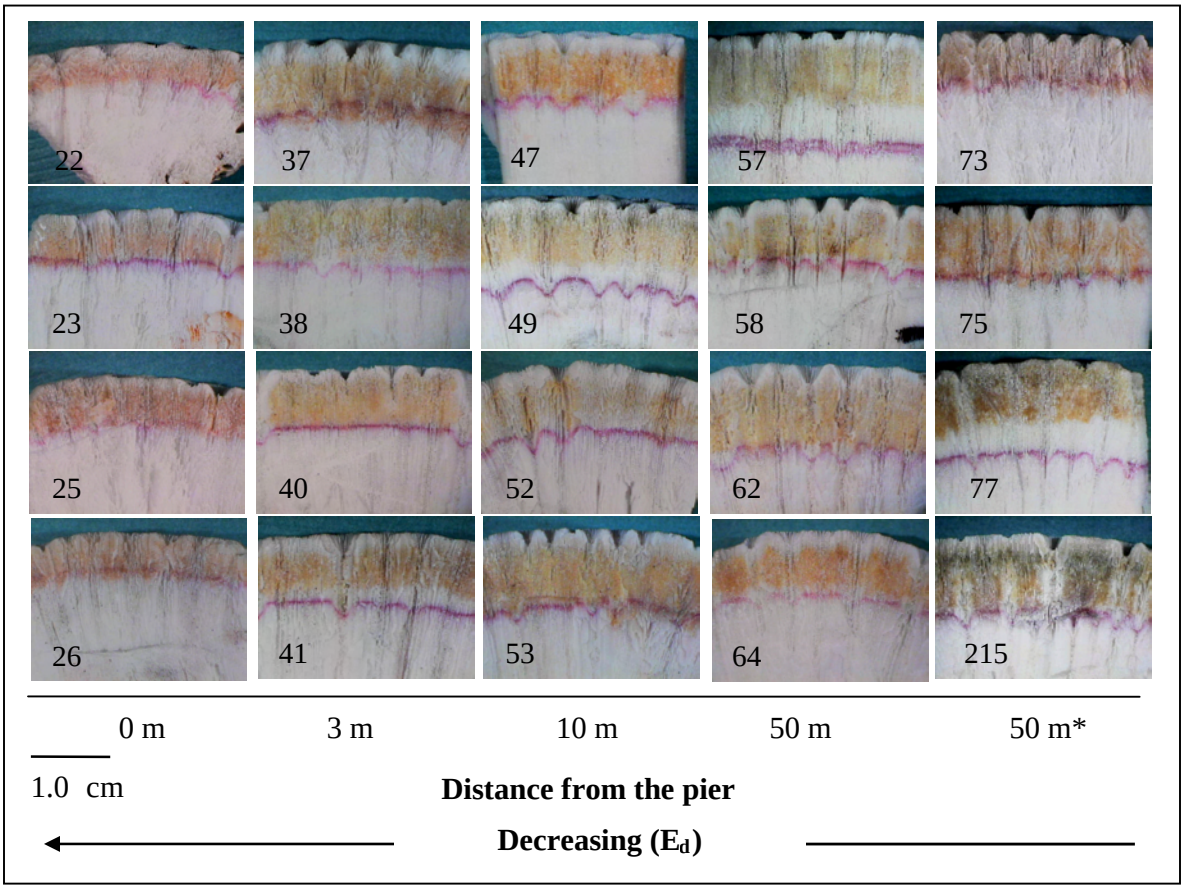

Figure 3.12. Photos (0.7x) of transplanted and control colonies of *S. siderea* (identified with numbers) showing skeletal extension variations with decreasing irradiance (E_d) due to the pier shadow. Colonies were sampled after sixteen-month following staining with Alizarin Red S (red mark on skeleton). 50 m* = control colonies in the 50 m zone.

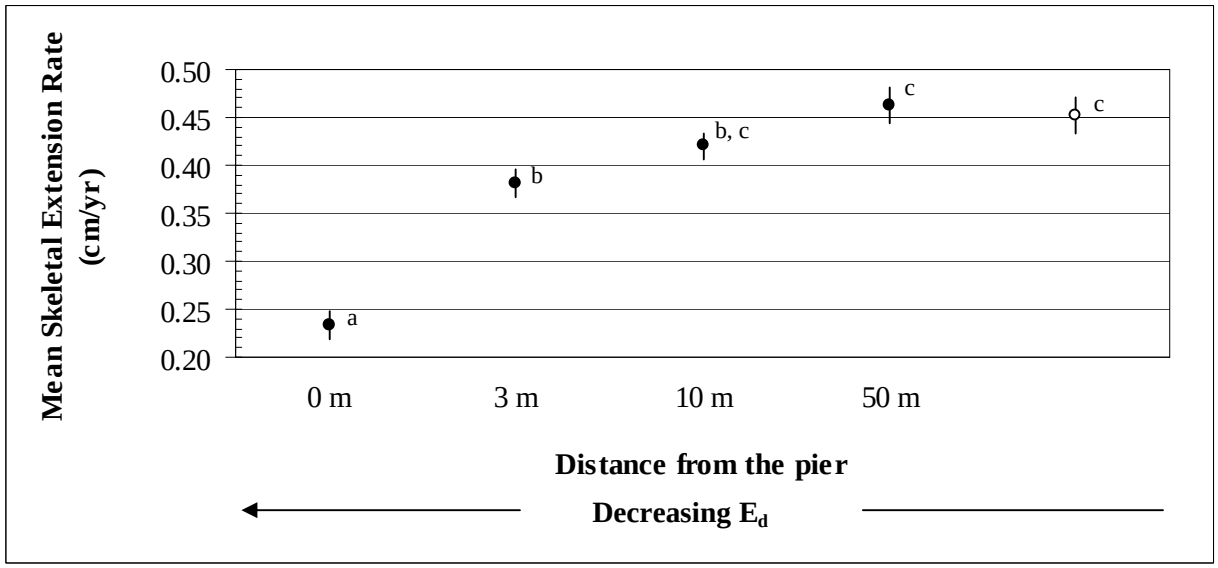

Figure 3.13. Mean skeletal extension rate (cm/yr) and standard error of transplanted and control colonies of *S. siderea* with decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

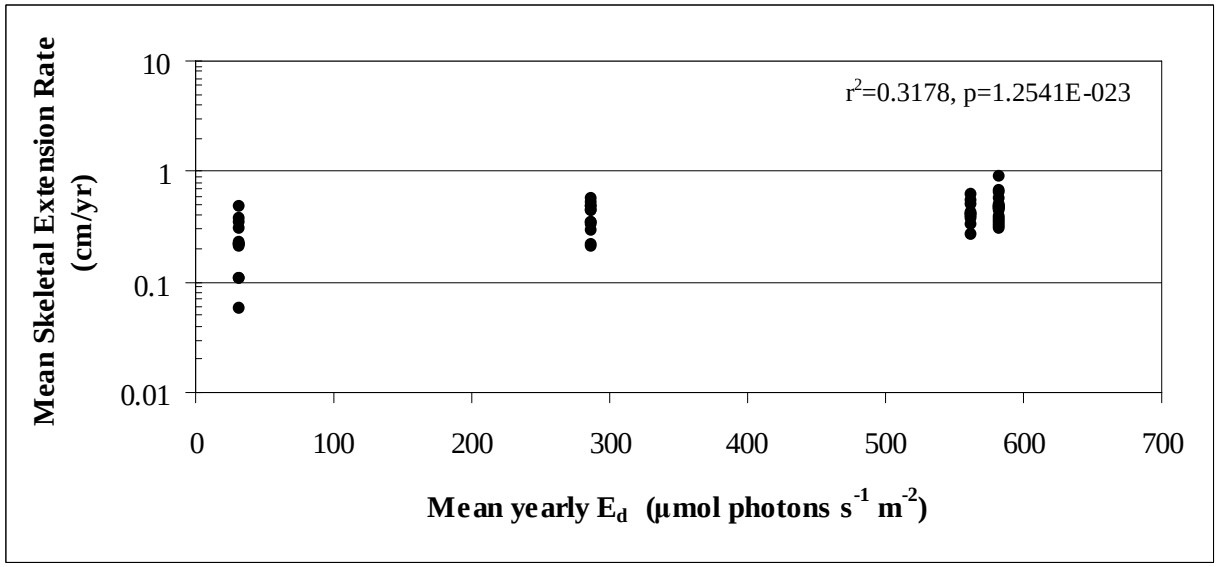

Figure 3.14. Correlation between mean skeletal extension rate of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.1.3. Skeletal Density (SkD, g/cm^3)

Mean SkD (g/cm^3) showed low variations among transplanted and control colonies of *S. siderea* (Figure 3.15). Mean SkD of transplanted and control colonies did not vary significantly across treatment zones (p=0.9386, One-Way ANOVA, Appendix IV.1.3). No significant correlation was found between SkD and irradiance (r= -0.08251, p=0.4394, n=96), suggesting that skeletal density was independent of changes in irradiance produced by the pier-shadow (Figure 3.16).

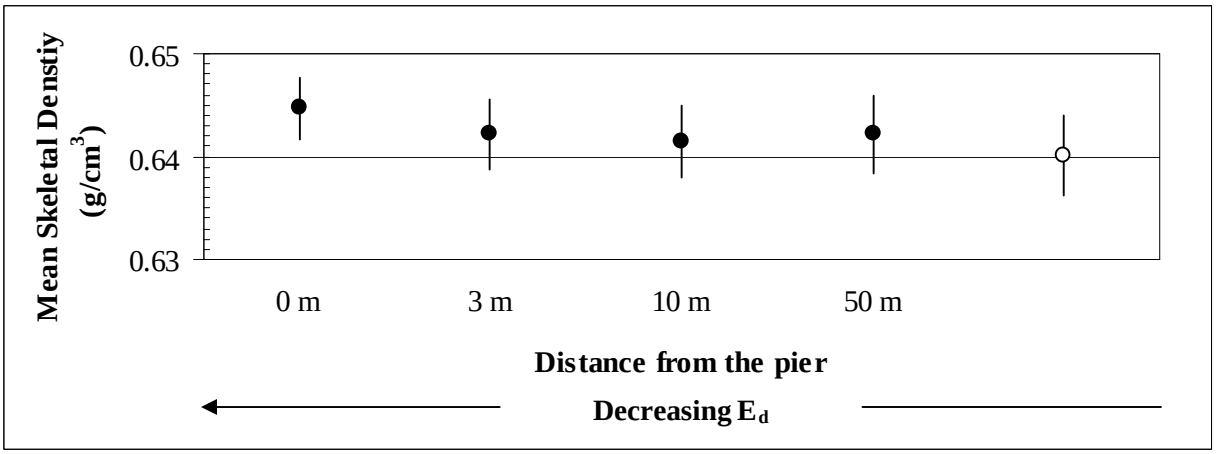

Figure 3.15. Mean skeletal density (g/cm^3) and standard error calculated for transplanted and control colonies of *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone.

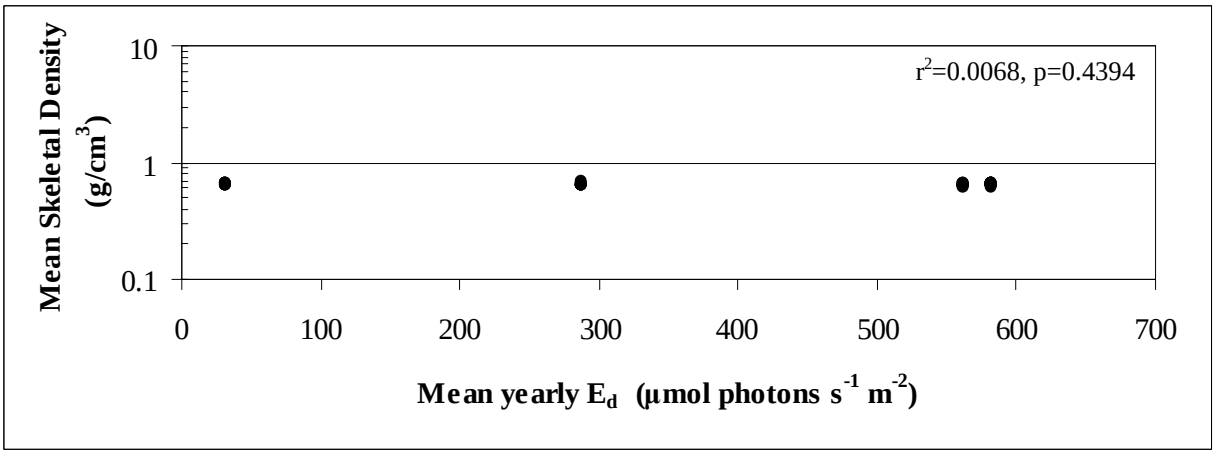

Figure 3.16. Correlation between mean skeletal density of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.1.4. Relative Calcification Rate (RCR, g/cm^2/yr)

Mean RCR (g/cm^2/yr) of *S. siderea* in the 0 m zone was significantly lower ($p<0.0001$, One-Way ANOVA, Appendix IV.1.4) than in the other treatment zones (Figure 3.17). Even though there is no significant differences among the 3 m, 10 m, and 50 m zones ($p>0.05$, Tukey Test), a significant positive correlation was found between RCR and irradiance ($r=0.5298$, $p=0.00000007896$, $n=96$) (Figure 3.18), suggesting that calcification might have a tendency to decrease to some extent due to changes in irradiance caused by the pier shadow.

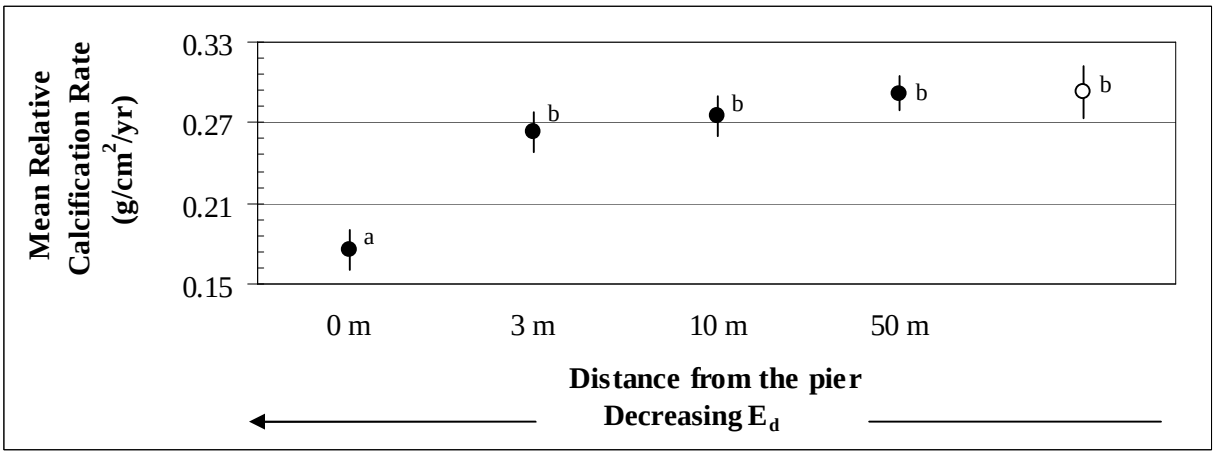

Figure 3.17. Mean relative calcification rate (g/cm^2/yr) and standard error calculated for *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

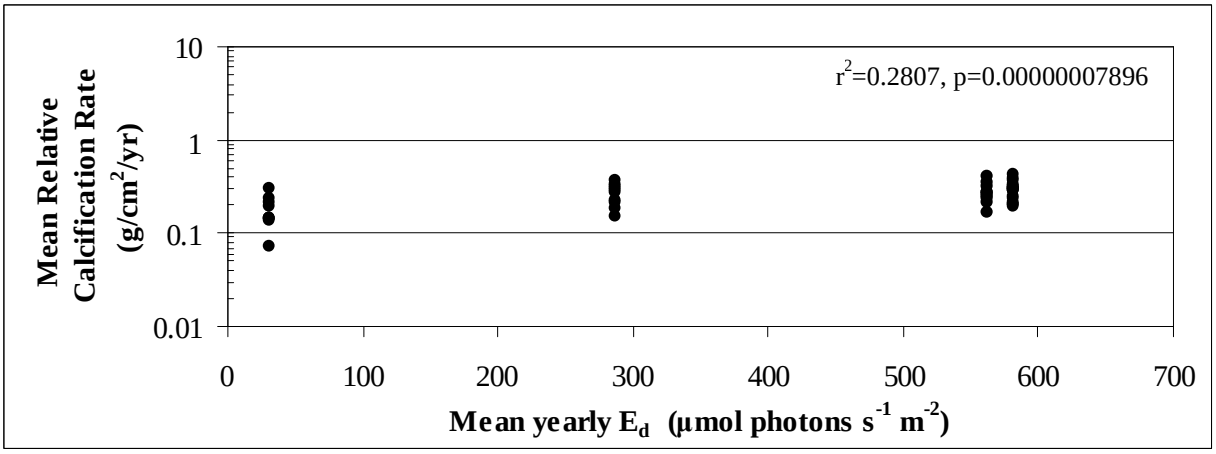

Figure 3.18. Correlation between mean relative calcification rate of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.1.5. Zooxanthellae Population Density (ZD)

Mean ZD (cells x $10^3/mm^2$) was significantly lower for transplanted and control colonies in the 50 m zone ($p=0.0330$, One-Way ANOVA, Appendix IV.1.5) than for colonies in the other treatment zones (Figure 3.19). There was a significant negative correlation (Figure 3.20) between irradiance and ZD ($r=-0.1325$, $p=0.02042$, $n=324$) implying that zooxanthellae densities increased to cope with a decrease in irradiance due to the pier shadow.

