SEXUAL REPRODUCTION AND THE EARLY LIFE HISTORY OF MONTIPORA CAPITATA IN KĀNE'OHE BAY, O'AHU, HAWAI'I

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By

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This work is dedicated to the memory of my father,

Frank Joseph Kolinski, Ph.D. (1931 – 1990),

and to MaryAnn,

Stella, and Jessica Ann Kolinski
ACKNOWLEDGEMENTS

I am grateful to Paul Jokiel, my committee chairperson, who opened his heart, mind and home and guided me towards research in coral reef ecology, and Evelyn Cox, whose shared interests, insights, assistance and guidance helped to make this effort possible. I am also indebted to the other members of my committee, Bob Kinzie, Jim Maragos and Mike Hamnett for insights, assistance and editorial review.

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ABSTRACT

The larval biology, early life history and energetic costs of sexual reproduction in the scleractinian coral *Montipora capitata* were assessed in Kāneʻohe Bay, Oʻahu, Hawaiʻi. Larvae were competent to settle three days post-spawning (DPS), and settled in large pulses days after syngamy in the laboratory and field. Ability to settle remained high (83% proportional settlement) at six weeks, but was reduced (≤11%) at 56 plus days. A few larvae survived and settled at 191 and 207 DPS, the longest lengths of competency recorded for a scleractinian coral. The larvae settled equally well on a variety of substrates including different species of crustose coralline algae and rubble covered with filamentous algae. Tests with antibiotics suggested bacteria play a role in inducing settlement.

The early life histories of *Montipora capitata* (hermaphroditic broadcast spawner), *Porites compressa* (gonochoric broadcast spawner) and *Pocillopora damicornis* (brooder) were monitored on field settlement plates. *Montipora capitata* had the highest number of overall settlers (91% of nearly 20,000 settlers), but displayed significantly lower levels of survivorship and growth than *P. compressa* and *P. damicornis*. Each species displayed Type III survivorship. The mean estimated time for settlers to reach 1 cm$^2$ projected area in the field was 4.9 years for *M. capitata* and 1.7 years for *P. compressa* and *P. damicornis*. Survival was not related to growth in *M. capitata*, in contrast to the other two species. These three species differ in their fertilization and early life history strategies. *Montipora capitata* emphasizes processes that achieve large quantities of larvae and settlers, while *P. compressa* and *P. damicornis* appear more dependent on settler quality (survival and growth).
The mean percent of annual net photosynthetic productivity allocated to sexual reproduction in *Montipora capitata* was estimated as 2.13 % for shallow reef-flat colonies and 3.50 % for deeper reef-slope colonies. This energy expenditure could be replaced by excess colony photosynthesis within two to six weeks (depending on depth) following summertime spawning. *Montipora capitata* may gain its early life history advantage through large repetitive, low cost, influxes of larvae settling in a variety of habitats. Management implications are discussed.
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CHAPTER 1
INTRODUCTION


Reproduction is one of the most critical components in the life histories of all living organisms. It is a means by which species persist, adapt and in many cases disperse in spatially and temporally fluctuating environments (Williams 1975, Maynard Smith 1978, Bell 1982, Jablonski and Lutz 1983, Bull et al. 1987, Veron 1995, Holt and

About 25 years ago, investigators began focusing on contributions of larvae to coral population recovery and maintenance (Connell 1973, Pearson 1981, Hughes and Jackson 1985). Paradigms regarding larval recruitment’s role in influencing coral community structure have shifted from the notion of a taxonomically diverse oversupply of larvae being acted upon by post-settlement selection factors to the confirmation of
taxonomic, spatial and temporal variability in larvae availability, settlement and recruitment success (Harrison and Wallace 1990, Fisk and Harriott 1990, Sammarco 1991, Tomascik 1991, Fitzhardinge 1993, Gleason 1996, Connell et al. 1997, Dustan and Johnson 1998, Hughes and Tanner 2000, Hughes et al. 1999, 2000, 2002). Corals are a highly diverse group of organisms with a variety of reproductive strategies. Although many generalities are known, the specifics of larval biology and early life history have only been elucidated for a small number of coral species (see Kinzie 1999, Nozawa and Harrison 2003). Coral larval biology and early life history need to be understood across a range of species and genera if we are to be able predict and potentially manage for coral responses to widespread environmental change (Kinzie 1999).

Reproductive patterns that lead to the production of larvae can be classified for corals by sexuality and location of embryogenesis (Harrison and Wallace 1990). Corals that form eggs and sperm within the same colony are hermaphroditic, while those that separate sexes among colonies are gonochoric. Species that develop and release planulae of either sexual or asexual origin are classified as brooders, while those that spawn their gametes into the surrounding water for fertilization and embryonic development are termed broadcast spawners. Nearly 85% of roughly 250 examined coral species broadcast spawn gametes (Richmond and Hunter 1990, Richmond 1997), and 75% are reported to be hermaphrodites (Harrison and Wallace 1990, Richmond and Hunter 1990, Richmond 1997, Veron 1995, 2000a). Broadcast spawning hermaphroditic species are found in at least 32 genera representing 9 families of Scleractinia (Richmond and Hunter 1990, Richmond 1997).
The general characteristics of larval development in most species of broadcast spawning hermaphrodites appear to be similar (Harrison and Wallace 1990, Richmond 1997). A majority release positively buoyant eggs-sperm bundles that rise to the ocean surface for fertilization in an essentially two-dimensional environment. The eggs remain viable for up to seven to eight hours (Heyward and Babcock 1986), which increases the potential for fertilization success, even for species at low population densities. Larval development typically occurs within seven days (Babcock and Heyward 1986, Harrison and Wallace 1990, Richmond 1997), which, depending on water circulation provides initial opportunity for dispersal away from reefs of origin. Larval competency, settlement, settler growth and survival are not well documented for the vast majority of species within this group, and interspecific variation is likely. This dissertation provides information related to these aspects for the common Hawaiian hermatypic broadcast spawner, *Montipora capitata*.

The dispersal potential of coral larvae is dependent on their period of competence to settle. Evidence suggests the larvae of broadcast spawning species can settle (i.e., attach to a substrate and metamorphose) rapidly (Harrison and Wallace 1990, Morse et al. 1996, Richmond 1997, Wilson and Harrison 1998, Nozawa and Harrison 2003, Miller and Mundy 2003). Yet, studies of larval competency periods in broadcast spawning hermaphrodites are few (Richmond 1988, Wilson and Harrison 1998, Baird 1998, Nozawa and Harrison 2003). In addition, evidence is accruing that coral larvae effect their distributions by actively selecting their settlement substrates, and settlement preferences do appear to differ between species (Fadlallah 1983, Morse et al. 1998, Harrison and Wallace 1990, Carlon and Olson 1993, Mundy and Babcock 2000,
Chapter 2 reports on laboratory and field experiments that elucidate larval settlement preferences, inducers, settlement timing and periods of competency in *Montipora capitata*.

Recruitment into a coral community is typically considered to occur once corals become easily visible in the field (Harrison and Wallace 1990). However, most coral larvae are small and early settlers of many species may only be visible when magnified (Wallace 1983). Since the critical links between larval influxes and recruitment typically occur in the “invisible” (sensu Wallace 1983) realm, manipulative experiments must be utilized to identify and understand settlement and early life history patterns in corals. Chapter 3 examines the settlement and long-term fate of seeded and natural *Montipora capitata* larvae to artificial plates placed on shallow water reefs. Comparisons of spatial and temporal settlement, settler growth and survival are made with a naturally settling brooding and gonochoric broadcast spawning species as a means to understand similarities and differences in early life history strategies.

Parental investments and costs associated with reproduction are not well known for coral species. However, resource allocation to reproduction is likely a reflection of the success of larval and early life history strategy (Vance 1973, Begon et al. 1986, Morgan 1995). Chapter 4 examines energetic costs associated with sexual reproduction in *Montipora capitata* with perspective to its early life history traits.
CHAPTER 2
LARVAL COMPETENCY AND SETTLEMENT PREFERENCE

Introduction


benthic biological communities that directly stimulate coral larvae settlement behavior (Morse and Morse 1991, Morse et al. 1996). However, most settlement inducing communities (biological) and/or molecules remain unknown for the vast majority of coral species.