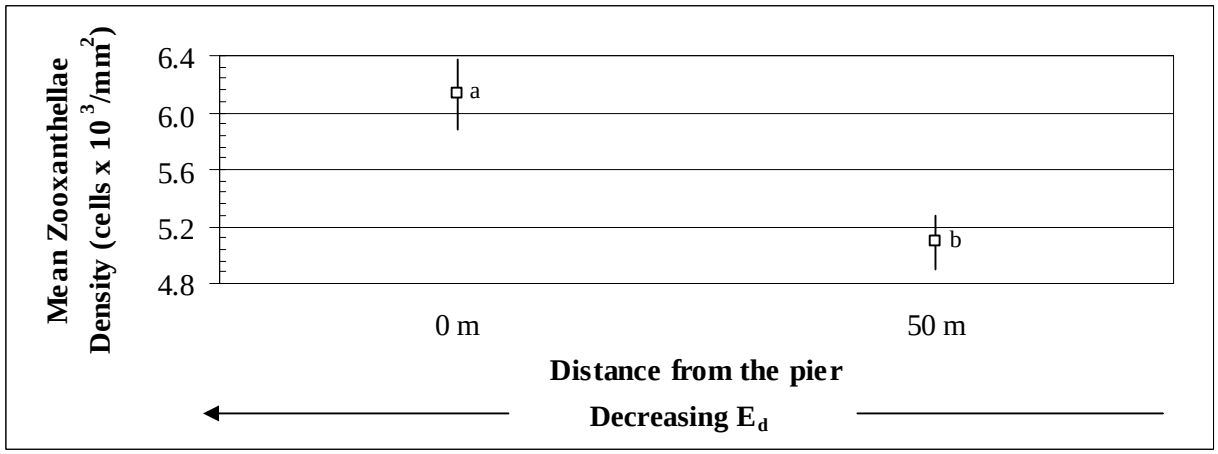

Figure 3.19. Mean zooxanthellae density (cells x $10^3/mm^2$) and standard error of *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

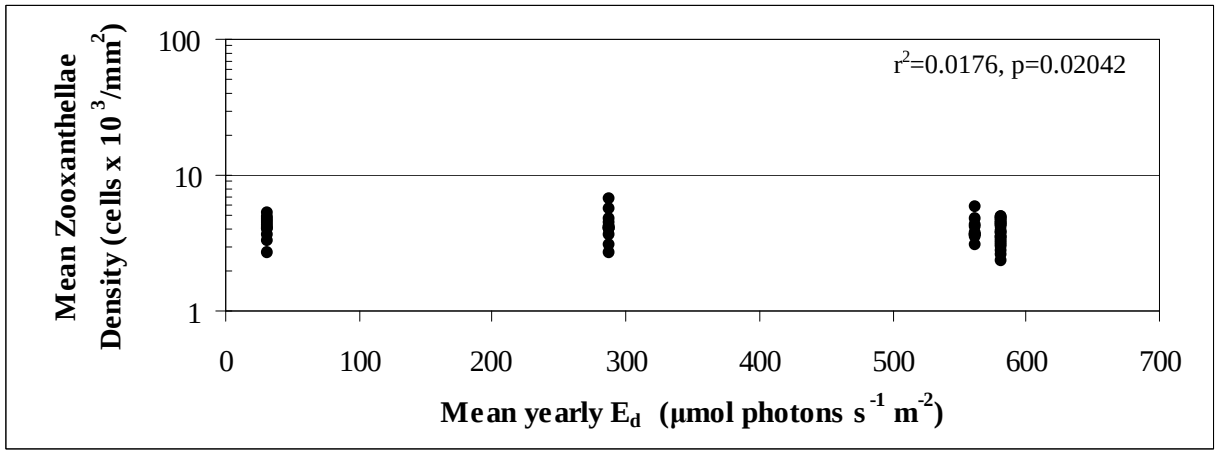

Figure 3.20. Correlation between mean zooxanthellae density of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.1.6. Gender determination

As a result of randomly selected colonies of *S. siderea* for transplanting and for controls, genders were not equally distributed across treatment zones at the pier (Table 3.2). The 3 m treatment zone had the least amount of colonies with oocytes (25%); three colonies in the 0 m zone were immature (25%). However, for all transplanted and control colonies of *S. siderea*, sex ratio was 1:1.

Table 3.2. Number of colonies of *S. siderea* bearing oocytes (F), spermaries (M), or immature (I) in each treatment zone at the pier, determined by histological procedures. Percentage within treatment zones is shown in parenthesis.

Treatment zones	F (%)	M (%)	I (%)
0 m	6 (50)	3 (25)	3 (25)
3 m	3 (25)	9 (75)	0 (0)
10 m	6 (60)	4 (40)	0 (0)
50 m	5 (42)	7 (58)	0 (0)
50 m*	6 (55)	5 (45)	0 (0)

50 m* = control colonies in the 50 m zone.

The criterion used to classify oocytes and spermaries developmental stages of *S. siderea* were that suggested by Szmant-Froelich et al. (1985) (see Appendix III.2). Oocytes from transplanted and control colonies of *S. siderea* were in stage IV. Although fertility was not measured in this study, all colonies of *S. siderea* with spermaries were found to be in the stage V (Figure 3.21), ready to spawn, at the moment of sampling (first two weeks of August 2001).

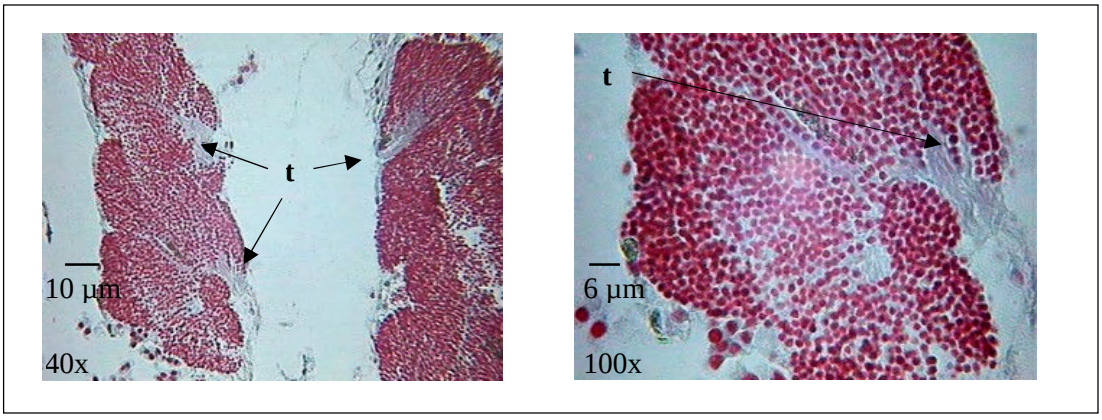

Figure 3.21. Photo of *S. siderea* (#67 in the 50 m zone) showing spermatocytes in stage V, specifically, spermatocytes with tail (t), ready to spawn, sensu Szmant-Froelich et al. (1985).

The smallest reproductive size (measurements done before sampling, on July 2001) for *S. siderea* colonies with spermaries was # 28 (96 cm^2) and for colonies with oocytes was # 22 (66 cm^2) both located in the 0 m zone. Mesenterial fecundity could not be determined for # 32 (99 cm^2) since only one oocyte was found in stage V; consequently, this colony was excluded from statistical analyses. Only three colonies in the 0 m zone (# 21, 26, and 29) were immature (stage 0) where no gametogenesis had occurred (Szmant-Froelich et al., 1985). Size seemed not to be the factor contributing to reproductive immaturity at least for colonies # 21 and 26, since they were over puberty size (Soong, 1993) (228, 308 cm^2, respectively), this was not the case with # 29 (75 cm^2). Colony # 22 had a much smaller size than puberty (66 vs. 110 cm^2) and was reproductive.

3.4.1.7. Mesenterial Fecundity (MF)

Mean MF was significantly lower in the 0 m and 3 m zone ($p<0.0001$, ANOVA, Appendix IV.1.6) than in the other zones (Figure 3.22). Colonies had similar fecundity in the 10 m and 50 m zones, but fecundity was lower in the 0 m than in the 3 m zone ($p<0.05$, Tukey Test). There was a significant positive correlation (Figure 3.23) between irradiance and MF ($r=0.7049$, $p=1.3824E-011$, $n=72$), thus, oocytes/mesentery decreased due to changes in irradiance caused by the pier shadow.

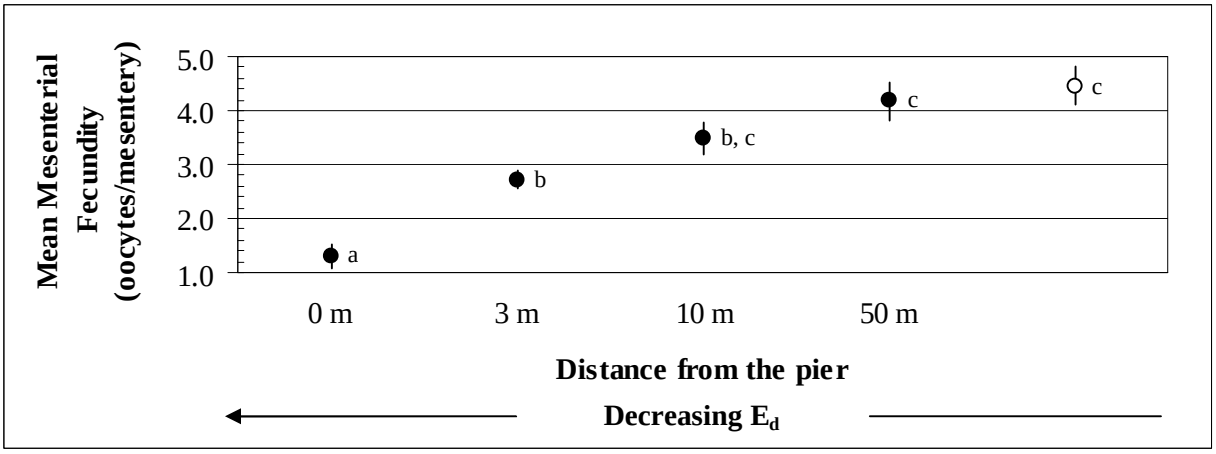

Figure 3.22. Mean mesenterial fecundity and standard error of *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

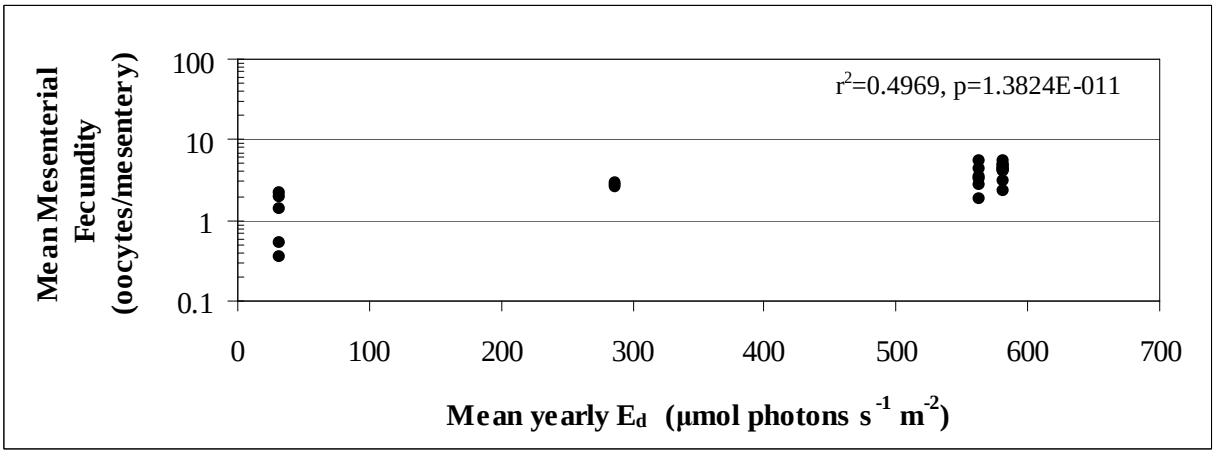

Figure 3.23. Correlation between mean mesenterial fecundity of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.1.8. Oocyte Diameter (OD)

Mean OD (µm) of *S. siderea* was significantly higher in the 0 m and 3 m zones ($p<0.0001$, One-Way ANOVA, Appendix IV.1.7) than in the 10 m and 50 m zones (Figure 3.24). Transplanted colonies in the 0 m and 3 m zones were similar ($p=0.3093$, Tukey Test). A significant negative correlation (Figure 2.25) was found between irradiance and mean OD ($r=-0.2918$, $p=1.4519E-026$, $n=1341$), implying that an increase in oocyte diameter occurred due to the shadow of the pier, which decreased irradiance across treatment zones.

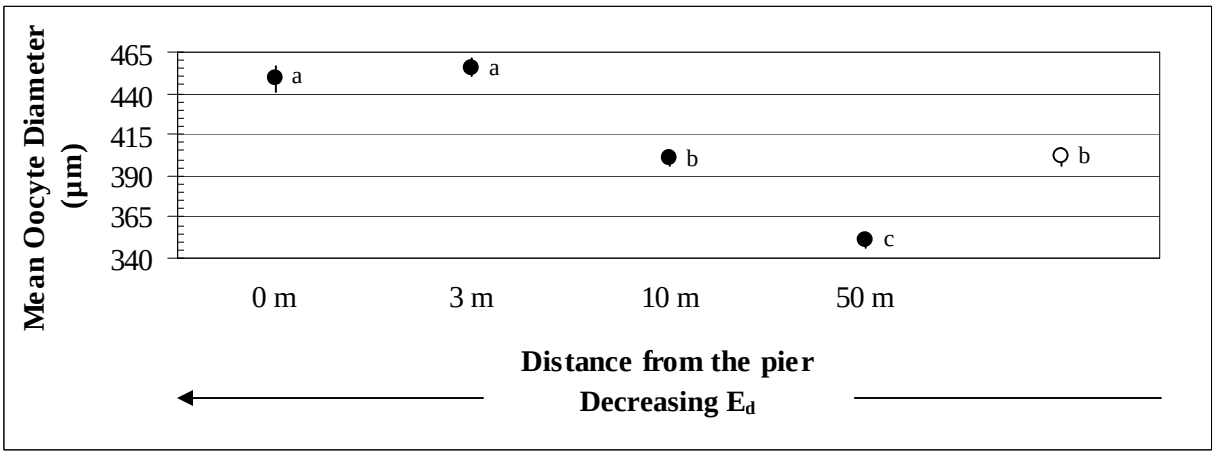

Figure 3.24. Mean oocyte diameter (µm) and standard error of *S. siderea* in relation to decreasing irradiance (E_d) across treatment zones. Dark circles represent transplanted colonies; open circles represent control colonies in the 50 m zone. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

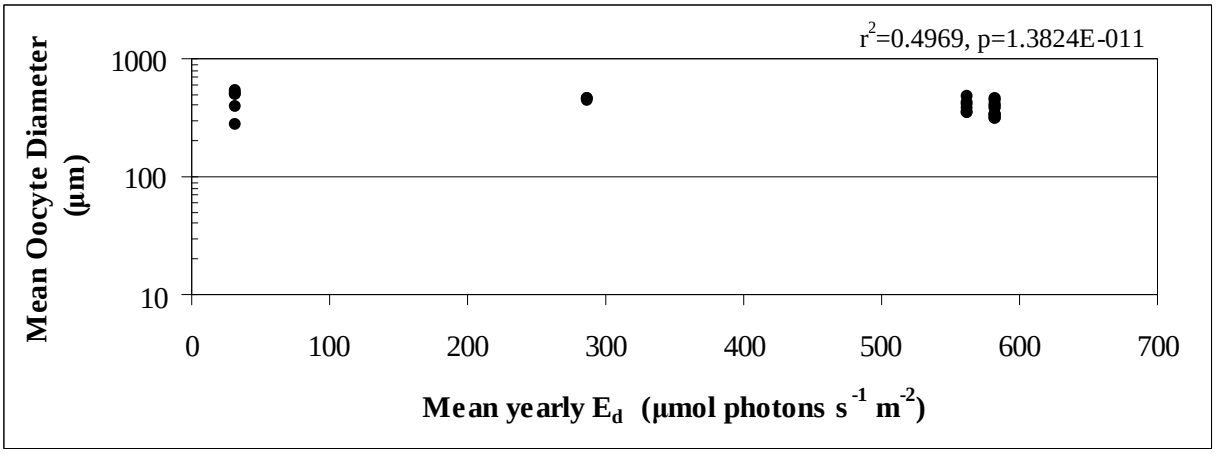

Figure 3.25. Correlation between mean oocyte diameter of transplanted and control colonies of *S. siderea* and mean yearly irradiance (E_d).

3.4.2. *D. clivosa*

Colonies selected for the study were over 100 cm^2 (LCT, cm^2) of surface tissue area (Table 3.3). All samples from *D. clivosa* were hermaphrodite with oocytes and spermaries in the same mesentery but not intermingled. To classify the developmental stages of oocytes and spermaries of *D. clivosa*, the criterion suggested by Szmant-Froelich et al. (1985) was used (see Appendix III.2). Oocytes from colonies of *D. clivosa* were in stage IV, and spermaries were found to be in the stage V.

Table 3.3. Mean (±standard deviations) colony size measured as live coral surface tissue (LCT - cm^2) of *D. clivosa* done on July 2001.

Distance from the pier	N	LCT (cm^2) July 2001
0 m	5	1257.80 (309.40)
50 m	4	1222.70 (840.80)

3.4.2.1. Zooxanthellae Population Density (ZD)

Mean ZD (cells x $10^3/mm^2$) of *D. clivosa* was significantly higher in the 0 m ($p=0.0018$, One-Way ANOVA, Appendix IV.2.1), than in the 50 m zone (Figure 3.26), implying that zooxanthellae densities increased as a response to the pier shadow; however, only two treatments and a small sample size were used (Table 3.3).

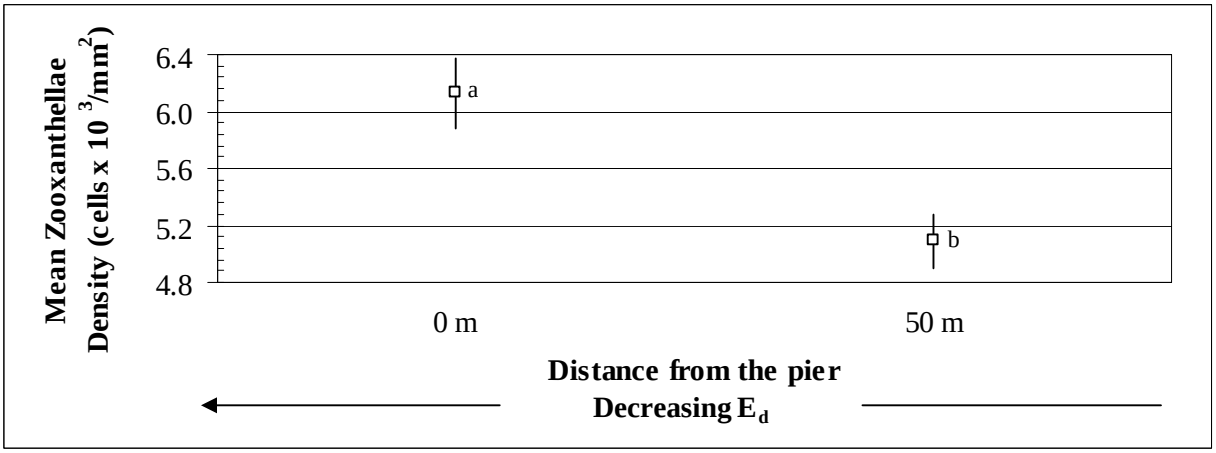

Figure 3.26. Mean zooxanthellae density (cells x $10^3/mm^2$) and standard error for *D. clivosa* in relation to decreasing irradiance (E_d) across treatment zones. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

3.4.2.2. Mesenterial Fecundity (MF)

Mean MF of *D. clivosa* was significantly lower in the 0 m zone ($p=0.0417$, One-Way ANOVA, Appendix IV.2.2) than in the 50 m zone (Figure 3.27), implying a significant negative effect on the production of oocytes per mesentery possibly due to lower resources available for reproduction because of decreasing irradiance across treatment zones.

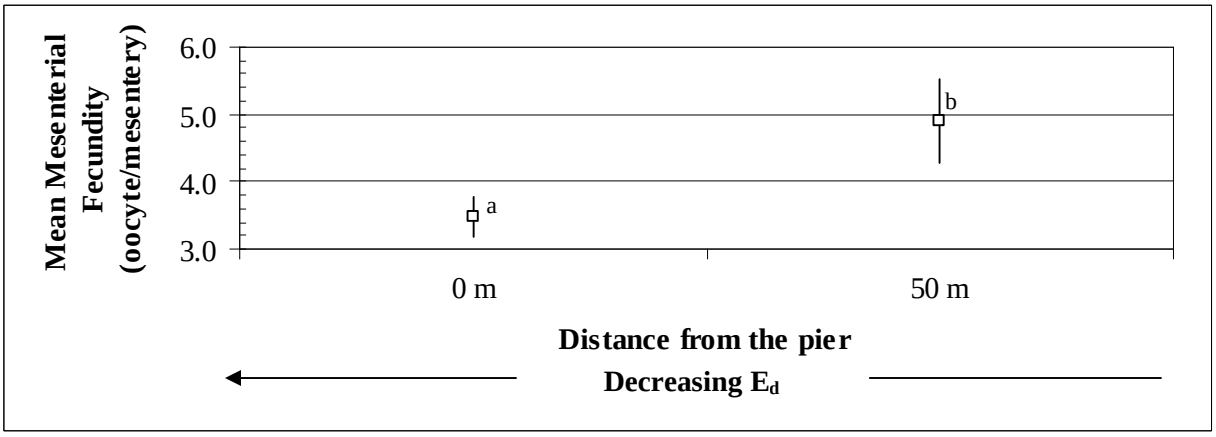

Figure 3.27. Mean mesenterial fecundity and standard error for *D. clivosa* in relation to decreasing irradiance (E_d) due to the pier shadow. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

3.4.2.3. Oocyte Diameter (OD, µm)

Mean OD (µm) of *D. clivosa* was significantly higher in the 0 m ($p<0.0001$, Mann-Whitney Rank Sum Test, Appendix IV.2.3) than in the 50 m zone (Figure 3.28), implying that a significant negative effect on the diameter of oocytes perhaps was due to decreasing irradiance across treatment zones.

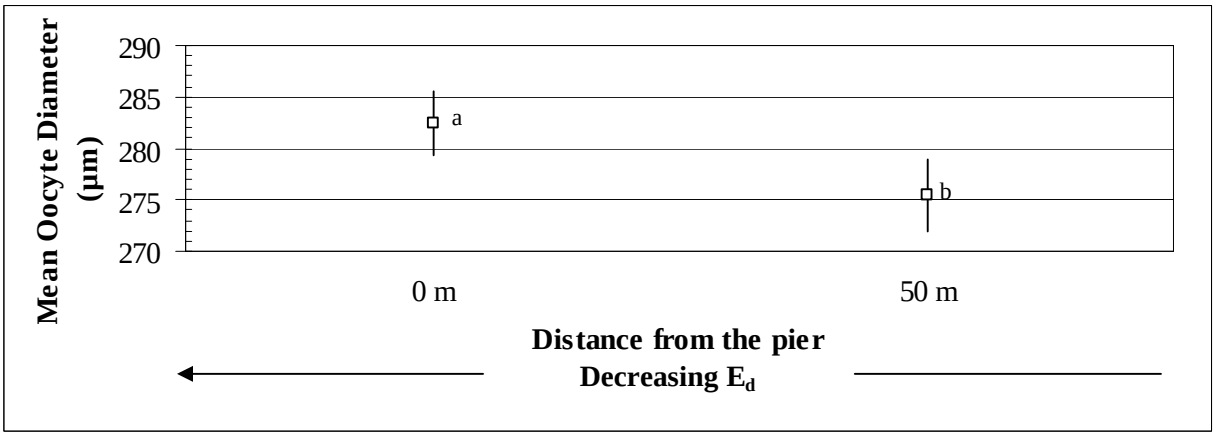

Figure 3.28. Mean oocyte diameter (µm) and standard error of *D. clivosa* in relation to decreasing irradiance (E_d) due to the pier shadow. Treatment zones with different letters were significantly different ($p<0.05$, Tukey Test).

3.4.3. Relationship among biological characteristic within treatment zones

When exploring the relationship among biological characteristics of *S. siderea* within treatment zones, a significant positive correlation (Figure 3.29) was found between SER and RCR in all zones ($r=0.9$, $p<0.0001$, $n=18$ to 20) (Appendix V.1.1 - V.1.5). A significant negative correlation (Figure 3.30) was found between SkD and SER in the 0 m ($r=-0.8953$, $p=0.0000005221$, $n=18$, Appendix V.1.1) and 3 m zones ($r=-0.5345$, $p=0.01518$, $n=20$, Appendix V.1.2), and between SkD and RCR in the 0 m ($r=-0.8644$, $p=0.000003725$, $n=18$, Appendix V.1.1) and 3 m zones ($r=-0.4735$, $p=0.03497$, $n=20$, Appendix V.1.2) (Figure 3.30).

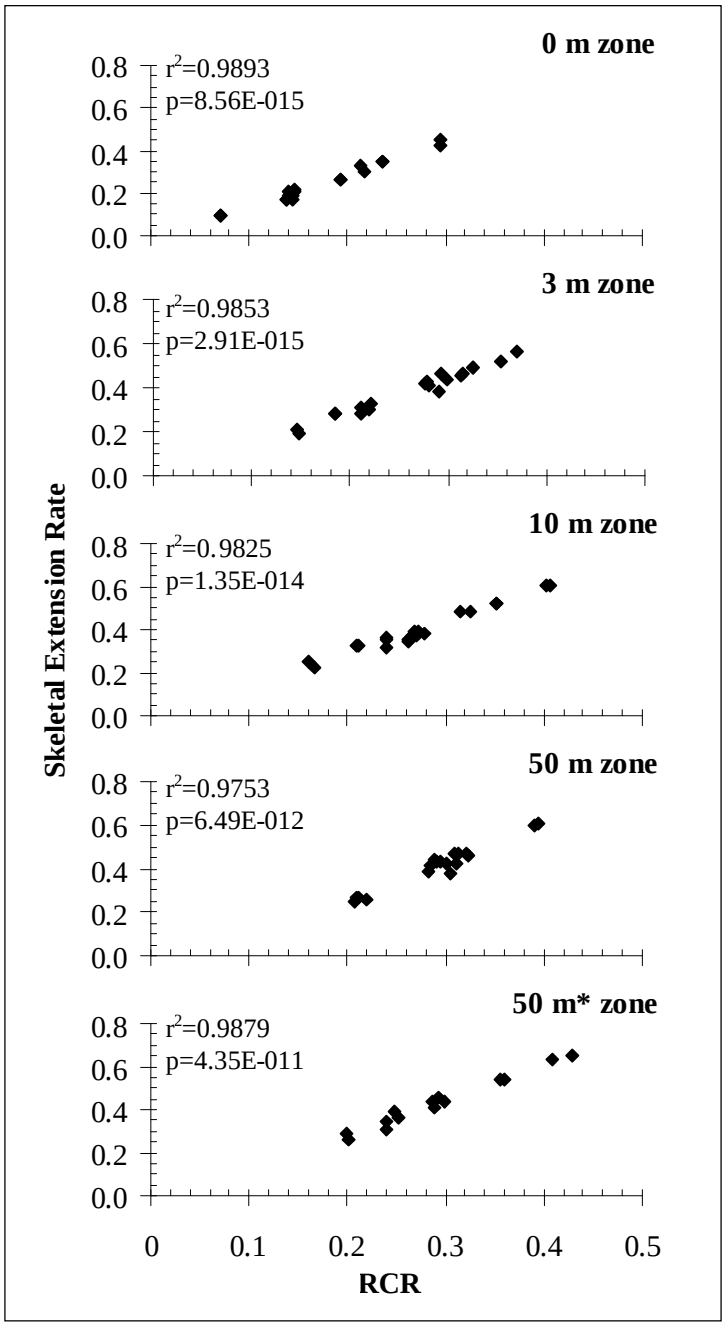

Figure 3.29. Correlation between mean skeletal extension rate (cm^2/yr) and relative calcification rate (RCR, g/cm^2/yr) of transplanted and control colonies of *S. siderea* in each treatment zone. 50 m* represents control colonies in the 50 m zone.

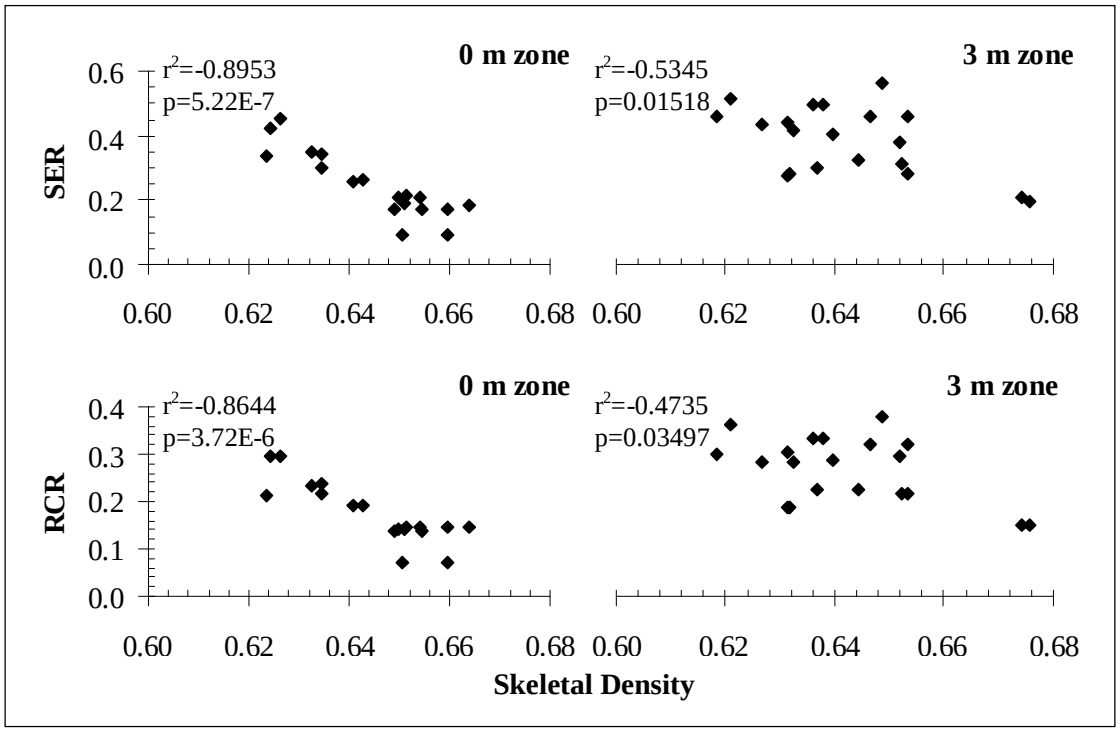

Figure 3.30. Correlation between mean skeletal density (g/cm^3) and mean skeletal extension rate (SER, cm^2/yr) (top), and relative calcification rate (RCR, g/cm^2/yr) (bottom) of transplanted colonies of *S. siderea* in the 0 m and 3 m zone.

Other significant relationships among biological characteristics where in the 0 m zone between growth and reproduction (Figure 3.31), such as between SER and OD (r= -0.5762, p=0.002572, n=25), between RCR and MF (r=-0.8204, p=0.04551, n=6), and between RCR and OD (r=-0.7921, p=0.06032, n=6), although some of the correlations have small sampling size they imply that growth and reproduction might compete for available resources (Harrison and Wallace, 1990).

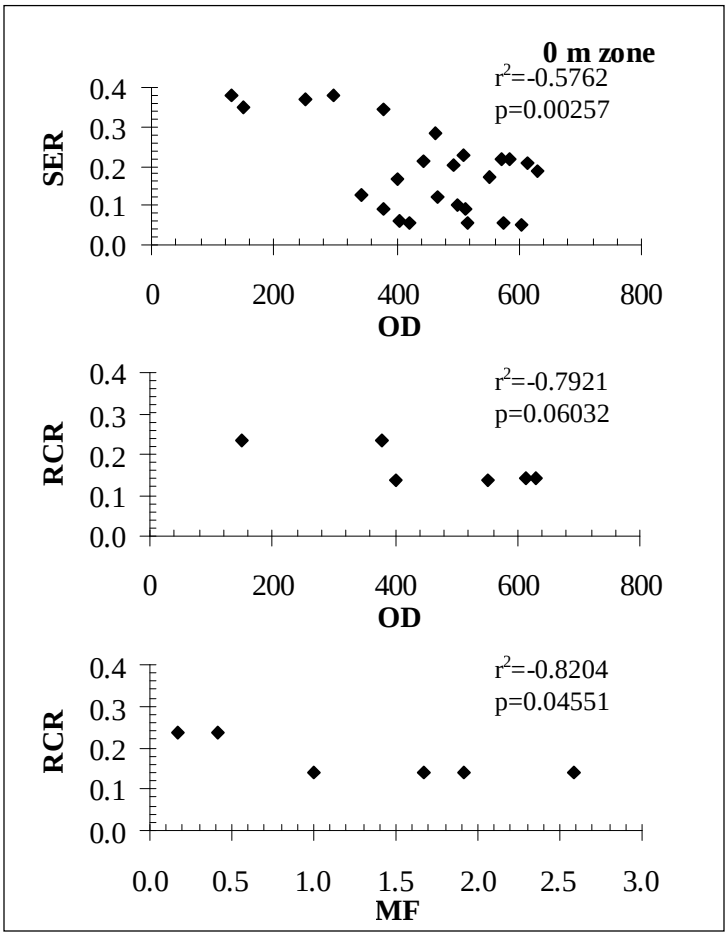

Figure 3.31. Correlation between mean skeletal extension rate (cm^2/yr) and oocyte diameter (μm) and mesenterial fecundity (oocytes/mesentery) (top), and between relative calcification rate (g/cm^2/yr) and mesenterial fecundity (oocytes/mesentery) (bottom) of transplanted colonies of *S. siderea* in the 0 m zone.

A significant positive correlation was found between SkD and MF (r=0.8330, p=0.03953, n=6), and between SkD and OD (r=0.8461, p=0.03372, n=6) in the 0 m zone (Figure 3.32), which suggests that growth and calcification are reduced when energy is allocated to reproduction. However, in the 10 m zone (Appendix V.1.3) the results imply that resources (i.e. irradiance) were available for both grow and reproduction, since a significant positive correlation was found between MF and SER (r=0.6983, p=0.001267, n=18), and MF and RCR (r= 0.6993, p=0.01137, n=12) (Figure 3.33). A negative correlation between OD and SER (r=-0.4550, p=0.01152, n=30), and between OD and RCR (r=-0.7056, p=0.01035, n=12) in the 10 m (Appendix V.1.C), and between OD and SER of control colonies in the 50 m zone (r=-

0.5791, p=0.02369, n=20) (Appendix V.1.5) indirectly suggest constrains in oocyte size due to mesenterial capacity (Figure 3.34).

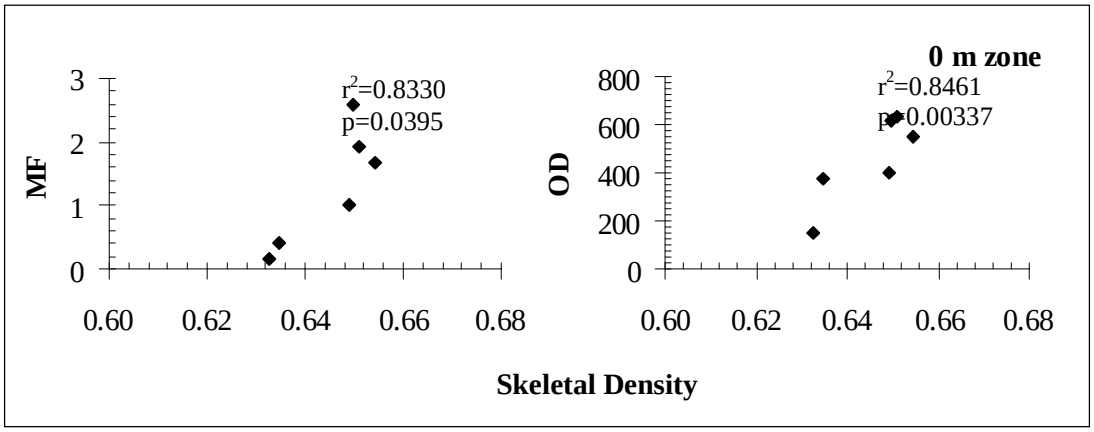

Figure 3.32. Correlation between mean skeletal density (g/cm^3) and mesenterial fecundity (MF, oocytes / mesentery) and oocyte diameter (OD, µm) of transplanted colonies of *S. siderea* in the 0 m zone.

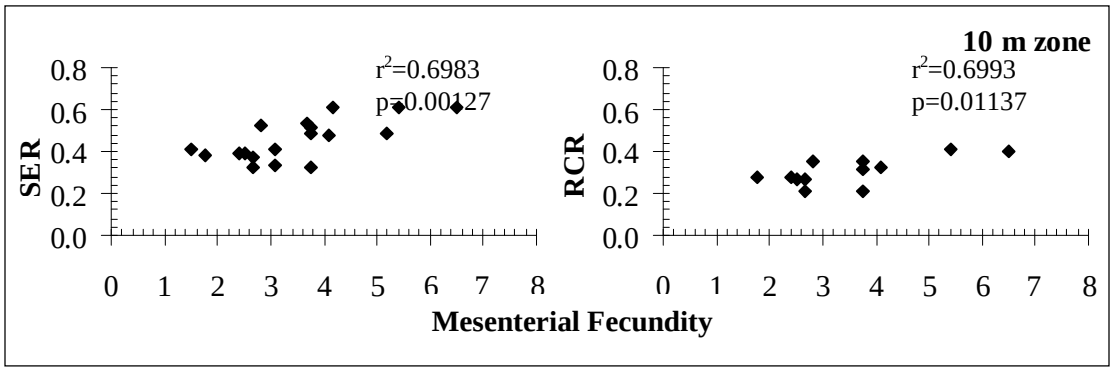

Figure 3.33. Correlation between mesenterial fecundity (oocytes/mesentery) and mean skeletal extension rate (SER, cm^2/yr) and relative calcification rate (RCR, g/cm^2/yr) of transplanted colonies of *S. siderea* in the 10 m zone.