The coral *Montipora capitata* (Anthozoa, Scleractinia; see Maragos 1977, 1995 for reported synonyms and reclassification) is widely distributed with geographic boundaries potentially reaching west Sumatra in the Indian Ocean, the Ryukyu Islands in the north Pacific, New Caledonia in the south Pacific and Hawai‘i in the east (Veron 1993, 2000b; note the geographic range is in presently in dispute. Maragos 1995 suggests a range restricted to Johnston, the Hawaiian and Line islands). Although noted to be uncommon elsewhere (Veron 2000b), in Hawai‘i it ranks third in statewide coral coverage in the Main Hawaiian Islands (Jokiel et al. 2001) and Northwestern Hawaiian Islands (Maragos et al. in press). *Montipora capitata* is found in a variety of habitats including deep, shallow, turbid, clear, calm and protected, and those directly exposed to high wave energy (Maragos 1972, 1977, Kolinski and Jokiel 2002). It is a broadcast spawning simultaneous hermaphrodite with buoyant egg-sperm bundles, surface water fertilization (Heyward 1986, Kolinski and Cox 2003) and an embryonic developmental period lasting two to three days (Mate et al. 1998, Kolinski pers. obs.). Very little is known, however, regarding its larval settlement tendencies or the period over which it remains competent to settle. This report presents results from a number of laboratory and field experiments, elucidating larvae settlement preferences, inducers, timing and competency in this species.
Methods

Field Studies

Laboratory and field studies were conducted from 1998 through 2001 at the Hawai‘i Institute of Marine Biology (HIMB) and in Kāne‘ohe Bay, O‘ahu, Hawai‘i. Field observations of Montipora capitata settlement were made on settlement plate sets established at six shallow water (depths 1.5 to 3.5 meters) sites, including one fringing (F) and patch (P) reef each in north (N), central (C) and south (S) Kāne‘ohe Bay (Figure 2.1). Each plate set consisted of two 10.0 x 9.5 x 1.2 cm unglazed terra-cotta tiles separated by a 0.75 x 1.5 x 2.5 cm piece of Plexiglas and attached in a horizontal position, two (1999-2000) to four (2000-2001) sets on each of seven polyvinyl chloride (PVC) posts at each site (Figure 2.2). Each set was held together with a 3.2 cm (1.25 in) stainless steel bolt and a stainless steel washer and wing nut. Four 0.4 cm thick PVC clips (1.9 cm diameter) were attached near each corner on each plate to allow for handling. Posts were positioned every 5 to 10 meters along the dominant reef contours, generally parallel to prevailing oncoming waves on the windward sides of reefs, and were set between corals with bottom surfaces approximately 15 cm above sand, mud, rubble, and/or hard reef substrates.

Initial plates (two to a post, seven posts at a site) were installed at sites in March, three months prior to the 1999 M. capitata summer spawning, with replicate sets being added three months prior to the 2000 summer spawning. Plate sets removed for analysis were always kept submerged in individual containers and were transferred by boat to the Hawai‘i Institute of Marine Biology (HIMB) for settler identification, measurement and mapping using a Wild Heerbrugg dissecting microscope (with the aid of a 10 x 10 cm
Figure 2.1. Location of settlement survey sites in Kaneʻohe Bay, O'ahu, Hawai'i (SF = South Fringing reef; SP = South Patch reef; CF = Central Fringing reef; CP = Central Patch reef; NF = North Fringing reef; NP = North Patch reef).
monofilament sectioned quadrat). In all cases, half the number of sets on each post at a site were collected at one time and analyzed, with collection schedules rotated among sites to ensure equivalent time-related proportionate sampling. Plates were held in their individual containers in a shaded flow-through seawater table while in the laboratory.
Container seawater was filtered (40 μm) and changed regularly. These procedures ensured that plates were not contaminated with larvae in seawater at the lab. All plate sets were returned to their respective posts within one to two days. Examination of all plate sets at each census was conducted in less than one month.

In June 1999, roughly half of the plate sets (one from each of five to six posts at a site) were inspected and then seeded with cultured *M. capitata* larvae for related experiments. These sets were enclosed within individual transparent Glad brand plastic disposable containers (739 ml) modified with 40 μm Nitex screen on all but the top surface to allow for adequate water exchange (Figure 2.2). The PVC clips ensured chamber (including mesh) and plate contact did not occur. Five hundred 6-day-old larvae were injected into each chamber in the field. Chambered sets were collected and settlement mapped and scored after 6 days. These seeded plates were returned (without chambers) to the field and were inspected with the other plates the following fall, winter-spring and summer through summer 2001.

**Culturing of Larvae**

Larvae of *Montipora capitata* were raised under laboratory conditions. Colonies from various locations in Kāne‘ohe Bay were placed in flow-through seawater tables prior to the June, July and/or August new moon spawnings. Seawater flow to the tables was terminated one hour before spawning. Egg-sperm bundles from three or more colonies were collected from the water surface and mixed in translucent 500 ml Nalgene™ polyethylene bottles (conditioned in seawater prior to use) filled one third full with either 0.45 μm or 100 μm filtered seawater (FSW). After two to three hours the containers and developing embryos were rinsed of excess sperm (using 0.45 μm FSW...
and 100-120 µm Nitex screen). The embryos were returned to containers filled with 0.45 µm FSW, which were then capped and placed in running seawater in shaded flow-through seawater tables. Embryonic development proceeded fairly rapidly, with blastulae and gastrulae apparent 11 hours after spawning, round spinning ciliated larvae evident at 36 hours (1.5 days), and actively swimming barrel-shaped larvae prevalent at 60 hours (2.5 days; see Mate et al. 1998). Bottles were cleaned of decomposed material daily by separating out live embryos and larvae using 100 - 120µm Nitex screen, then scrubbing and rinsing the bottles with 0.45 µm FSW. Over time, larvae were consolidated into fewer bottles. Water changes and scrubbing of bottles containing larvae used for long-term settlement competency experiments were accomplished every day post spawning for the first two to three weeks, but then proceeded on the order of every three to 21 days.

**Settlement Preference**

**Tests of General Substrate Preference**

Substrates for testing the settlement preference of *Montipora capitata* larvae were collected from throughout Kāneʻohe Bay. One branching and seven encrusting forms of crustose coralline algae (CCA) were collected from the tops, sides and undersides of hard substrata. The eight CCA differed in appearance, collection location and exposure (Table 2.1), and were assumed to represent eight different species from an undetermined number of genera. Dead coral substrate covered with filamentous algae (FA), dead and dried coral rubble from Coconut Island (Moku o Loe) beach deposits, and terra-cotta tile fragments (from plates conditioned in a flow-through seawater table for 1.5 months) were also collected. Substrates were cut into 1 cm² replicate samples, inspected for previous coral recruits, and were inspected and cleaned (except for the tile pieces) to ensure that
Table 2.1. Appearance, collection location and exposure of crustose coralline algae used in settlement preference experiments.

<table>
<thead>
<tr>
<th>Species</th>
<th>Description of form and location</th>
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<tr>
<td>CCA1</td>
<td>Attached; branching; purple-pink; exposed to direct sunlight; reef flat Chinamen’s Hat (Mo’okoli’i), North Bay. Identified as <em>Hydrolithon setchelli</em> (Shelly James pers. comm.).</td>
</tr>
<tr>
<td>CCA2</td>
<td>Unattached; bulbous with large nodules; light purple; exposed to direct sunlight; reef flat Chinamen’s Hat, North Bay.</td>
</tr>
<tr>
<td>CCA3</td>
<td>Encrusting; rough with numerous conceptacles; red; cryptic, undersides of dead <em>M. capitata</em> plates; reef flat Wai’ahole-Waikane, North Bay. Identified as <em>Hydrolithon gardineri</em> (Shelly James pers. comm.).</td>
</tr>
<tr>
<td>CCA4</td>
<td>Encrusting; smooth; pinkish-yellow; exposed to direct sunlight, covering shallow water carbonate; reef flat Marine Corps. Base sandbar reef, Central Bay.</td>
</tr>
<tr>
<td>CCA5</td>
<td>Encrusting; rough; dark purple; cryptic, inside reef framework; reef flat Wai’ahole-Waikane, North Bay.</td>
</tr>
<tr>
<td>CCA6</td>
<td>Encrusting; smooth and velvety; dark red; cryptic, inside reef framework; reef flat Coconut Island, Central Bay. Possibly <em>Peysonella</em> sp. Almost always observed competing with CCA8.</td>
</tr>
<tr>
<td>CCA7</td>
<td>Encrusting; rough with numerous conceptacles, light red; exposed to direct sunlight; reef flat Coconut Island, Central Bay. Competing with adult <em>M. capitata</em>.</td>
</tr>
<tr>
<td>CCA8</td>
<td>Encrusting, smooth; cryptic, inside reef framework; reef flat Coconut Island, Central Bay. Almost always observed competing with CCA6. Identified as <em>Sporolithon</em> c.f. <em>ptychoides</em> (Shelly James pers. comm.).</td>
</tr>
</tbody>
</table>

desired biological forms were not contaminated by multiple algal or invertebrate species.