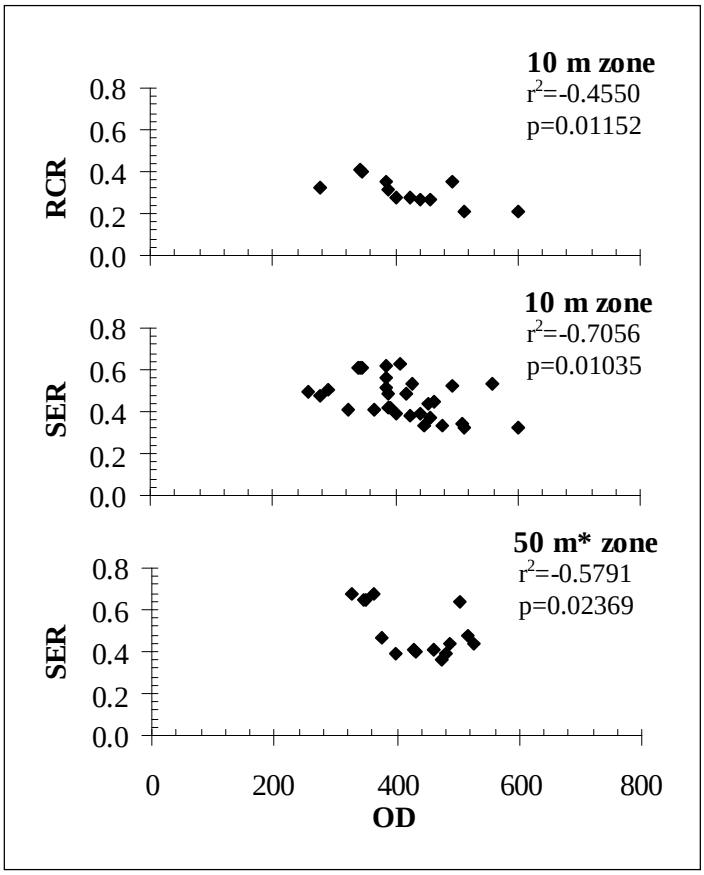

Figure 3.34. Correlation between oocyte diameter (µm) and relative calcification rate (g/cm^2/yr) and mean skeletal extension rate (cm^2/yr) of transplanted colonies of *S. siderea* in the 10 m zone, and control colonies (50 m*) in the 50 m zone.

3.5. DISCUSSION

This chapter highlights the importance of irradiance to some aspects of the ecology and biology of two Caribbean coral reef species. The lost of live coral tissue of transplanted colonies of *S. siderea* in the 0 m zone indicated that low irradiance might not be providing enough energy (mean monthly irradiance from approaching 0 to less than 100 µmol photons s^{-1} m^{-2}) to support new tissue growth and/or outcompete other sessile organisms growing on the surface tissue. Even though this study did not quantify the organisms overgrowing the colonies of *S. siderea*, it was observed that some colonies under the pier were overgrown by sponges, green and coralline algae, while colonies on the other treatment zones were not. Studies have found that shading might be beneficial for other sessile invertebrates such

as subtidal epibiotic assemblages (Glasby, 1999a). For instance, epibiotic assemblages underneath overwater structures were found to differ significantly from those on adjacent natural reefs (Connell and Glasby, 1999; Glasby, 1999b). As shown in this study, the pier shadow caused a significant decrease in irradiance up to 10 m away, which could have affected tissue and skeletal growth of *S. siderea* colonies. This might have affected their recovery, tissue regeneration, and competitive ability perhaps due to a reduction in energy from photosynthesis. These results might agree to those obtained by Nagelkerken et al. (1999), who found that recovery of artificial lesions of scleractinian corals were negatively related to water depth, implying that a decrease in irradiance affected the availability of energy from photosynthesis, which consequently might have affected tissue regeneration.

Skeletal extension, skeletal density, and calcification rate were three parameters used in this study to characterize coral growth under a gradient of irradiance due to pier shading. Only a few studies in the Caribbean have examined linear growth rates of *S. siderea* (Huston, 1985; Hubbard and Scaturo, 1985; Guzmán et al., 1991; Guzmán and Tudhope, 1998; Torres and Morelock, 2002), but unlike this study, they used X-radiographic measurement of annual density bands to determine skeletal extension rates. Although none of these previous studies on *S. siderea* measured irradiance, some used depth as a proxy for light and reported a negative correlation between *S. siderea* growth rate and depth (Huston, 1985; Hubbard and Scaturo, 1985). These results are similar to the results from this study where a decrease in skeletal extension was correlated with decreasing irradiance due to shading by the pier. Few studies on skeletal density of *S. siderea* have been done, however, Jiménez and Cortés (1993) suggested a positive correlation between skeletal density (from 1.6 to 1.9 g/cm^3) and increasing sedimentation in the Caribbean coast of Costa Rica; however, sedimentation was inferred from qualitative observations and no quantitative approach was done. Although their results could not be compared with this study because sedimentation did not vary across treatment zones, skeletal densities of *S. siderea* were in general lower (0.64 g/cm^3) than those reported by Jiménez and Cortés (1993). Skeletal densities were independent from changes in irradiance. Relative calcification rates of *S. siderea* found in this study were positively related to irradiance. Similar results in calcification rates were found for *Porites compressa* by Marubini et al.

(2001) in Hawaii, although they used depth as a proxy for light. Meesters et al. (1994) also found similar results for *M. annularis* in the Caribbean, a linear relationship between calcification and the amount of irradiance received by a colony.

Changes in irradiance have shown to trigger morphological and physiological changes in the zooxanthellae symbiont, although, the mechanisms to maximize the light harvesting capacity may vary. This study showed that and increase in zooxanthellae densities occurred as a biological response, in both species studied, to decreasing irradiance across treatment zones. Similarly, changes in zooxanthellae densities with depth have been observed in other scleractinian coral species as well (Drew, 1972; Dustan, 1979; Titlyanov et al., 2000, 2001a). Acclimation to changes in light intensity involves various responses that are not mutually exclusive: changes in the concentration of photosynthetic pigments (Falkowski and Dubinsky, 1981; Dustan, 1982; Porter et al., 1984), increase in the size of the photosynthetic unit (PSU) (Dustan, 1982), changes in zooxanthellae population densities (Drew, 1972; Titlyanov et al., 2000, 2001a), and morphological change of the coral colony (Barnes, 1973). Although the study of photosynthetic pigments was beyond the scope of this study, future research on *S. siderea* could also consider changes at the molecular level in relation to the decreasing irradiance, i.e. zooxanthellae pigments concentration.

Results of this study confirmed the gonochoric sexual pattern and sex ratio (1:1) reported for *S. siderea* for the Caribbean (Szmant, 1986; Soong, 1991; Guzmán and Holst, 1993), and the hermaphroditic sexual pattern of *D. clivosa* reported for the Caribbean (Soong, 1991; Vargas-Toledo, 2002) with oocytes and spermaries in the same mesentery, but not intermingled.

Colony size in corals is an important species characteristic, which controls many life history traits like reproduction (Connell, 1973). In scleractinian coral species, a minimum size must be attained before sexual reproduction can occur (Kojis and Quinn, 1985; Szmant-Froelich, 1985; Soong and Lang, 1992; Soong, 1993). Soong and Lang (1992) reported puberty size (the colony size beyond which more than 90% of the colonies becomes fertile) for *S. siderea* to be 156 cm^2; however, Soong (1993) found later that maturity or puberty size could range from 110 to 414 cm^2 (95% confidence interval). In this study, the

smallest reproductive size for transplanted colonies of *S. siderea* was 66 cm^2, below the minimum size reported before in the literature. Moreover, three colonies of *S. siderea* were found to be below the minimum size reported for reproductive colonies of *S. siderea*, two colonies with oocytes (66, and 99 cm^2) and one colony with spermaries (96 cm^2); all three were found under the pier, at the 0 m zone. Even though colonies of *S. siderea* were selected with similar dimensions, size and condition, it is a difficult task to determine if they were young colonies or if they came from older colonies that suffered partial mortality, fusion or fission of tissue; this might have influenced minimum breeding size found in this study (Kojis and Quinn, 1985). Another factor to consider is the increase in zooxanthellae densities found in the 0 m zone and their contribution to the nutritional requirements of the coral. Rinkevich (1989) found that energy requirements for planula production in the hermatypic coral *Stylophora pistillata* were supported by translocation of products from zooxanthellae photosynthesis. Wellington and Glynn (1983) found that coral growth and calcification are reduced when energy is allocated to reproduction. At the 0 m zone, results showed a significant increase in zooxanthellae densities compared to the other treatment zones, which could suggest that reproduction might have occurred due to allocation of energy from the zooxanthellae, at least during this study, considering that this zone was not in complete darkness, had the smallest reproductive size, and significantly lower growth than the other treatment zones. Future research could consider long-term studies to investigate these relationships further.

The reproductive parameters examined in this study were mesenterial fecundity and oocyte diameter. The results showed that mean mesenterial fecundity of control colonies of *S. siderea* and colonies of *D. clivosa* were comparable to other localities in the Caribbean (Szmant, 1986; Soong, 1991; Guzmán and Holst, 1993; Vargas-Toledo, 2002). However, reduced irradiance seems to have affected negatively mesenterial fecundity of both species studied. Similarly, Kojis and Quinn (1984) reported that decreasing irradiance with depth was the primary factor significantly decreasing fecundity in *Acropora palifera.* A decrease in oocytes/mesentery can have implications in reproductive success of coral species, with less oocytes to be fertilized by spermatocytes, and eventually, fewer recruits contributing to the population, affecting population dynamics and structure.

Oocyte diameters of control colonies of *S. siderea* were different, but similar for *D. clivosa*, to other results reported for the Caribbean (Szmant, 1986; Soong, 1991; Guzmán and Holst, 1993; Vargas-Toledo, 2002). In this study, mean oocyte diameter for control colonies of *S. siderea* was smaller than other reports from Puerto Rico (Szmant, 1986) and Panamá (Soong, 1991; Guzmán and Holst, 1993) for the same species. Mean oocyte diameter reported here for *D. clivosa* (control colonies 50 m from the pier) was comparable with reports from Puerto Rico by Vargas-Toledo (2002), but smaller than reported by Soong (1991) for Panamá. Although conclusions cannot be drawn from only one year of data, oocyte diameters of *S. siderea* (though sample size was small) appeared to show an increase with a decrease in irradiance due to shading by the pier. Oocyte diameter of *S. siderea* transplanted colonies increased gradually from 351 µm (50 m from the pier) to 449 µm (under the pier). An increase in mean oocyte diameter was observed for *Diploria clivosa* from 275 µm (50 m away from the pier) to 282 µm (under the pier), but this was not significant (perhaps due to few samples size and variability introduced by the methodology). Even though this study provided evidence that a decrease in irradiance might have affected oocyte diameters of *S. siderea*, the consequences of larger diameters in coral's oocytes is uncertain. Nevertheless, Bagenal (1971) and Ware (1977) found that larger oocytes in fishes could be an adaptive advantage (due to an increase in yolk reserves) if food supply is sparse or variable, and is likely to increase juvenile survival because of the positive correlation between oocyte size and larval size. They also found that growth rate of fishes increased with increasing egg size, probably due to increased feeding success, better swimming, and larger mouth gapes. Although the literature in coral reproduction is extensive (see reviews from Fadlallah, 1983; Harrison and Wallace, 1990; Richmond and Hunter, 1990; and Fautin, 2002), few studies have investigated the variations in oocyte diameter in relation to light, and how this might affect the reproductive success of the species. Future research might focus on long-term studies to determine the consequences that increased diameters could cause on oocyte viability, fertilization, and planulae development.

Correlations among biological parameters within treatment zones showed an expected positive relationship between skeletal extension and calcification rates since calcification was a product of skeletal

extension and skeletal density, and the latter was not significantly different among treatment zones. significant negative correlations found in this study between skeletal density and skeletal extension, and between skeletal density and calcification in the low irradiance zones (0 m and 3 m), are consistent with other studies that found an increase in skeletal density and decrease in skeletal extension and calcification with depth (Baker and Weber, 1975; Highsmith, 1979, Hughes, 1987), suggesting that transplanted colonies of *S. siderea* in the 0 m and 3 m behave similar to colonies growing in deeper waters where irradiance is low when compared to shallower waters.

Another significant relationship among biological characteristics was between growth and reproduction, which potentially compete for available resources (Harrison and Wallace, 1990). Wellington and Glynn (1983) found similar results for *Pavona gigantea* when a negative correlation was found between skeletal accretion and gamete production. The negative correlation between growth and reproduction of *S. siderea* under the pier (0 m zone) suggests that transplanted colonies in this zone could have been allocating their available resources (from an increase in zooxanthellae densities, but probably limited due to conditions of low irradiance) more to reproduction than to skeletal extension and calcification (growth) during the reproductive cycle parallel to this study. Moreover, the results showed that some reproductive colonies were below the smallest reproductive size reported before in the literature. In addition, previous results from this study showed significantly larger oocyte diameter and lower skeletal extension and calcification under the pier than in other treatment zones.

The results from the 10 m zone suggest that resources (i.e. irradiance and energy from photosynthesis of the zooxanthellae) were available for both grow and reproduction, since a significant positive correlation was found between mesenterial fecundity and skeletal extension. Oocyte diameter could to be restricted by the capacity of a mesentery to bear a certain number of oocytes or vice versa, but direct evidence of this was not found in this study. However, the negative correlation between oocyte diameter and skeletal extension in the 10 m zone, and between oocyte diameter and calcification in the 10 m and 50 m zones, indirectly suggest that this might be the case. That is, in the 10 m and 50 m zones, with plenty of resources, growth and fecundity increases, but oocyte diameter decreases probably due to

constrains in space within the mesentery, thus, it seems that fecundity increases at the expense of oocyte diameter or size.

Coral transplantation has potential role in the restoration of coral reef habitats affected by human activities, similar to terrestrial reforestation projects (Harriot and Fisk, 1988). The use of coral transplantation as a possible mitigating tool was first explored by Maragos (1974) in the early 1970's, however nowadays, the restoration of coral reefs is still considered to be at the experimental phase (Edwards and Clark, 1998). It has been suggested that for restoration purposes the faster-growing branching coral species may be beneficial on the short-term, for instance through an immediate increase in coral cover, but for long-term stability, the use of massive species is more advantageous because they tend to have higher survivorship after transplantation than the branching forms (Edwards and Clark, 1998). However, when discussing the potential benefits and drawbacks of coral transplantation in general, Edwards and Clark (1998) mentioned five specific disadvantages of the method: loss of coral colonies from donor reef areas, loss of transplanted colonies from the reef as a result of wave action (attachment failure), high mortality rates, reduced growth rates, and reduced fecundity of transplanted corals. However, the use of a massive coral species such as *S. siderea* as a mitigating tool is supported by the following characteristics that were found in this study when comparing transplanted and control colonies, both from the 50 m zone (control zone):

- no colonies were lost from the donor area, since transplanted colonies where mostly from under the pier (which proved disadvantageous for coral colonies), transplanted next to the pier (optimum zone was 50 m from the pier)
- the method used for coral-substrate attachment proved to be efficient and no colonies were lost due to attachment failure
- no mortality was recorded among transplanted or control colonies; moreover, mortality of 130 colonies from different species (67 colonies of *S. siderea*), transplanted from around the pier to a recipient site (offshore spur and groove reef), was only ten percent in five years (Vicente and Associates unpublished data)
- coral growth was similar between transplanted and control colonies at the 50 m zone, thus was not affected by the transplant method
- reproductive characteristics such as mesenterial fecundity and oocyte diameter were similar between transplanted and control colonies at the 50 m zone

The above observations and results underline the potential of *S. siderea* as a mitigating tool for restoration/mitigation purposes. In addition, other observations supporting this statement include:

- recruitment of *S. siderea* occurred among groups of transplanted colonies
- good transplant size would be at/or exceeding puberty (>100 cm^2 - 400 cm^2) because of the likelihood of sexual reproduction and ease of logistical procedures (manipulation, transporting, etc.)
- densities of zooxanthellae were similar among transplanted and control colonies, showing no effect after transplantation

Other studies emphasized that *S. siderea* is a tolerant species capable of adapting to:

- eutrophic environments (Lewis, 1997)
- extensive coastal development (Debrot et al., 1998)
- high sedimentation rates (Foster, 1979, 1980)
- acute temperature fluctuations (Burns, 1985)
- salinity fluctuations (Muthiga and Szmant, 1987)
- oil-spills (Guzmán et al., 1991; Guzmán and Holst, 1993)

The marked differences in the mesenterial fecundity of two coral species (*S. siderea* and *D. clivosa*) associated with differences in irradiance at the pier suggest that coral reproduction could be used as a biological indicator of sublethal effects of stress as proposed by Kojis and Quinn (1984). Further quantitative experimental work is suggested to determine:

- the maximum time a colony could remain in an unfavorable habitat (i.e. under a pier with low irradiance) without affecting reproductive characteristics
- if decreases in irradiance affects the complete gametogenic cycle
- how long it takes colonies to recover from changes in reproductive characteristics if moved from the stressed area to a more favorable one
- reverse the effects of shading using light mitigating techniques such as the use of artificial under-pier daytime lighting, which could be beneficial to corals while they are transplanted, or as a permanent solution if corals can not be transplanted because of logistical procedures (i.e. size of the colonies)

In light of these results, this study provided evidence to accept the alternative hypothesis established since changes in irradiance due to the pier shadow did affect living coral tissue, skeletal extension rates, relative calcification rates, and oocyte diameter of *S. siderea*, and mesenterial fecundity and zooxanthellae densities of both species studied. The results obtained on skeletal density of *S. siderea*,

and on oocyte diameter of *D. clivosa* did not provide evidence to reject the null hypothesis since it showed independence to changes in irradiance.

3.6. CONCLUSIONS

- This chapter underlines the importance of irradiance to the ecology and biology of two Caribbean coral reef species.
- Tissue growth, skeletal extension, calcification, mesenterial fecundity, oocyte diameters, and zooxanthellae densities of *S. siderea* decreased with decreasing irradiance due to the pier-shadow effect.
- An increase in zooxanthellae density was found to be a biological response strategy to a decrease in irradiance in both species studied.
- A decrease in mesenterial fecundity in *S. siderea* and *D. clivosa* might be related to a decrease in irradiance and lower photosynthetic activity of the zooxanthellae, produced by the pier shadow.
- The use of *S. siderea* as a mitigating tool in coastal zone areas where coral communities are threatened by pier constructions is supported by specific characteristics of the species found in this study.
- As developers and resource managers address issues such as the placement and design of overwater structures and the protection of marine resources, information on the ecology and biology of reef corals need to be a fundamental component of the decision-making process, and future coastal zone management policies.

CHAPTER 4. Effects of a pier shadow on recruitment patterns and recruit survival of the tropical reef-building coral *Siderastrea siderea* (Ellis and Solander)

4.1. ABSTRACT

Natural variations in irradiance occur inevitably over coral reef habitats; however, piers and docks can cause further alterations in light regimes to phototrophic organisms like reef corals. This study was conducted in Guayanilla Bay, where a liquefied natural gas power plant and terminal pier was constructed. The purpose of this study was to assess changes in recruitment and recruit survival of *S. siderea* with changes in irradiance due to shading by the pier. Juvenile colonies (2 to 40mm) of *S. siderea* found for the first time in 2000 were denominated **juveniles** and were monitored until 2002. New juvenile colonies found during the monitoring of 2001 were denominated **recruits**, and were monitored until 2002. Monitoring was done using a 50 m transect parallel to the pier at each of four treatment zones: 0 m, 3 m, 10 m, and 50 m (control zone). After establishing the transect, a one-m^2 quadrat was used to sample systematically every other meter, for a total sampling area of 25 m^2 per treatment zone. Each juvenile and recruit colony of *S. siderea* found within the quadrat was counted, measured along its maximum perceived diameter of surface tissue, and recorded. Results showed that juvenile density was significantly lower in the 0 m and 3 m zones when compared to the other treatment zones, and gradually decreased throughout the years of the study ($p<0.0001$, Two-Way ANOVA). A significant ($p<0.05$) positive correlation was found between irradiance and juvenile density for 2000 ($r=0.2174$) and 2001 ($r=0.2209$), although this results showed a weak relationship. Recruit survival of *S. siderea* was not significantly different between treatment zones ($df = 2$, $p>0.025$, X^2). Recruit densities and survival were similar to other localities in the Caribbean. It is postulated that post-settlement processes might have been influencing the densities and survival rates of *S. siderea* juveniles and recruits more than decreasing irradiance.