Each substrate sample was randomly assigned, along with controls (FSW only), to a cell within a set of Corning™ brand 6-cell, flat bottom culture trays (20 ml cells), with a total of 5 replicates for each treatment. Trays were covered and translucent. All cells contained 0.45 μm FSW.

Ten cultured, actively swimming, barrel-shaped larvae (5.5 days post fertilization) were pipetted into each treatment and control cell. All trays were partially submerged in flowing seawater in a semi-shaded flow-through seawater table to maintain seawater temperatures close to ambient. Every other day, approximately one third of the FSW in each cell was exchanged. On the seventh day, cells and substrates were examined at 12x using a Wild Heerbrugg dissecting microscope and scored for settlement. Larvae displaying strong adherence to a substrate and morphological change (from squat form to tentacle development) were considered settled. Proportional data were arcsine square-root
transformed and analyzed using ANOVA. In the case of no settlement in replicated FSW controls (no substrate), control values were excluded from the ANOVA due to lack of variance with the justification that proportional settlement in cells with substrates represented the difference from mean settlement in controls. Post-hoc comparisons were made using a Tukey HDS test with $\alpha = 0.05$.

**Antibiotic Treatments**

Experiment 1

A potential role of bacteria in stimulating *Montipora capitata* larvae to settle was examined by exposing substrates and larvae to an antibiotic treatment. Three species of crustose coralline algae (CCA2, CCA6 and CCA8; those which induced the highest mean settlement in the previous experiment) and dead coral substrate covered with filamentous algae were collected from source areas within Kane’ohe Bay. Additionally, terra-cotta tile fragments were newly broken from settlement plates conditioned in running seawater for 2.5 months in a flow-through seawater table. The substrates were trimmed to approximately 1 cm$^2$ in size, inspected for previous recruits, and were inspected and cleaned (except for the tile pieces) to ensure desired biological forms were not contaminated by multiple algal/other species. All substrate samples were randomly assigned to control and experimental (antibiotic) groups with a total of five replicates for each substrate for each treatment.

Experimental substrates were washed and soaked 5 times in separate 5 mg L$^{-1}$ concentrations of antibiotic (chloramphenicol in 0.45 μm FSW) for 1 hr periods (total 5 hrs. each substrate). Control substrates were similarly washed and soaked in 0.45 μm FSW. Each substrate sample was placed in a randomly assigned cell in a set of Corning™
brand 6-cell culture trays with a medium corresponding to treatment (i.e. 0.45 μm FSW or antibiotic solution). Trays were covered and translucent. Appropriate replicated control cells (antibiotic; no antibiotic) without substrates were established. Ten cultured, actively swimming, barrel-shaped *M. capitata* larvae (9 days post fertilization) were pipetted into each cell. The trays were partially submerged in running seawater in a semi-shaded flow-through seawater table. Fluid mediums in each cell were replaced on a daily basis. On the seventh day cells and substrates were examined at 12x using a Wild Heerbrugg dissecting microscope and scored for settlement (defined above). Proportional data were arcsine square-root transformed for factorial ANOVA analysis. In the case of no settlement in replicated FSW controls (no substrate), control values were excluded from the ANOVA due to lack of variance with the justification that proportional settlement in cells with substrates represented the difference from mean settlement in controls. Post-hoc comparisons were made using a Tukey HDS test with $\alpha = 0.05$.

Experiment 2

An additional experiment was conducted to determine whether the antibiotic might effect larval settlement through direct effects on the larvae as opposed to its effects on the substrate bacterial community. This experiment involved four treatment groups including: larvae pre-exposed to antibiotic put in cells with substrates containing antibiotic solution; larvae pre-exposed to antibiotic put in cells with substrates containing FSW only; larvae pre-exposed only to FSW put in cells with substrates containing FSW only; and larvae pre-exposed only to FSW put in cells with substrates containing antibiotic solution.
Two species of crustose coralline algae (CCA6 and CCA8), dead coral substrate covered with filamentous algae, and terra-cotta tile fragments newly broken from settlement plates (conditioned in running seawater for 12 months in a flow-through seawater table) were collected and processed as described above. Substrate samples were randomly assigned to antibiotic and 0.45 μm FSW treatment groups, and were separately exposed to their respective treatments for a period of six days. The substrates were maintained in preconditioned plastic cups half submerged in running seawater in a semi-shaded flow-through seawater table. Treatment fluids were exchanged daily and substrates were rinsed rigorously.

Ten 500 ml Nalgene™ polyethylene bottles (translucent) containing high concentrations of cultured Montipora capitata larvae (7 days post fertilization) were selected and randomly assigned, five to pre-exposure with antibiotic solution and five to continued exposure to 0.45 μm FSW only, for a period totaling seven days. Bottles were capped and allowed to float in running seawater in a semi-shaded flow-through seawater table. Bottles were cleaned and fluids exchanged daily. Larvae and cleaning apparatus were exposed only to their respective treatment medium.

Each substrate sample was placed in a randomly assigned cell in a set of Corning™ brand 6-cell culture trays with its corresponding treatment medium. The replicate bottles of cultured larvae were combined by treatment, and ten actively swimming, barrel shaped larvae were pipetted into each cell corresponding to their assigned treatment. Antibiotic exposed larvae assigned to FSW cells were rinsed thoroughly and repeatedly with 0.45 μm FSW prior to placement in their cells (to avoid contamination of the medium with antibiotic). All other groups of larvae were treated
similarly within their respective treatment medium. Six replicates of each substrate in each treatment were established along with replicated controls of larvae in cells with only the treatment mediums. Trays were partially submerged in running seawater in a semi-shaded flow-through seawater table to maintain seawater temperatures close to ambient. Fluids were replaced on a daily basis. On the seventh day cells and substrates were examined at 12x using a Wild Heerbrugg dissecting microscope and scored for settlement (as defined above). Proportional data were arcsine square-root transformed for factorial ANOVA analysis, with control (no substrate) values treated as described in Experiment 1. Post-hoc comparisons were made using a Tukey HDS test ($\alpha = 0.05$).

GABA Treatments

The effect of gamma aminobutyric acid (GABA) on *Montipora capitata* larvae settlement was examined by exposing replicates of 10 cultured, actively swimming, barrel-shaped larvae (13 days post fertilization) to approximately 10 ml of $10^{-6}$ M, $10^{-5}$ M, $10^{-4}$ M, $10^{-3}$ M, and $10^{-2}$ M concentrations of GABA (in 0.45 μm FSW) in FSW conditioned glass scintillation vials (see Morse et al. 1979). Five replicates of each treatment were established with replicate controls (0.45 μm FSW), and were capped and maintained half submerged in running seawater in a semi-shaded flow-through seawater table. Vials were examined every day for three days and at three weeks at 12x with a Wild Heerbrugg dissecting microscope and scored for settlement and survival. Proportional data were arcsine square-root transformed prior to statistical analysis.

Settlement Substrates in the Field

Natural and artificial substrates selected for settlement were recorded and
categorized in an effort to identify the range of substrates selected for natural and seeded settlement on field plate sets over a two year period. A description of the data is presented. Preference could not be determined statistically as data collection was haphazard and substrate availability between sites was inconsistent. Substrates upon which larvae settle do not necessarily identify inducer communities (Morse et al. 1988, Morse et al. 1996, Heyward and Negri 1999, Negri et al. 2001). Available substrates with no settlement were also recorded.

**Settlement and Field Plate Conditioning**

Settlement preference for plate sets differing in lengths of time of field conditioning was examined in two separate trials at each of four field sites. Summer settlement in 2000 was compared between 3.3 and 15.8 month conditioned plates, and in 2001 between 15.8 and 28.3 month conditioned plates. Full examination of plates occurred over a three-week period in a pair-wise fashion (i.e., one new and one old plate set from each post at a site were always examined on the same day). Preference was examined by calculating the proportional difference between the sum of all settlers on plates of similar age on each post (two plates for each age group), divided by the total of all settlers on the four plates of each post ((sum of old – sum of new)/total). Posts with less than two natural settlers were excluded from the analysis; thus, comparisons were restricted to Central and South Bay sites. Only natural settlement in summer months was scored. Data for each year were analyzed separately using ANOVA, testing whether the mean preference differed from zero (no preference) at the four sites. Post-hoc comparisons were made for each site in each year using single sample t-tests applying a Bonferroni correction for multiple comparisons (Moore and McCabe 1993).
Settlement and Surface Orientation in the Field