4.2. INTRODUCTION

Coral reefs are inevitably exposed to natural variations in irradiance and spectral quality, and such changes can occur over a wide range of temporal and spatial scales. Irradiance can be affected by variations in the optical properties of water (absorption and scattering), depth, and cloud cover (Kirk, 1994). Overwater structures, like piers and docks, can further alter light regimes, which largely determine the habitat characteristics that support phototrophic organisms and associated organisms. For instance, the comparison of sessile epibiotic assemblages of shaded (serpulid polychaetes, bryozoans, sponges and ascidians) and unshaded pilings (spirorbid polychaetes, filamentous and foliose algae) showed significant differences in community composition, diversity, and abundance when unshaded pilings were experimentally shaded (Glasby, 1999a). Other investigations of the effects of shading on marine organisms included fishes (Able et al., 1998), algae, and sponges (see Simenstad et al., 1999, Appendix E for summary), but have often focused on seagrasses, such as the eelgrass *Zostera marina* (Simenstad et al., 1995; Burdick and Short, 1999; Fresh et al., 2001), the turtlegrass *Thalassia testudinum* (Shafer and Robinson, 2001), *Posidonia oceanica* (Ruiz and Romero, 2003), and the shoalgrass, *Halodule wrightii* (Shafer, 1999), perhaps because of their ecological distribution (common, shallow, coastal marine communities) and economic value of seagrasses to coastal zones (Ogden and Gladfelter, 1983; Parrish, 1989). Results showed detrimental changes in seagrass populations due to shading by piers and docks.

Scientific investigations have characterized light requirement and light reduction levels under and near residential pier structures for submerged aquatic vegetation (Dennison et al., 1993; Kemp et al., 2000). Experimental methods to reduce shading impacts included the use of particular construction materials, such as glass blocks (Steinmetz et al., 2003), grid platforms (Shafer and Lundin, 1999; Shafer and Robinson, 2001), and gratings (Fresh et al., 2001). Results of these studies have been used to provide a scientific basis for establishing dock construction guidelines and regulations for the protection of seagrasses, such as structural design specifications, like height, width, and sun orientation; though, more research is needed (Kelty and Bliven, 2003).

Few investigations have been done for scleractinian corals, which are generally considered phototrophic organisms due to their symbiotic association with zooxanthellae (Wellington, 1982; Battey and Porter, 1988; Muller-Parker and D'Elia, 1996). Zooxanthellae are responsible for the high productivity observed on coral reefs (Hatcher, 1990), thus, light is an essential requirement for the nutrition of scleractinian corals, and also enhances calcification rates (Goreau, 1959). Mundy and Babcock (1998) found irradiance-dependent settlement of planulae from five scleractinian corals consistent with the adult vertical distribution patterns in the field. It seems that irradiance is not only important for zooxanthellae photosynthesis, coral growth, distribution, and reef zonation, but seems to play a mayor role for planula larvae to identify optimum habitats for adult survival (Mundy and Babcock, 1998). However, No information has been published, however, on how shading might affect coral recruitment and recruit survival.

The survival of coral reefs is dependent on successful recruitment and growth of reef-building coral larvae, thus, literature on coral recruitment is extensive. Patterns of recruitment and recruit survival of scleractinian corals are important to the recovery and replenishment of coral reefs after disturbances (Gittings et al., 1988; Sammarco et al., 1991; Johnson and Preece, 1992), and are suggested to be major determinants of scleractinian community structure and population dynamics (Connell, 1973). Knowledge of recruitment processes had been identified as a research priority (Harrison and Wallace 1990; Wells 1995), and could help in the implementation of conservation and management decisions on coral reefs (Dunstan and Johnson, 1998). Thus, the purpose of this chapter was to determine how changes in irradiance at the EcoEléctrica LP pier in Guayanilla Bay, affect recruitment maximum perceived diameter of surface tissue, and recorded and recruit survival of *S. siderea*. The objectives of this investigation were:

1) to determine if changes in irradiance across treatment zones cause changes in recruitment and recruit survival.

The null hypothesis was that changes in irradiance do not affect juvenile and recruit density or recruit survival of *S. siderea*.

4.3. METHODOLOGY

4.3.1. Experimental Design

Four treatment zones were selected at the EcoEléctrica LP pier, characterized by distance from the pier and movement of the shadow (Ch 2, section 2.3).

4.3.2. Juvenile and Recruit Densities

Juvenile colonies of *S. siderea* were surveyed and monitored using a 50 m transect that ran northeast, parallel to the pier at each of the treatment zones: 0 m, 3 m, 10 m, and 50 m. Juvenile colonies of *S. siderea* were defined as colonies with maximum perceived diameter of surface tissue between 2 to 40mm, following the criteria established by Bak and Engel (1979), Rogers et al. (1984) and Edmunds (2000) for determining juvenile coral densities.

After establishing the transect, a one-m^2 quadrat was used to sample systematically every other meter, for a total sampling area of 25 m^2 per treatment zone. Quadrats were surveyed by parting algae and fanning out sediment to locate small juveniles. Each *S. siderea* juvenile colony (Figure 4.1) found within the one-m^2 quadrat was marked, measured (mm) *in situ* along its maximum perceived diameter of surface tissue, and recorded.

Figure 4.1. Photo of *S. siderea* juvenile colony from the 50 m zone.

The survey was performed for the first time on December 2000. Juvenile colonies of *S. siderea* found for the first time in 2000 and monitored until 2002 were denominated **juveniles**. New juvenile colonies of *S. siderea* found during the monitoring of 2001 were denominated **recruits**, and were monitored until 2002.

4.3.3. Juvenile and Recruit Survival Rates

To determine survival, juveniles and recruits were revisited, and recorded as alive or dead (missing colonies were counted as dead). Juveniles found in December 2000 were revisited in September 2001 and July 2002, while recruits found during the survey of September 2001 were revisited in July 2002. To determine annual survival rates (colonies/yr) of juvenile corals, **S**, (defined as the number of juvenile corals, which survived during a year, divided by the initial number), the following equation was used:

$$\mathbf{S = e^{Z},} \qquad \mathbf{(4.1)}$$

where Z is the natural logarithm of the survival rate, defined as the ratio of number of survivors per unit of time to population abundance during that time. To calculate Z, the following equation was used:

$$\mathbf{Z = Ln\ [(N_{t+1}) / (N_{t0})] / t,} \qquad \mathbf{(4.2)}$$

where *t* is time (in years), *N* is number of recruits.

4.3.4. Statistical Analyses

The normality and homogeneity of variance assumption for the juvenile and recruit density data was tested using the Kolmogorov-Smirnov and the Levene Test, respectively. The data violated the normality and homogeneity assumption, even after transformation (log x+1, square root). Consequently, the data was ranked and a Two-Way ANOVA by Ranks (at $p<0.05$ confidence level) was used to test for significant differences among treatment zones, among years and among years within treatment zones. To identify the zone with significantly higher or lower juvenile or recruit densities, a multiple comparison test, Tukey Test (at $p<0.05$ confidence level), was used. If significant differences were found, a Pearson Correlation was used to explore the relationship among juvenile and recruit densities with irradiance.

To test for significant differences in survival of juveniles and recruits across treatment zones, a Chi square (X^2) test was performed. Zones were pooled into low (0 m and 3 m zone) and high (10 m and 50 m zone) irradiance treatment zones due to small sample size.

4.4. RESULTS

4.4.1. Juvenile and Recruit Densities

Mean juvenile density (juveniles/m^2) of *S. siderea* (Figure 4.2) in the 0 m and 3 m zones was significantly lower ($p<0.0001$, Two-Way ANOVA, Appendix VI.1) than in the 10 m and 50 m zones. Moreover, the 0 m and 3 m zones were similar throughout the study, as well as the 10 m and 50 m zones ($p>0.05$, Tukey Test, Appendix VI.1). These results imply that similar environmental conditions might have existed in the 0 m and 3 m, as well as in the 10 m and 50 m zones for coral recruitment. Juvenile density among years within treatment zones significantly decreased from 2000 to 2001, and from 2000 to 2002; however, no differences were found from 2001 to 2002 ($p<0.0001$, Tukey Test, Appendix VI.1), which suggest that juvenile densities decreased gradually throughout the years.

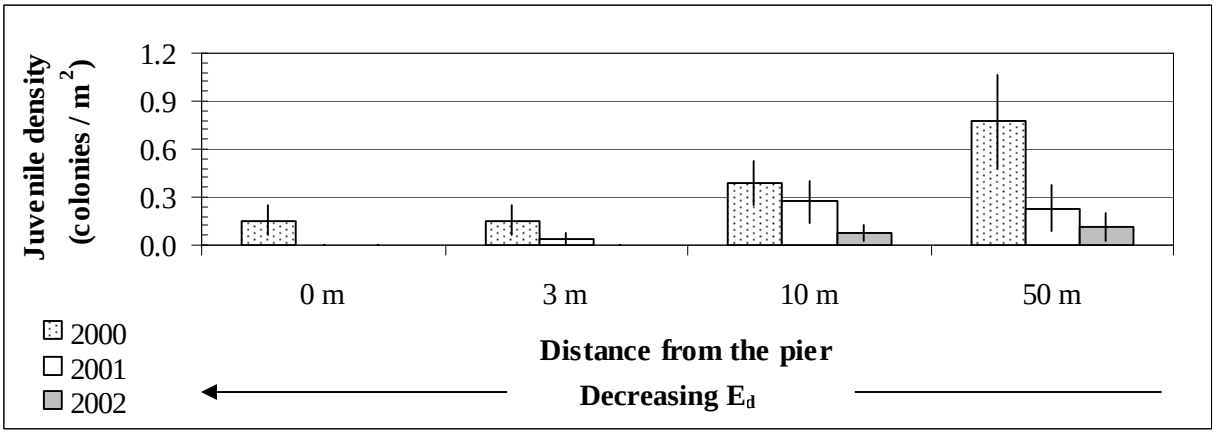

Figure 4.2. Juvenile density (juveniles/m^2) and standard error of *S. siderea* related to decreasing irradiance (E_d) across treatment zones.

There was a significant positive correlation (Figure 4.3) between irradiance and juvenile density for 2000 ($r=0.2174$, $p=0.02663$, $n=104$) and for 2001 ($r=0.2209$, $p=0.02423$, $n=104$), although this results showed a weak relationship. No significant correlation was found between irradiance and juvenile

density for 2002 (r=0.1743, p=0.07679, n=324). These results imply that irradiance might have contributed little to the observed decrease in juvenile densities across treatment zones.

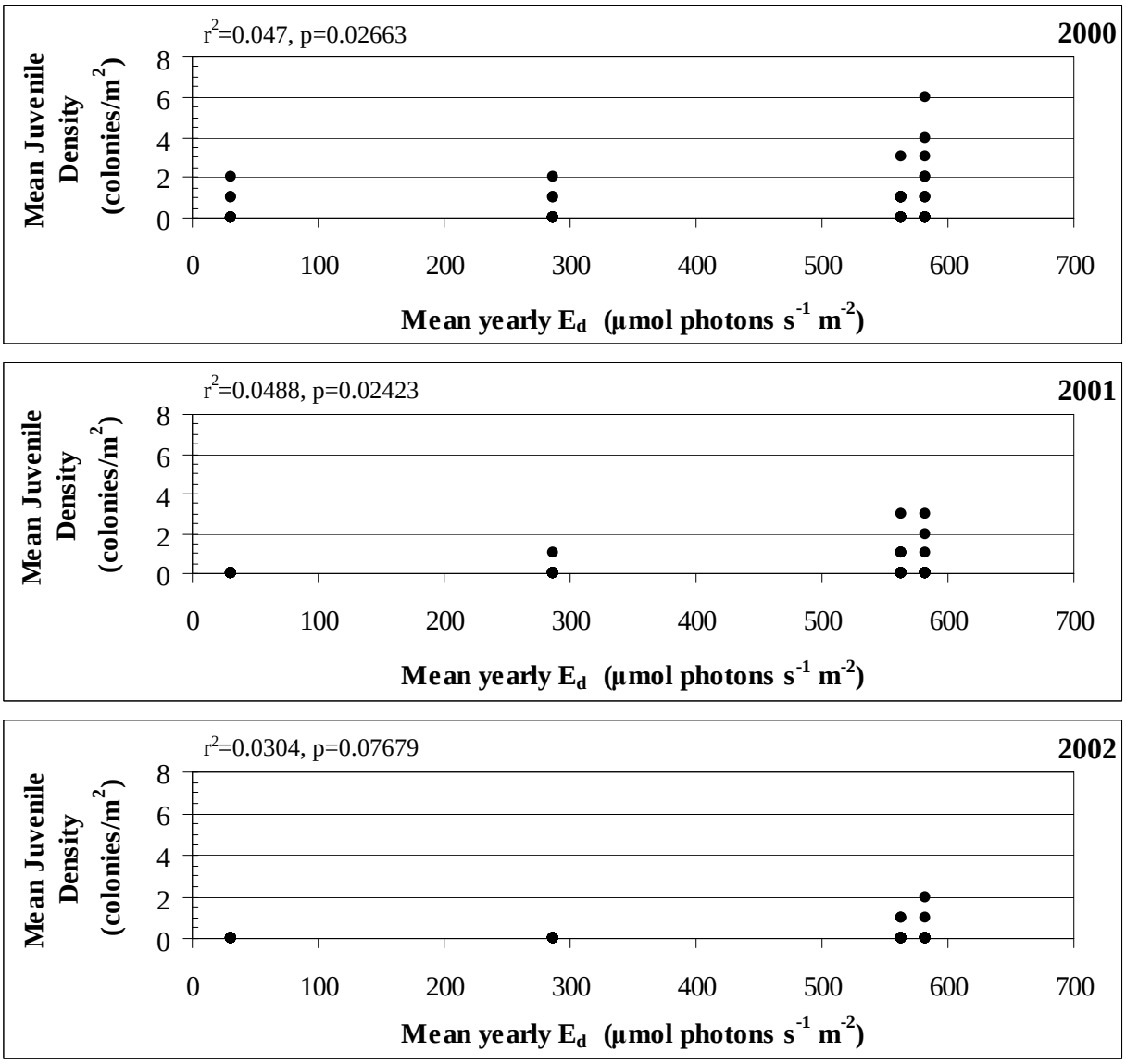

Figure 4.3. Correlation between mean juvenile density of *S. siderea* (from 2000 to 2002) and mean yearly irradiance (E_d).

Mean recruit density (recruit/m^2) of *S. siderea* (Figure 4.3) was slightly different across treatment zones (p=0.0454), but not within years among treatment zones (p>0.05) (Two-Way ANOVA, Appendix VI.1). However, no significant differences among treatment zones were found by a Tukey Test (p>0.05).

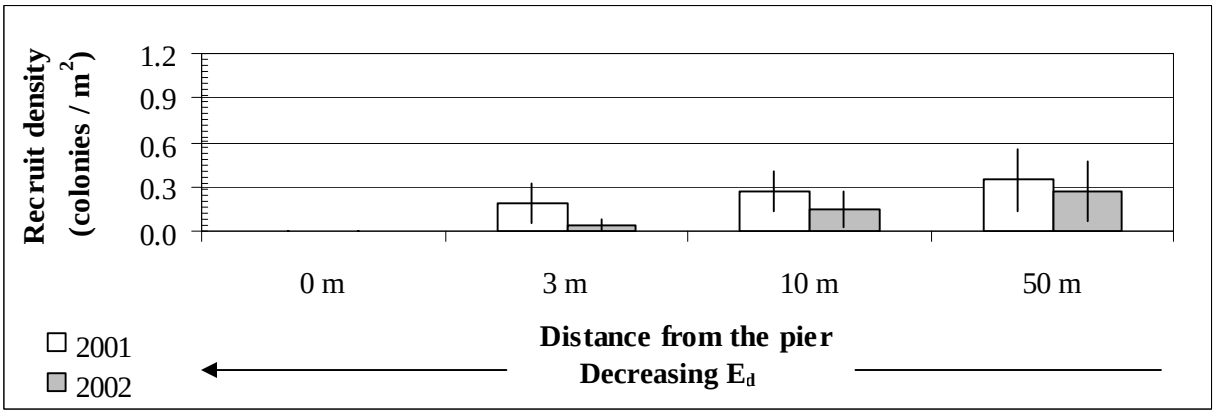

Figure 4.4. Recruit density (recruits/m^2) and standard error of *S. siderea* related to decreasing irradiance (E_d) across treatment zones.

No significant correlation was found between irradiance and recruit density for 2001 (r=0.1754, p=0.07494, n=104) or 2002 (r=0.1724, p=0.08011, n=104).

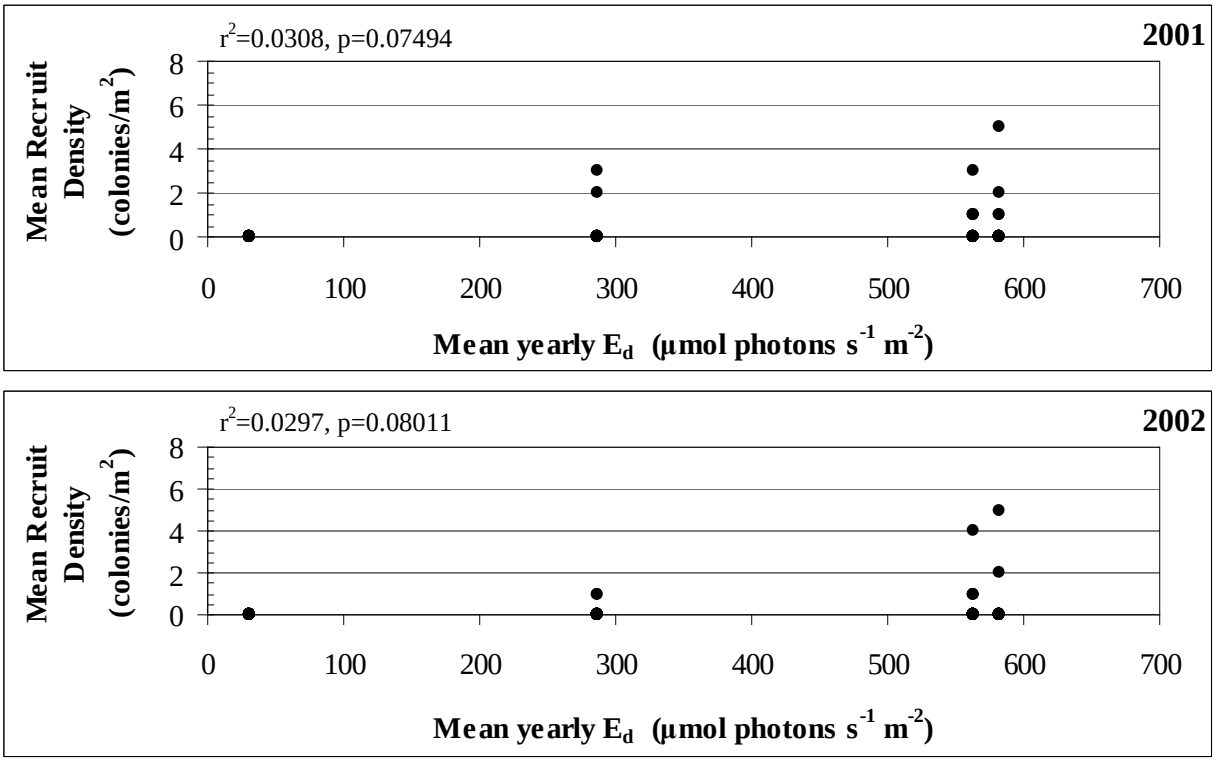

Figure 4.5. Correlation between mean recruit density of *S. siderea* (2001 and 2002) and mean yearly irradiance (E_d).