Proportional settlement on plate surfaces was compared to ascertain larval settlement preference for surface orientation. Plate surfaces were categorized as top, bottom, middle and sides. Natural summer settlement of *Montipora capitata* in each surface category was determined and pooled across plates within each of four sites, including South Fringing, South Patch, Central Fringing and Central Patch reefs in 2000 and 2001. Low settlement at North Bay sites prohibited their inclusion. Proportional data were arcsine square-root transformed. A Factorial ANOVA and Tukey HDS tests (α = 0.05) were used to examine surface preference, with the plate top surface category removed prior to analysis (due to negligible settlement) to meet model assumptions. Year was treated as a replicate factor, but was dropped from the final analysis due to limited degrees of freedom and its insignificant effect in exploratory analyses.

Settlement Competency

Proportional Settlement Over Time

Proportional settlement of cultured *Montipora capitata* larvae over time was examined in five replicate nine-liter glass aquaria. Five 10.0 x 9.5 x 1.2 cm unglazed terra-cotta tile plates were conditioned in running seawater in a semi-shaded flow-through seawater table for approximately two months. Prior to use in the experiment, these plates were examined to ensure coral larvae caught in the seawater system had not settled to the plates during conditioning. Sea anemones that had settled on the plates were removed. Each plate was rinsed thoroughly with 0.45 μm FSW and was placed, with six liters of 0.45 μm FSW, in an individual aquarium. Three 0.4 cm thick PVC clips (1.27 cm diameter, pre-conditioned in running seawater) were attached to each plate. This raised
the plates above aquaria glass bottom surfaces and allowed for plate transfer without directly handling plate surfaces. The aquaria were maintained half submerged in running seawater in a semi-shaded flow-through seawater table to maintain seawater temperatures close to ambient. Daytime temperatures in the aquaria ranged between 26.5 and 27.9°C. Water levels in each aquarium were maintained over time by adding 0.45 µm FSW. Aeration and water motion were maintained in each aquarium by bubbling a slow but constant stream of air through a Pasteur pipette fitted to an air-line.

One thousand cultured *M. capitata* larvae (2.5 days post spawning) were added to each aquarium. The following day, each plate was transferred to a large glass bowl containing 0.45 µm FSW, briefly examined at 12x with a Wild Heerbrugg dissecting microscope, and returned. Plates consistently remained submerged during transport and inspection. Settlement was scored and locations mapped (with the aid of a 10 x 10 cm monofilament sectioned quadrat) for each plate surface four, seven, 12, 17 and 22 days post spawning. Larvae displaying strong adherence to the substrate with evident morphological change (from squat form to tentacle development) were considered settled. The low levels of settlement observed on the clips and aquarium walls were recorded but not included in the plate settlement tallies. Although new settlement was observed to have occurred, significant mortality of settlers on two of the plates between days seven and 12 made their results on day 12 difficult to interpret. Original plates were replaced by similarly sized and conditioned terra-cotta tiles on day 12 to ease mapping efforts. A repeated measures ANOVA comparing settlement day⁻¹ between each of the first three census periods (times within which settlement occurred) was conducted for the three plates not affected by mass mortality. Settlement values were log₁₀ transformed to
meet model assumptions. All aquaria were considered to be saturated with larvae; thus, settlement rates were not proportionally adjusted (circumventing the need for multiple transformations on data that exhibited analogous trends).

**Long-term Settlement Competency**

Long-term settlement competency of *Montipora capitata* larvae was investigated directly through experimentation. Actively swimming, barrel-shaped larvae raised in 500 ml Nalgene™ culture bottles were added to cells in Corning™ brand 6-cell culture trays containing 0.45 μm FSW with filamentous covered coral substrate, CCA6 and/or CCA8. The trays were partially submerged in running seawater in a semi-shaded flow-through seawater table to maintain seawater temperatures close to ambient. Cells were monitored over time with FSW changes occurring daily, weekly or biweekly as needed. Settlement (as defined above) was scored at each inspection, and competency was calculated as the interval between the date of colony spawning and relevant inspection dates flanking settlement events. Monitoring continued until all viable larvae had settled or perished. Additional information related to larval settlement competency was gained through examination of larval age and settlement timing in the larval settlement preference experiments.