4.4.2. Juvenile and Recruit Survival Rates

Survival rates (colonies/yr) of juvenile and recruit colonies of *S. siderea* for each zone per year are shown on Table 4.1. Survival rates for both juveniles and recruits seem to be lower for the 0 m and 3 m zones, than for the 10 m and 50 m zones during the study. However, the results from the X^2 test (zones pooled) found no significant differences in juvenile survivorship for 2000-2001 (df=2, p=1.42), for 2001-2002 (df=2, p=0.09), or for 2000-2002 (df=2, p=0.423), neither for recruit survivorship for 2001-2002 (df=2, p=1.97).

Table 4.1. Annual survival rates (S, colonies/yr) of juveniles of *S. siderea* found in 2000 and monitored until 2002, and for recruits found in 2001 and monitored for survival until 2002, with relation to distance from the pier.

Treatment Zones	S 2000-2001 Juveniles	S 2001-2002 Juveniles	S 2000-2002 Juveniles	S 2001-2002 Recruits
0 m	0.00	0.00	0.00	0.00
3 m	0.25	0.00	0.00	0.20
10 m	0.70	0.29	0.44	0.57
50 m	0.30	0.50	0.38	0.78

4.5. DISCUSSION

This chapter describes the juvenile and recruit density patterns and survival of a scleractinian coral in response to a decrease in irradiance caused by shading of a pier. In this study, even though densities of juveniles and recruits of *S. siderea* seem to decrease across treatment zones and across time, it seems that irradiance might not to be the primary factor affecting juvenile and recruit densities of *S. siderea*, as shown by the weak correlation between them. Furthermore, results from the X^2 test showed no significant differences in juvenile and recruit survival among treatment zones. The low sampling size and the consequent pooling of the data into two treatment zones: low (0 m and 3 m zones) and high (10 m and 50 m zones) irradiance zones, might have contributed to these results, among other factors to be discussed. Annual survival rates of *S. siderea* juveniles and recruits were similar to those reported for shallow waters by Edmunds (2000) in St. John (USVI) and by Smith (1997) in the Florida Keys for the same species. Albeit the causes of the decline on density and low survival are uncertain for juveniles and

recruits of *S. siderea* near the pier, it is well known that size dependent mortality is a feature of most coral populations (Connell, 1973). Higher rates of mortality have been reported for younger corals (small recruits) than for older (larger size) corals (Babcock, 1985; Hughes and Connell, 1987), which agreed with the results of this study, since coral mortality was not observed in transplanted or control colonies of *S. siderea* (adult colonies) at the pier (Chapter 3), but very low survival was recorded among juveniles and recruits (this chapter).

There is increasing agreement among scientists on the importance of understanding the factors influencing survival and mortality of newly recruiting corals, and how this may affect coral demographics (Caley et al., 1996; Hughes and Tanner, 2000). Studies on this subject suggest that the reduction of ambient light levels decrease recruitment rates directly underneath tabulate corals by the process of overtopping (Connell, 1973; Sheppard, 1981; Stimson, 1985; Porter et al., 1981; Lang and Chornesky, 1990). However, this study did not provide evidence to prove that shading by a pier structure might have adversely affected coral recruitment and survival of *S. siderea*. Other process, like post-settlement mortality, has often been suggested as a mechanism influencing successful patterns of coral recruitment (Harriot, 1985; Sammarco, 1991). Post-settlement processes (personal observations) that might have contributed to the low densities and low survival of *S. siderea* juveniles and recruits, and that have also been reported in the literature, are preemption of space, smothering or overgrowth by macroalgae (Bak and Engel, 1979; Hughes et al., 1987), smothering by sediments (Hodgson, 1990; Babcock and Davies, 1991), or grazing by fish and echinoids (Sammarco, 1985). Even though this study did not quantify macroalgae overgrowth over recruits or adult corals (transplanted colonies of *S. siderea* were 4 cm above the substrate, and both transplanted and control colonies were cleaned frequently from macroalgae), this process was frequently observed in the area and probably contributed to the results observed in this study. Recruits smothered by sediments were observed around the pier due to the sedimentation (see Chapter 2), and perhaps it is occurring within Guayanilla Bay in general, due to runoff by three mayor tributaries to the main channel of Guayanilla Canyon (Morelock, 1979). Even though coral grazing by fish from the families Chaetodontidae and Scaridae was observed a few times on colonies of *S. siderea* and on other

corals species, their contribution to low densities and low survival of coral recruits might have been negligible due to their low densities around the pier (0.07, 0.03 / m^2, respectively) (Mateo et al., in press).

The relationship between abundance of adult corals and number of recruits has received considerable attention (Connell, 1973; Bak and Engel, 1979; Harriot, 1985; Chiappone and Sullivan, 1996; Edmunds, 2000). At Guayanilla Bay, *S. siderea* relative abundance of adult colonies was higher than other coral species around the pier and in patch reefs and keys near the pier (personal observations; V.P. Vicente, unpublished data). However, juvenile densities of *S. siderea* around the pier were low (0 to 0.7 juveniles/m^2 during the study) when compared to shallow waters in St. John, USVI (>3 juveniles/m^2) (Rogers et al., 1984), but within results reported by Chiappone and Sullivan (1996) for the Florida Keys (0.04 to 0.58 juveniles/m^2) for the same species. Thus, the disproportion between the abundance of adult colonies of *S. siderea* observed at Guayanilla Bay and the low recruit density of *S. siderea* reported in this study, agrees with Bak and Engel (1979), Rylaarsdam (1983), and Edmunds (2000) who reported that the composition of the parental coral community was not a direct function of recruit abundance, probably because of high variations in recruitment patterns in space and time (Connell, 1973; Wallace, 1985), although other studies have presented data against this view (Harriot, 1985; Chiappone and Sullivan, 1996).

The results obtained in this study for juvenile and recruit densities and survival provided evidence to accept the null hypothesis, since processes other than decreasing irradiance due to shading by the pier might be controlling coral recruitment and recruit survival.

4.6. CONCLUSIONS

- This chapter presents the juvenile and recruit density patterns and survival of a scleractinian coral in response to a decrease in irradiance caused by the shadow of a pier.
- Juvenile and recruit densities were significantly lower in the 0 m and 3 m zones when compared to the other treatment zones, and gradually decreased throughout the years of the study.

- A low correlation ($r=0.22$, $p<0.05$) between irradiance and juvenile and recruit densities suggested that irradiance might not to be the main factor influencing recruitment of *S. siderea*.
- Recruit survival of *S. siderea* was comparable to other areas in the Caribbean.
- Recruit survival of *S. siderea* was not significantly different between treatment zones; it might have been influenced more by post-settlement processes than by irradiance.

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APPENDIX I. Tables for Chapter 2

I.1. Mean monthly irradiance (µmol photons s^{-1} m^{-2})

Mean monthly irradiance (µmol photons s^{-1} m^{-2}) and ± standard deviations (Std) calculated for the 0 m zone.

	Surface		Subsurface		1 m		2 m	
Month	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**
Aug-00	146.5	39.0	86.0	16.2	54.9	10.9	38.2	7.3
Sep-00	127.2	60.4	75.3	16.9	52.9	22.2	34.8	11.5
Oct-00	85.7	7.6	55.5	9.0	33.2	2.9	23.7	6.4
Nov-00	136.0	119.6	89.5	69.9	38.7	16.5	20.8	5.5
Dec-00	105.5	39.3	64.4	10.7	29.8	9.9	18.1	14.1
Jan-01	149.1	70.4	102.0	40.7	82.0	38.4	69.9	27.2
Feb-01	103.6	53.8	80.7	38.0	50.6	22.8	31.8	13.9
Mar-01	85.8	18.3	62.8	15.1	38.2	7.0	30.0	9.1
Apr-01	145.2	69.5	100.3	55.0	76.8	52.9	41.2	18.3
May-01	129.5	66.5	78.1	42.4	41.0	20.8	22.0	8.2
Jun-01	121.3	40.4	75.4	29.0	40.2	18.1	26.9	18.5
Jul-01	102.0	27.7	64.3	16.1	39.0	7.4	23.9	6.5
Aug-01	94.1	23.4	68.1	18.7	46.3	7.4	33.0	7.5
Sep-01	80.9	15.6	54.0	8.1	36.2	7.2	26.5	9.2

Mean monthly irradiance (µmol photons s^{-1} m^{-2}) and ± standard deviations (Std) calculated for the 3 m zone.

	Surface		Subsurface		1 m		2 m	
Month	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**
Aug-00	2701.9	163.1	1699.7	123.8	973.7	137.5	499.9	22.8
Sep-00	1366.6	1346.4	928.8	925.8	506.5	491.7	289.0	259.3
Oct-00	161.1	72.2	106.7	43.6	58.2	19.6	43.7	18.2
Nov-00	150.1	112.1	111.2	88.5	47.2	35.8	26.6	5.5
Dec-00	141.2	40.3	77.3	16.0	37.3	9.6	19.2	11.4
Jan-01	299.6	236.7	197.3	158.5	140.3	113.3	96.8	77.3
Feb-01	200.0	140.9	122.4	69.5	77.6	50.4	56.3	41.6
Mar-01	160.4	50.9	98.6	28.2	70.2	31.1	49.5	19.2
Apr-01	1754.1	1037.3	1128.6	839.2	746.1	591.1	463.9	404.2
May-01	1647.1	1100.7	1104.7	794.2	574.5	415.9	262.4	195.3
Jun-01	2490.7	128.1	1648.7	71.6	881.4	209.4	464.5	197.7
Jul-01	2377.8	356.4	1501.5	146.7	849.6	202.9	424.3	166.9
Aug-01	2359.5	191.7	1593.2	73.6	1119.2	143.0	751.6	199.8
Sep-01	2390.2	62.1	1658.0	144.1	1021.6	53.0	571.0	151.5

Mean monthly irradiance (µmol photons s^{-1} m^{-2}) and ± standard deviations (Std) calculated for the 10 m zone.

	Surface		Subsurface		1 m		2 m	
Month	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**
Aug-00	2755.6	177.6	1855.8	183.6	965.6	166.3	507.0	50.7
Sep-00	2531.3	274.4	1772.4	69.5	1097.0	151.5	647.1	198.2
Oct-00	2546.5	75.1	1610.5	109.7	975.0	79.6	642.1	162.0
Nov-00	2068.8	674.9	1341.5	388.4	795.7	415.7	467.4	313.7
Dec-00	2105.1	54.9	1442.3	159.6	651.5	233.0	328.6	241.0
Jan-01	2114.4	719.7	1414.1	511.6	887.8	300.0	576.0	189.2
Feb-01	2063.9	911.5	1353.0	687.0	877.9	447.2	543.8	298.3
Mar-01	2628.7	107.5	1699.7	97.0	1150.0	128.0	720.6	231.0
Apr-01	2113.7	847.7	1292.0	714.6	879.2	532.0	564.7	362.1
May-01	1870.7	1137.1	1254.7	854.0	655.4	442.4	320.0	228.5
Jun-01	2560.8	150.9	1773.5	152.7	903.0	248.0	547.5	233.9
Jul-01	2531.3	148.8	1738.3	127.8	927.7	141.8	478.4	187.6
Aug-01	2487.5	132.7	1753.2	188.8	1201.2	211.3	776.2	194.3
Sep-01	2483.6	46.8	1774.9	54.8	1147.5	100.8	757.9	177.5

Mean monthly irradiance (µmol photons s^{-1} m^{-2}) and ± standard deviations (Std) calculated for the 50 m zone.

	Surface		Subsurface		1 m		2 m	
Month	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**
Aug-00	2707.3	49.3	1557.6	388.2	885.6	332.5	506.9	186.0
Sep-00	2625.0	160.3	1812.8	229.8	1025.3	93.0	669.5	244.6
Oct-00	2603.9	211.8	1723.3	69.3	1037.5	171.9	636.0	241.4
Nov-00	2140.7	549.7	1374.4	345.9	811.6	334.6	432.1	241.5
Dec-00	2162.0	85.6	1527.0	46.3	700.9	239.7	339.2	233.3
Jan-01	2205.0	688.4	1447.9	426.8	992.2	312.3	633.0	203.1
Feb-01	2107.1	955.7	1389.9	664.2	867.4	451.8	544.0	303.1
Mar-01	2663.8	83.6	1990.9	475.3	1126.9	140.0	742.3	216.2
Apr-01	2209.9	877.3	1438.3	647.8	898.6	537.9	547.6	390.2
May-01	1848.2	1148.1	1211.1	830.2	634.1	491.8	325.8	235.5
Jun-01	2640.5	184.3	1861.3	195.3	1015.6	280.1	545.8	228.7
Jul-01	2567.7	142.0	1820.6	169.2	990.4	164.0	544.8	184.9
Aug-01	2530.4	129.3	1781.4	145.6	1193.0	229.8	863.6	249.6
Sep-01	2528.9	22.1	1806.6	59.8	1192.7	135.3	817.1	196.6

I.2. Irradiance (µmol photons s^{-1} m^{-2}) at the surface

Results of the Kruskal-Wallis One-Way ANOVA on ranks to test for significant differences in measurements of irradiance at the surface among treatment zones at the pier.

Treatment zones	N	Missing	Median	25%	75%
0 m	60	2	91.715	82.180	134.000
3 m	60	2	855.850	135.600	2468.600
10 m	60	2	2489.300	2329.900	2675.200
50 m	60	2	2545.100	2375.000	2693.300

H = 136.936 with 3 degrees of freedom, (P = <0.001).

Results of a Pairwise Multiple Comparison Test (Dunn's Method) to isolate the treatment zone at the pier with significant differences in measurements of irradiance at the surface.

Comparison	Diff of Ranks	Q	P<0.05
50 m vs. 0 m	129.233	10.369	S
50 m vs. 3 m	58.664	4.707	S
50 m vs. 10 m	7.724	0.620	NS
10 m vs. 0 m	121.509	9.749	S
10 m vs. 3 m	50.940	4.087	S
3 m vs. 0 m	70.569	5.662	S

S = significant differences, NS = not significant.

I.3. Irradiance (µmol photons s^{-1} m^{-2}) at the subsurface

Results of the Kruskal-Wallis One-Way ANOVA on ranks to test for significant differences in measurements of irradiance at the subsurface among treatment zones at the pier.

Treatment zones	N	Missing	Median	25%	75%
0 m	60	2	63.65	53.92	84.52
3 m	60	2	404.75	91.40	1635.80
10 m	60	2	1701.35	1528.10	1816.40
50 m	60	2	1730.10	1551.80	1850.70

H = 136.897 with 3 degrees of freedom, (P = <0.001).

Results of a Pairwise Multiple Comparison Test (Dunn's Method) to isolate the treatment zone at the pier with significant differences in measurements of irradiance at the subsurface.

Comparison	Diff of Ranks	Q	P<0.05
50 m vs. 0 m	128.233	10.289	S
50 m vs. 3 m	59.724	4.792	S
50 m vs. 10 m	6.112	0.490	NS
10 m vs. 0 m	122.121	9.798	S
10 m vs. 3 m	53.612	4.302	S
3 m vs. 0 m	68.509	5.497	S

S = significant differences, NS = not significant.

I.4. Irradiance (µmol photons s^{-1} m^{-2}) at 1 m depth

Results of the Kruskal-Wallis One-Way ANOVA on ranks to test for significant differences in measurements of irradiance at 1 m depth among treatment zones at the pier.

Treatment zones	N	Missing	Median	25%	75%
0 m	60	2	39.735	32.88	51.34
3 m	60	2	268.350	52.70	975.80
10 m	60	2	1026.250	824.20	1101.70
50 m	60	2	1033.000	849.30	1153.00

H = 130.063 with 3 degrees of freedom, (P = <0.001).

Results of a Pairwise Multiple Comparison Test (Dunn's Method) to isolate the treatment zone at the pier with significant differences in measurements of irradiance at 1 m depth.

Comparison	Diff of Ranks	Q	P<0.05
50 m vs. 0 m	123.914	9.942	S
50 m vs. 3 m	58.276	4.676	S
50 m vs. 10 m	3.983	0.320	NS
10 m vs. 0 m	119.931	9.623	S
10 m vs. 3 m	54.293	4.356	S
3 m vs. 0 m	65.638	5.267	S

S = significant differences, NS = not significant.

I.5. Irradiance (µmol photons s^{-1} m^{-2}) at 2 m depth

Results of the Kruskal-Wallis One-Way ANOVA on ranks to test for significant differences in measurements of irradiance at 2 m depth among treatment zones at the pier.

Treatment zones	N	Missing	Median	25%	75%
0 m	60	2	26.635	19.99	38.89
3 m	60	2	135.255	34.00	509.40
10 m	60	2	561.500	414.60	728.70
50 m	60	2	607.700	384.80	759.20

H = 131.930 with 3 degrees of freedom, (P = <0.001).

Results of a Pairwise Multiple Comparison Test (Dunn's Method) to isolate the treatment zone at the pier with significant differences in measurements of irradiance at 2 m depth.

Comparison	Diff of Ranks	Q	P<0.05
50 m vs. 0 m	123.741	9.928	S
50 m vs. 3 m	61.388	4.926	S
50 m vs. 10 m	2.940	0.236	NS
10 m vs. 0 m	120.802	9.693	S
10 m vs. 3 m	58.448	4.690	S
3 m vs. 0 m	62.353	5.003	S

S = significant differences, NS = not significant.

I.6. Number of hours of shading

Results of One-Way ANOVA to test for significant differences in mean number of hours of shading among treatment zones.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	4	0	7.00	1.4142	0.7071
3 m	4	0	5.00	1.1547	0.5774
10 m	4	0	1.75	1.2583	0.6292
50 m	4	0	0.00	0.0000	0.0000

Source of Variation	DF	SS	MS	F	P
Between zones	3	119.1875	39.7292	32.3220	<0.0001
Residual	12	14.7500	1.2292		
Total	15	133.9375			

Power of performed test with alpha = 0.050: 1.0000

Results of a pairwise multiple comparison test (Tukey Test) to isolate treatment zone with significantly higher or lower average number of hours of shading.

Comparison	Diff of Means	p	q	P	P<0.05
0 m vs. 50 m	7.0000	4	12.6277	0.0002	S
0 m vs. 10 m	5.2500	4	9.4707	0.0003	S
0 m vs. 3 m	2.0000	4	3.6079	0.1016	NS
3 m vs. 50 m	5.0000	4	9.0198	0.0004	S
3 m vs. 10 m	3.2500	4	5.8628	0.0066	S
10 m vs. 50 m	1.7500	4	3.1569	0.1698	NS

S = significant differences, NS = not significant.

I.7. Sediment Rates (g/cm^2/d)

Results of the Two-Way ANOVA to test for significant differences in sediment rates among treatment zone, among trap position, and among trap position within treatment zones.

Source of variation	DF	SS	MS	F	P
Zones	3	1143.532	381.177	7.354	<0.001
Trap Position	1	591.331	591.331	11.408	0.001
Zone x Trap Position	3	529.416	176.472	3.404	0.020
Residual	104	5390.955	51.836		
Total	111	7655.234	68.966		

Power of performed test with alpha = 0.0500: for Zones: 0.971
Power of performed test with alpha = 0.0500: for Trap Position: 0.911
Power of performed test with alpha = 0.0500: for Zones x Trap Position: 0.581

Results of a pairwise multiple comparison test (Tukey Test) to isolate the treatment zone at the pier with significant differences in mean sediment rates.

Comparison	Diff of Means	p	q	P	P<0.050
50 m vs. 3 m	8.420	4	6.189	<0.001	S
50 m vs. 0 m	2.086	4	1.533	0.700	NS
50 m vs. 10 m	1.720	4	1.264	0.808	NS
10 m vs. 3 m	6.700	4	4.924	<0.004	S
10 m vs. 0 m	0.366	4	0.269	0.998	NS
0 m vs. 3 m	6.334	4	4.655	0.007	S

S = significant differences, NS = not significant.

Results of a pairwise multiple comparison test (Tukey Test) to isolate the treatment zone at the pier with significant differences in mean sediment rates within UST (upper sediment traps).

Comparison	Diff of Means	p	q	P	P<0.050
50 m vs. 3 m	3.012	4	1.565	0.686	NS
50 m vs. 0 m	1.260	4	0.655	0.967	NS
50 m vs. 10 m	1.247	4	0.648	0.968	NS
10 m vs. 3 m	1.765	4	0.917	0.916	NS
10 m vs. 0 m	0.013	4	0.007	1.000	NS
0 m vs. 3 m	1.753	4	0.911	0.918	NS

S = significant differences, NS = not significant.

Results of a pairwise multiple comparison test (Tukey Test) to isolate the treatment zone at the pier with significant differences in mean sediment rates in LST (lower sediment traps).

Comparison	Diff of Means	p	q	P	P<0.050
50 m vs. 3 m	13.829	4	7.187	<0.001	S
50 m vs. 0 m	2.913	4	1.514	0.708	NS
50 m vs. 10 m	2.193	4	1.140	0.852	NS
10 m vs. 3 m	11.636	4	6.047	<0.001	S
10 m vs. 0 m	0.720	4	0.374	0.994	NS
0 m vs. 3 m	10.916	4	5.673	<0.001	S

S = significant differences, NS = not significant.

I.8. Water Temperature Fluctuations(^{o}C)

Results of the One-Way ANOVA to test for significant differences in water temperature among two treatment zones at the pier.

Treatment zone - year	N	Missing	Mean	Std Dev	SEM
0 m - 2000	8	0	84.270	1.563	0.553
0 m - 2001	9	0	83.908	1.420	0.473
0 m - 2002	7	3	85.194	0.343	0.172
50 m - 2000	8	0	84.674	1.645	0.582
50 m - 2001	9	1	84.279	1.350	0.477
50 m - 2002	7	3	85.247	0.329	0.165

Source of Variation	DF	SS	MS	F	P
Between Zones	5	8.287	1.657	0.884	0.502
Residual	35	65.617	1.875		
Total	40	73.905			

Power of performed test with alpha = 0.050: 0.050

APPENDIX II. Density Determination Procedures

II.1. Principle of Density Determination of Solids with the Ohaus Explorer Analytical Balance

Density determinations (g/cm^3) were normally performed by Archimedes' principle, which is also used with the density determination kit (DDK) installed to the Ohaus Explorer Analytical Balance (Model E11140) (Figure II.1). This principle states that every solid body immersed in a fluid loses weight by an amount equal to that of the fluid it displaces.

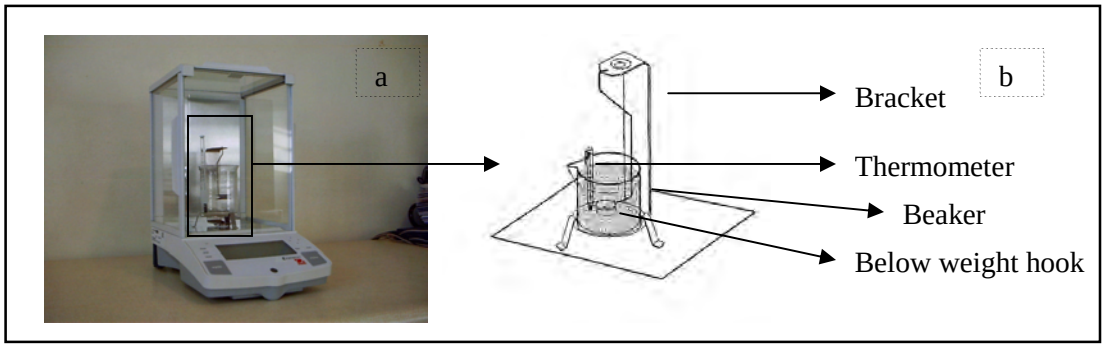

Figure II-1. Photo showing the Ohaus Explorer Analytical Balance (a) and the density determination kit (b) installation.

The density of the coral sample was determined with an auxiliary liquid, in this case distill water (DH_20), whose density Q_0 is known. The coral sample is weighed in air (A) and then in the auxiliary liquid (B). The density Q can be calculated from the two weightings as follows: $Q = A / A\text{-}B * Q_0$

The balance allows direct determination of the buoyancy P (P=A-B) and consequently the above formula can be simplified: $Q = A / P * Q_0$, where Q is the density of the solid, A is the weight of the solid in air, B is the weight of the solid in the auxiliary liquid, Q_0 is the density of the auxiliary liquid at a given temperature (this value depends on the temperature and must be taken form a density table), P is the buoyancy of the solid in the auxiliary liquid (A – B).

II.2. Preparing the Balance for Density Determination

For density determinations, the analytical balance was prepared with the DDK as in Figure II-1. The balance was warmed up (20 minutes) and calibrated before making measurements. A standard glass

beaker (250 ml) and a precision thermometer (0 to 30 ^{o}C) were used. The beaker was filled with DH_2O, and then the balance was ready for the weight measures.

II.3. Performing Density Determination

After the preparation steps, the balance was tarred. The sample was placed on the top of the bracket (weight A). After tarring the balance, the sample was placed on the weight hook, this is the buoyancy of the sample, P. To ensure that there were no bubbles on the sample, it was placed in another container with DH_2O before weighting and air bubbles were removed cautiously by means of a soft brush, only then the sample was placed on the below weight hook. The temperature was observed and recorded for each measure.

APPENDIX III. Histology Procedures

III.1. Sample fixation, decalcification and preservation

Sample Fixation with Zenker Formalin (Helly's Solution)

Coral samples were fixed in Zenker Formalin (Helly's solution) (Appendix III) for 10 to 15 hrs followed by rinse in running tap water for 24 hrs to remove the Helly's solution. Rinsed cores were placed in glass containers with 10% hydrochloric acid (HCl) solution (Appendix III). Solutions of 10% HCl were changed daily until decalcification was completed. Remains of $CaCO_3$ in decalcified coral tissue were checked using the 5% ammonium oxalate test, 5 ml of the HCl solution taken from the containers with the samples and adding 1 ml of 4% ammonium oxalate in a clean container and allowed to stand for five minutes. When a white precipitate was formed, decalcification was not completed; a clear solution indicated a completed process. After decalcification, tissues were rinsed with distilled water and carefully cleaned of endolithic algae and other organisms that may have been embedded in the skeleton. Samples were then preserved in 70% ethanol until the embedding process (Appendix III).

Zenker Formalin = 100 ml of Zenker Base + 5 ml of 37% of formalin

Zenker Base 1L:

- 10 g Sodium Sulfate
- 25 g Potassium Dichromate
- 50 g Mercuric Chloride
- 1000 ml Distilled Water (D H_20)

The Helly's Solution was allowed to stand 3 to 4 days before sample collecting.

Sample Decalcification

Decalcification with 10% Hydrochloric acid (HCL):

- 1L 10% HCL = 900 ml of DH_20 + 100 ml of 100% HCL

Sample Preservation

Preservation with 70% of Ethanol (ETOH)

- 1L 70% ETOH = 750 ml of 95% ETOH + 250 ml of D H_20

III.1.1. Tissue Processing: Dehydrating, Embedding, Sectioning and Staining

Dehydrating

Preserved tissue samples were dehydrated in a series of alcohol treatments (ethanol and isopropanol) and cleared in xylene solution using an automatic rotary tissue processor (Tissue Tek Rotary Tissue Processor Model 4640B). The last step on the processor was to fill the tissues with paraplast (Appendix III).

Dehydration and clearing was done with a rotary tissue processor (Tissue Tek Rotary Tissue Processor Model Number 4640B) (Figure III.1).

The rotary tissue processor consisted, of nine beakers of 1000 ml and two containers with the following reagents (in order of tissue processing):

- Beakers number 1 and 2 = 70% ETOH (Dehydration process)
- Beaker number 3 = 95% ETOH (Dehydration process)
- Beaker number 4, 5 and 6 = Isopropanol (Tissue Dry) (Dehydration process)
- Beaker number 7, 8 and 9 = Xylene (Tissue Clear III)
- Beakers number 10 and 11 = Paraplast (Tissue Prep, melting point 56^{o}C)

Two baskets were filled with 15 to 20 capsules with tissue samples and stay one hour in each of the beakers.

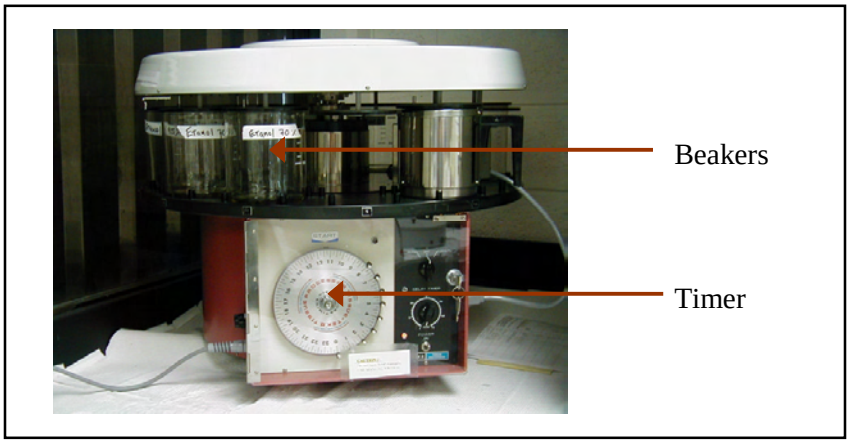

Figure III-1. Tissue Tek Rotary Tissue Processor (Model Number 4640B) used for dehydrating and clearing coral tissue.

Embedding

Samples were embedded in paraplast (Tissue Prep, melting point - 56 to 57°C) using the

Tissue Tek Tec Embedding Equipment, placed in a cold plate (Tissue-Tek) at approximately 3°C until the paraplast-tissue block solidified. Afterward, samples were stored in the freezer for at least 24 hrs before sectioning.

Samples were embedded in paraplast (Tissue Prep, melting point 56 to 57°C) using the Tissue Tek Tec Embedding Equipment (Figure III.2), and placed in a cold plate at approximately 3°C until the paraffin-tissue block solidified.

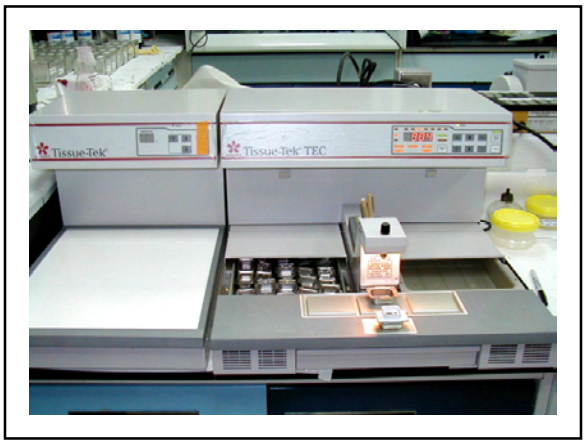

Figure III-2. Tissue Tek Tec Embedding Equipment used for embedding coral tissue.

Sectioning

A rotary microtome (Leitz Model 1512) was used to obtain longitudinal and cross sections (7 µm) form the paraplast-tissues block samples. Long ribbon-like sections were placed in a warm bath (Boekel) at 48-50°C and allowed to expand before lifting on the slide. Subsequently, the slide was placed on a slide warmer (Precision) at approximately 48°C for about 1 to 1.5 hrs. Slides with tissue samples were then stored at room temperature for at least 24 hrs to allow the tissue to fix to the slide and dry before the staining procedure.

A rotary microtome was used to obtain longitudinal and cross sections of 7 µm form the paraplast-tissues block samples (Figure III.3). Long ribbon-like sections were placed in a warm bath

(Boekel) at 48 to 50°C and allowed to expand before lifting on a slide previously coated with albumin fixative (Figure III.3). Subsequently, the slide was placed on a slide warmer at approximately 48°C for about 1 to 1.5 hrs (Figure III.3). Slides with tissue samples were then stored at room temperature for at least 24 hrs to allow the tissue to fix to the slide and dry before staining.

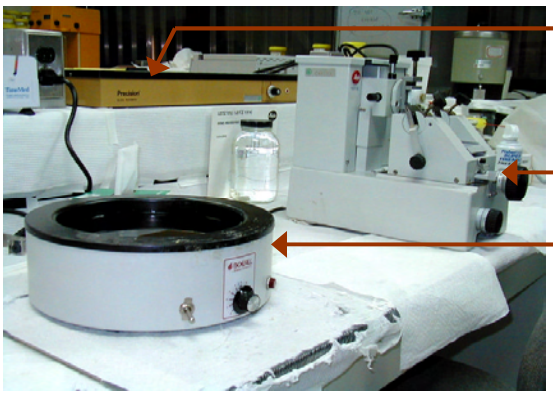

Figure III-3. Laboratory equipment used for the sectioning tissue and related procedures.

Staining

Tissue samples were stained with the Heidenhain's Aniline-Blue method to study the maturation stage of gametocytes. For a detailed description of the Heidenhain's Aniline-Blue method, see Appendix III. Briefly, tissue thin sections were first deparaffinized with xylene solution, slowly hydrated with ethanol solutions. Slides were stained in preheated (56°C) Azocarmine B solution, and rinsed. Afterward, samples were soaked in Aniline-Alcohol, mordant in Phosphotungstic acid and stained with Aniline-Blue-Orange G solution. Finally, samples were dehydrated through ethanol solutions, cleared with xylene solution and mounted with a Cytoseal on the slides.

The Heidenhain's Aniline-Blue method for staining coral tissue was used. A detailed description follows due to some changes in the amount of chemical reactive and time of reaction that can vary among coral species. For *S. siderea* tissue samples were:

1. First deparaffinized with xylene (3 glass containers of 300 ml with xylene at 3 minutes interval in each container)

2. Hydrated with ETOH solutions:
    - 100% ETOH - 3 glass containers - 3 minutes interval in each container
    - 90% ETOH - 1 glass containers - 3 minutes interval
    - 70% ETOH - 1 glass containers - 3 minutes interval
3. Stained in preheated (56^{o}C) 1% Azocarmine B solution, and maintained for 28 to 30 minutes in the oven at 56^{o}C.
    - 1% Azocarmine = 3g Azocarmine B + 300 ml boiling DH_2O + 3 ml glacial acetic acid
4. Rinsed in tap water, then one minute in DH_2O.
5. Soaked in 90% Aniline-Alcohol for 8 minutes
    - 300 ml 90% ETOH + 3 ml Aniline
6. Rinsed in D H_2O for 2 minutes
7. Mordant in 5% Phosphotungstic acid solution for 15 minutes
    - 300 ml bottle water (NAYA worked better) + 9g Phosphotungstic acid
8. Rinsed in D H_2O for 2 minutes
9. Stained with Aniline-Blue-Orange G solution for 17-20 minutes
    - 300 ml DH2O + 0.5 g Aniline Blue + 2 g Orange G + 8 ml glacial acetic acid
10. Rinsed in tap water, then in D H_2O for 2 minutes
11. Dehydrated through ETOH solutions,
    - 70% ETOH 1 glass containers - 2 minutes interval
    - 90% ETOH 1 glass containers - 2 minutes interval
    - 100% ETOH 3 glass containers - 2 minutes interval in each container
12. Cleared with xylene solution
    - 3 glass containers of 300 ml with xylene at 3 minutes interval in each container
13. Mounted with a Cytoseal on the slides

III.2. Criteria established by Szmant-Froelich et al., (1985), and used for classifying oocytes and spermaries of *S. siderea* and *D. clivosa* into developmental stages after histological procedures.

Stages	Oocytes	Spermaries	Embryos
0	No ova in mesentery.	No spermaries in mesentery.	No planulae in coelenteron
I	Enlarged interstitial cells with large nuclei in mesoglea of mesentery.	Small clusters of interstitial cells near or entering the mesoglea.	Same size and staining properties as eggs, but free from mesentery. Includes development up to the two-layered gastrula stage.
II	Accumulation of small amount of cytoplasm around nuclei.	Cluster of spermatocytes with distinct spermary boundary, large nuclei.	Early planula, mesoglea present, oral pore and coelenteron form. No longer stains red.
III	Oocytes of variable size, main period of vitellogenesis.	Spermatocytes smaller with smaller nuclei; number of cells within spermary much larger.	Mesenteries forming as invaginations of mesoglea and endoderm.
IV	Oocytes full size with indented nucleus; stains dark red with H-H.	Spermatocytes with little cytoplasm; tails not evident.	Well developed septa; mature planula.
V		Spermatozoa with tails; ready to spawn.	

(H-H refers to Heidenhain's azocarmine-aniline blue stain used in this study).

APPENDIX IV. Tables for Chapter 3

IV.1. S. siderea

IV.1.1. Tissue Growth Rate (cm^2/yr)

Results of the One-Way ANOVA to test for significant differences among treatment zones for tissue growth rate (cm^2/yr) of *S. siderea* transplanted and control colonies. Data was transformed (log x+1).

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	12	0	0.4876	0.7428	0.2144
3 m	12	0	1.3676	0.7201	0.2079
10 m	10	0	1.7604	0.3811	0.1205
50 m	12	0	1.7388	0.8474	0.2446
50 m*	11	0	1.3360	0.7467	0.2251

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Groups	4	12.3882	3.0971	6.0646	0.0004
Residual	52	26.5554	0.5107		
Total	56	38.9437			

Power of performed test with alpha = 0.050: 0.9565

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower tissue growth rate.

Comparison	Diff of Means	p	q	P	P<0.05
10 m vs. 0 m	1.2728	5	5.883	0.0012	S
10 m vs. 50 m*	0.4245	5	1.923	0.6558	NS
10 m vs. 3 m	0.3928	5	1.816	0.7023	NS
10 m vs. 50 m	0.0216	5	0.100	1.0000	NS
50 m vs. 0 m	1.2512	5	6.065	0.0008	S
50 m vs. 50 m*	0.4029	5	1.910	0.6614	NS
50 m vs. 3 m	0.3712	5	1.799	0.7091	NS
3 m vs. 0 m	0.8800	5	4.266	0.0310	S
3 m vs. 50 m*	0.0317	5	0.150	1.0000	NS
50 m* vs. 0 m	0.8483	5	4.022	0.0479	S

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.1.2. Skeletal extension rate (cm/yr)

Results of the One-Way ANOVA to test for significant differences among treatment zones for skeletal extension rates (cm/yr) of *S. siderea* transplanted and control colonies.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	60	0	0.2327	0.1145	0.01478
3 m	60	0	0.3805	0.1114	0.01438
10 m	50	0	0.4198	0.1014	0.01435
50 m	60	0	0.4623	0.1509	0.01948
50 m*	50	0	0.4517	0.1141	0.01928

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Groups	4	1.9669	0.4917	33.6836	<0.0001
Residual	275	3.7955	0.0146		
Total	279	5.7624			

Power of performed test with alpha = 0.050: 1.0000

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower skeletal extension rates.

Comparison	Diff of Means	p	q	P	P<0.05
50 m vs. 0 m	0.22970	5	14.7239	<0.0001	S
50 m vs. 3 m	0.08183	5	5.2463	0.0019	S
50 m vs. 10 m	0.04253	5	2.5999	0.3513	NS
50 m vs. 50 m*	0.01062	5	0.5844	0.9939	NS
50 m* vs. 0 m	0.21900	5	12.0546	<0.0001	S
50 m* vs. 3 m	0.07121	5	3.9190	0.0443	S
50 m* vs. 10 m	0.03191	5	1.6950	0.7523	NS
10 m vs. 0 m	0.18710	5	11.4388	<0.0001	S
10 m vs. 3 m	0.03930	5	2.4023	0.4347	NS
3 m vs. 0 m	0.14780	5	9.4776	<0.0001	S

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.1.3. Skeletal Density (g/cm^3)

Results of the One-Way ANOVA to test for significant differences among treatment zones for skeletal density (g/cm^3) of *S. siderea* transplanted and control colonies.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	18	0	0.6447	0.01271	0.002997
3 m	20	0	0.6422	0.01524	0.003409
10 m	20	0	0.6415	0.0156	0.003489
50 m	18	0	0.6422	0.01597	0.003764
50 m*	20	0	0.6401	0.01483	0.003964

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Groups	4	0.000177	0.0000443	0.1983	0.9386
Residual	91	0.018980	0.0002233		
Total	95	0.019160			

Power of performed test with alpha = 0.050: 0.0494

IV.1.4. Relative Calcification Rates (g/cm^2/yr)

Results of the One-Way ANOVA to test for significant differences among treatment zones for relative calcification rate (g/cm^2/yr) of *S. siderea* transplanted and control colonies.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	18	0	0.1753	0.06411	0.01511
3 m	20	0	0.2625	0.06662	0.01490
10 m	20	0	0.2751	0.06754	0.01510
50 m	18	0	0.2920	0.05406	0.01274
50 m*	20	0	0.2930	0.07179	0.01919

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Zones	4	0.1674	0.041860	9.9514	<0.0001
Residual	91	0.3575	0.004206		
Total	95	0.5249			

Power of performed test with alpha = 0.050: 0.9996

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower relative calcification rate.

Comparison	Diff of Means	p	q	P	P<0.05
50 m* vs. 0 m	0.11780	5	7.2062	0.0001	S
50 m* vs. 3 m	0.03053	5	1.9105	0.6604	NS
50 m* vs. 10 m	0.01787	5	1.1183	0.9327	NS
50 m* vs. 50 m	0.00106	5	0.0647	1.0000	NS
50 m vs. 0 m	0.11670	5	7.6346	0.0001	S
50 m vs. 3 m	0.02947	5	1.9782	0.6302	NS
50 m vs. 10 m	0.01681	5	1.1285	0.9306	NS
10 m vs. 0 m	0.09989	5	6.7044	0.0002	S
10 m vs. 3 m	0.01266	5	0.8729	0.9720	NS
3 m vs. 0 m	0.08723	5	5.8547	0.0009	S

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.1.5. Zooxanthellae Density (cells/mm^2)

One-Way ANOVA to test for significant differences significant differences in zooxanthellae densities (cells x 10^3/mm^2) of *S. siderea* transplanted and control colonies among treatment zones.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	72	0	4.1333	1.1013	0.1298
3 m	72	0	4.2264	1.3835	0.1630
10 m	60	0	4.0050	1.1877	0.1533
50 m	72	0	3.6306	1.1272	0.1328
50 m*	48	0	3.8500	1.1793	0.2153

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Zones	4	15.3954	3.8488	2.6584	0.033
Residual	319	435.7961	1.4478		
Total	323	451.1915			

Power of performed test with alpha = 0.050: 0.5001

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower zooxanthellae densities.

Comparison	Diff of Means	p	q	P	P<0.05
3 m vs. 50 m	0.5958	5	4.2018	0.0248	S
3 m vs. 50 m*	0.3764	5	2.0357	0.6020	NS
3 m vs. 10 m	0.2214	5	1.4886	0.8307	NS
3 m vs. 0 m	0.0931	5	0.6562	0.9905	NS
0 m vs. 50 m	0.5028	5	3.5456	0.0890	NS
0 m vs. 50 m*	0.2833	5	1.5324	0.8151	NS
0 m vs. 10 m	0.1283	5	0.8629	0.9735	NS
10 m vs. 50 m	0.3744	5	2.5177	0.3851	NS
10 m vs. 50 m*	0.1550	5	0.8147	0.9786	NS
50 m* vs. 50 m	0.2194	5	1.1869	0.9184	NS

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.1.6. Mesenterial Fecundity

Results of the One-Way ANOVA to test for significant differences in mesenterial fecundity of *S. siderea* transplanted and control colonies among treatment zones.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	15	0	1.2889	0.8410	0.2171
3 m	9	0	2.7130	0.4825	0.1608
10 m	18	0	3.4861	1.2803	0.3018
50 m	15	0	4.1667	1.3408	0.3462
50 m*	15	0	4.4583	1.1713	0.3381

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Zones	4	91.3691	22.8423	18.3001	<0.0001
Residual	67	79.8851	1.2482		
Total	71	171.2542			

Power of performed test with alpha = 0.050: 1.0000

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower mesenterial fecundity.

Comparison	Diff of Means	p	q	P	P<0.05
50 m* vs. 0 m	3.1694	5	10.3588	0.0001	S
50 m* vs. 3 m	1.7454	5	5.0103	0.0066	S
50 m* vs. 10 m	0.9722	5	3.3022	0.1474	NS
50 m* vs. 50 m	0.2917	5	0.9533	0.9614	NS
50 m vs. 0 m	2.8778	5	9.9761	0.0001	S
50 m vs. 3 m	1.4537	5	4.3642	0.0242	S
50 m vs. 10 m	0.6806	5	2.4641	0.4160	NS
10 m vs. 0 m	2.1972	5	7.9556	0.0001	S
10 m vs. 3 m	0.7731	5	2.3972	0.4443	NS
3 m vs. 0 m	1.4241	5	4.2753	0.0287	S

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.1.7. Oocyte Diameter (µm)

Results of the One-Way ANOVA to test for significant differences in oocyte diameter (µm) of *S. siderea* transplanted and control colonies among treatment zones.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	211	0	2.6335	0.13530	0.009312
3 m	170	0	2.6538	0.06544	0.005019
10 m	360	0	2.5930	0.09317	0.004911
50 m	300	0	2.5309	0.11330	0.006541
50 m*	300	0	2.5940	0.09129	0.005893

50 m* = control colonies in the 50 m zone.

Source of Variation	DF	SS	MS	F	P
Between Zones	4	2.1303	0.53260	50.2929	<0.0001
Residual	1336	13.5120	0.01059		
Total	1340	15.6422			

Power of performed test with alpha = 0.050:

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower oocyte diameter.

Comparison	Diff of Means	p	q	P	P<0.05
3 m vs. 50 m	0.12290	5	17.5899	<0.0001	S
3 m vs. 10 m	0.06078	5	8.9753	<0.0001	S
3 m vs. 50 m*	0.05976	5	8.1929	<0.0001	S
3 m vs. 0 m	0.02031	5	2.7079	0.3093	NS
0 m vs. 50 m	0.10260	5	15.6879	<0.0001	S
0 m vs. 10 m	0.04047	5	6.4146	<0.0001	S
0 m vs. 50 m*	0.03945	5	5.7456	0.0005	S
50 m* vs. 50 m	0.06311	5	10.0148	<0.0001	S
50 m* vs. 10 m	0.00101	5	0.1672	1.0000	NS
10 m vs. 50 m	0.06209	5	10.9163	<0.0001	S

50 m* = control colonies in the 50 m zone.
S = significant differences, NS = not significant.

IV.2. D. clivosa

IV.2.1. Zooxanthellae Density (cells/mm^2)

Results of the One-Way ANOVA to test for significant differences in zooxanthellae densities (cells x 10^3/mm^2) of *D. clivosa* colonies among treatment zones. Data was transformed (log x+1).

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	50	0	0.7713	0.1183	0.01673
50 m	40	0	0.6953	0.1012	0.01599

Source of Variation	DF	SS	MS	F	P
Between Zones	1	0.1282	0.12820	10.4012	0.0018
Residual	88	1.0846	0.01232		
Total	89	1.2128			

Power of performed test with alpha = 0.050: 0.8763

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *D. clivosa* with significantly higher or lower zooxanthellae densities.

Comparison	Diff of Means	p	q	P	P<0.05
0 m vs. 50 m	0.07595	2	4.561	0.0019	S

S = significant differences, NS = not significant.

IV.2.2. Mesenterial Fecundity

Results of the One-Way ANOVA to test for significant differences in mesenterial fecundity of *D. clivosa* transplanted and control colonies among treatment zones.

Treatment zones	N	Missing	Mean	Std Dev	SEM
0 m	10	0	3.4833	0.9261	0.2929
50 m	8	0	4.9062	1.7584	0.6217

Source of Variation	DF	SS	MS	F	P
Between Zones	1	8.9986	8.9986	4.9031	0.0417
Residual	16	29.3644	1.8353		
Total	17	38.3630			

Power of performed test with alpha = 0.050: 0.04492

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *D. clivosa* with significantly higher or lower mesenterial fecundity.

Comparison	Diff of Means	p	q	P	P<0.05
0 m vs. 50 m	1.4229	2	3.1315	0.0418	S

S = significant differences, NS = not significant.

IV.2.3. Oocyte Diameter (µm)

Results of a Mann-Whitney Rank Sum Test to test for significant differences in oocyte diameter (µm) of *D. clivosa* among treatment zones.

Treatment zones	N	Missing	Median	25%	75%
0 m	282	0	275.6795	245.1613	319.2897
50 m	240	0	272.8300	239.2540	308.0089

T = 60492.0000, n(small)= 240 - n(big)= 282, P = 0.1868.

APPENDIX V. Correlation among biological characteristics within treatment zones

V.1. S. siderea

V.1.1. Pearson Correlation – 0 m zone

	SER	SkD	RCR	ZD	MF	OD
TRG	-0.1039	0.3464	-0.4431	0.1937	-0.5728	-0.5997
	0.629	0.1591	0.06555	0.3645	0.0835	0.06685
	24	18	18	24	10	10
SER		-0.8953	0.9893	0.1729	-0.2206	-0.5762
		5.22E-07	8.56E-15	0.1864	0.4294	0.002572
		18	18	60	15	25
SkD			-0.8644	-0.192	0.833	0.8461
			0.000003725	0.4453	0.03953	0.03372
			18	18	6	6
RCR				0.04652	-0.8204	-0.7921
				0.8546	0.04551	0.06032
				18	6	6
ZD					0.1518	0.07354
					0.5892	0.6993
					15	30
MF						0.5593
						0.03018
						15
OD						

Cells contents:
Correlation coefficient
P value
Number of samples

V.1.2. Pearson Correlation – 3 m zone

	SER	SkD	RCR	ZD	MF	OD
TRG	-0.03335	-0.5086	0.1812	0.08097	-0.471	-0.1075
	0.8771	0.02201	0.4446	0.7068	0.3458	0.8394
	24	20	20	24	6	6
SER		-0.5345	0.9853	-0.3772	-0.4112	-0.1467
		0.01518	2.92E-15	0.002969	0.2715	0.6018
		20	20	60	9	15
SkD			-0.4735	0.09594	0.792	-0.4347
			0.03497	0.6874	0.208	0.5653
			20	20	4	4
RCR				-0.3571	0.3314	-0.4564
				0.1222	0.6686	0.5436
				20	4	4
ZD					0.6123	-0.02611
					0.07967	0.9181
					9	18
MF						0.4458
						0.2291
						9
OD						

Cells contents:
Correlation coefficient
P value
Number of samples

V.1.3. Pearson Correlation – 10 m zone

	SER	SkD	RCR	ZD	MF	OD
TRG	-0.1116	0.04331	-0.1295	-0.06935	-0.2768	0.4833
	0.6396	0.8561	0.5864	0.7714	0.3837	0.1114
	20	20	20	20	12	12
SER		0.3782	0.9825	0.06789	0.6983	-0.455
		0.1001	1.35E-14	0.6395	0.001267	0.01152
		20	20	50	18	30
SkD			0.4762	-0.02646	-0.2536	-0.4669
			0.0338	0.9118	0.4263	0.1259
			20	20	12	12
RCR				0.1953	0.6993	-0.7056
				0.4092	0.01137	0.01035
				20	12	12
ZD					0.2266	-0.3301
					0.3659	0.04926
					18	36
MF						-0.265
						0.288
						18
OD						

Cells contents:
Correlation coefficient
P value
Number of samples

V.1.4. Pearson Correlation – 50 m zone

	SER	SkD	RCR	ZD	MF	OD
TRG	0.1668	-0.243	0.4258	0.1145	0.3179	0.382
	0.4359	0.3313	0.0781	0.5943	0.3707	0.276
	24	18	18	24	10	10
SER		-0.1257	0.9753	0.1015	0.2047	-0.1772
		0.6193	6.50E-12	0.4405	0.4643	0.3968
		18	18	60	15	25
SkD			-0.05631	-0.04522	0.2544	-0.3058
			0.8244	0.8586	0.6266	0.5556
			18	18	6	6
RCR				0.07676	0.632	0.8803
				0.7621	0.1782	0.02063
				18	6	6
ZD					0.3745	0.06189
					0.169	0.7453
					15	30
MF						-0.2407
						0.3874
						15
OD						

Cells contents:
Correlation coefficient
P value
Number of samples

V.1.5. Pearson Correlation – 50 m zone – Control Colonies

	SER	SkD	RCR	ZD	MF	OD
TRG	0.1307	0.09553	0.1325	-0.3294	-0.02352	-0.86
	0.6559	0.7453	0.6515	0.2128	0.9559	0.006158
	20	20	20	22	10	10
SER		-0.5784	0.9879	0.1664	0.03881	-0.5791
		0.03024	4.35E-11	0.3393	0.921	0.02369
		20	20	50	12	20
SkD			-0.493	0.02164	-0.4619	-0.7146
			0.07329	0.9415	0.3564	0.1105
			20	20	8	8
RCR				0.1446	0.01167	-0.529
				0.6218	0.9825	0.2805
				20	8	8
ZD					0.2358	0.5532
					0.4606	0.005043
					15	30
MF						0.2753
						0.3865
						15
OD						

Cells contents:
Correlation coefficient
P value
Number of samples

V.2. D. clivosa

V.2.1. Pearson Correlation –0 m zone

	MF	OD
ZD	-0.0709	-0.06814
	0.8457	0.6382
	10	50
MF		0.2334
		0.5164
		10
OD		

V.2.2. Pearson Correlation –50 m zone

	MF	OD
ZD	-0.1429	-0.04521
	0.7357	0.7818
	8	40
MF		0.7416
		0.03521
		8
OD		

Cells contents:
Correlation coefficient
P value
Number of samples

APPENDIX VI. Tables for Chapter 4

VI.1. Juvenile Density (juvenile/m^2)

Results of the Two-Way ANOVA by Ranks to test for significant differences in juvenile density among treatment zones, among years and among years within treatment zones. Data was ranked.

Source of Variation	DF	SS	MS	F	P
Zones	3	35339.1731	11779.7244	5.2259	0.0016
Years	2	40938.3317	20469.1659	9.0808	0.0001
Zones x Years	6	6235.5529	1039.2588	0.4611	0.8369
Residual	300	676232.4423	2254.1081		
Total	311	758745.5000	2439.6961		

Power of performed test with alpha = 0.05000: for Zone : 0.8661
Power of performed test with alpha = 0.05000: for Years : 0.9681
Power of performed test with alpha = 0.05000: for Zone x Years : 0.05000

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower juvenile density among zones.

Comparison	Diff of Means	p	q	P	P<0.05
10 m vs. 0 m	23.3910	4	4.3512	0.0113	S
10 m vs. 3 m	21.4679	4	3.9935	0.0245	S
10 m vs. 50 m	2.5256	4	0.4698	0.9874	NS
50 m vs. 0 m	20.8654	4	3.8814	0.0308	S
50 m vs. 3 m	18.9423	4	3.5237	0.0612	NS
3 m vs. 0 m	1.9231	4	0.3577	0.9943	NS

S = significant differences, NS = not significant.

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower juvenile density among years.

Comparison	Diff of Means	p	q	P	P<0.05
2000 vs. 2002	27.1875	3	5.8398	0.0001	S
2000 vs. 2001	19.6010	3	4.2102	0.0082	S
2001 vs. 2002	7.5865	3	1.6296	0.4819	NS

S = significant differences, NS = not significant.

VI.2. Recruit Density (recruit/m^2)

Results of the Two-Way ANOVA by Ranks to test for significant differences in recruit density among treatment zones, among years and among years within treatment zones. Data was ranked.

Source of Variation	DF	SS	MS	F	P
Zones	3	6175.9615	2058.6538	2.7247	0.0454
Years	1	1812.4808	1812.4808	2.3989	0.1230
Zones x Years	3	937.4423	312.4808	0.4136	0.7434
Residual	200	151111.6154	755.5581		
Total	207	160037.5000	773.1280		

Power of performed test with alpha = 0.05000: for Zones : 0.4366
Power of performed test with alpha = 0.05000: for Years : 0.2029
Power of performed test with alpha = 0.05000: for Zones x Years : 0.05000

Results of a pairwise multiple comparison test (Tukey Test) to isolate the colonies of *S. siderea* with significantly higher or lower recruit density among zones.

Comparison	Diff of Means	p	q	P	P<0.05
10 m vs. 0 m	13.7885	4	3.6173	0.0515	NS
10 m vs. 3 m	7.7500	4	2.0332	0.4757	NS
10 m vs. 50 m	1.6154	4	0.4238	0.9907	NS
50 m vs. 0 m	12.1731	4	3.1935	0.1080	NS
50 m vs. 3 m	6.1346	4	1.6094	0.6660	NS
3 m vs. 0 m	6.0385	4	1.5841	0.6771	NS

S = significant differences, NS = not significant.