**Field Settlement Over Time**

Natural *Montipora capitata* settlement on 33 to 168 recruitment plate sets established at the six Kane‘ohe Bay field sites (Figure 2.1) was examined with respect to settlement timing as defined by six census periods over a two-year period (1999 to 2001). Data from 11 plate sets were pooled to give a total proportional estimate of new settlement versus census period. Data corresponding to similar monitoring during the 1999 summer
spawning period were not included, as replicates were not equally examined over the course of the year due to the larval seeding experiments.

Results

Settlement Preference

Test of General Substrate Preference

Mean settlement (± S.E.) of *Montipora capitata* larvae on tested substrates is shown in Figure 2.3. A significant difference was found in settlement between substrates (ANOVA, \( n = 55, F_{10,54} = 3.12, P = 0.004 \)). Two groups of substrates overlapped in terms of settlement preference, but only CCA6 and CCA8 (encrusting forms of crustose coralline algae) experienced significantly higher levels of settlement than CCA1 (branching form of crustose coralline algae) and unconditioned beach rubble. No settlement was evident in the controls.

![Graph showing mean settlement of *Montipora capitata* larvae on various substrates](image)

**Figure 2.3.** Mean (± S.E.) proportional settlement of *M. capitata* larvae on various substrates (CCA = crustose coralline algae; FA = filamentous algae covered coral skeleton; * = no settlement).
Antibiotic Treatments

Experiment 1

No settlement of larvae occurred in cells without substrates. Substrates exposed to the antibiotic treatment showed significantly lower levels of settlement across all substrate groups (Table 2.2, Figure 2.4). There were no significant differences in settlement between the three CCA types and the filamentous algae covered coral skeleton; however, the four differed significantly from plate fragments (Table 2; FA=CCA8=CCA6=CCA2>Plate) in contrast to earlier findings (Figure 2.3).

Table 2.2. Factorial ANOVA of mean proportional M. capitata settlement (arcsine square-root transformed) on antibiotic treated versus FSW control substrates.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1</td>
<td>1.7065</td>
<td>1.7065</td>
<td>20.73</td>
<td>0.0000</td>
</tr>
<tr>
<td>Substrate</td>
<td>4</td>
<td>4.8914</td>
<td>1.2229</td>
<td>14.86</td>
<td>0.0000</td>
</tr>
<tr>
<td>Treatment x Substrate</td>
<td>4</td>
<td>0.0086</td>
<td>0.0022</td>
<td>0.03</td>
<td>0.9986</td>
</tr>
<tr>
<td>Residual</td>
<td>40</td>
<td>3.2922</td>
<td>0.0823</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>49</td>
<td>9.8987</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2.4. Mean (± S.E.) proportional settlement of M. capitata larvae on substrates treated with an antibiotic compared to substrates in FSW controls (CCA = crustose coralline algae; FA = filamentous algae covered coral skeleton).
Experiment 2

Larvae did not settle in cells without substrates. No significant effect of larvae pre-exposure to antibiotic was detected (Table 2.3). Pre-exposed larvae actually displayed a tendency for higher mean proportional settlement across treatments (Figure 2.5). Substrate treatments with antibiotic solution had significantly lower settlement than comparable controls for all substrates with the exception of CCA8, which displayed a similar trend (Table 2.3, Figure 2.6). There was a significant substrate effect for the combined treatments (Table 2.3; FA = CCA8 > CCA8 = CCA6 > CCA6 = Plate).

Table 2.3. Factorial ANOVA examining the effects of larvae pre-exposure to antibiotics, substrate exposure to antibiotics and substrate type on mean proportional settlement of *M. capitata* larvae.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larvae Pre-Trmt (L)</td>
<td>1</td>
<td>0.1455</td>
<td>0.1455</td>
<td>2.25</td>
<td>0.1377</td>
</tr>
<tr>
<td>Substrate Trmt (ST)</td>
<td>1</td>
<td>2.5524</td>
<td>2.5524</td>
<td>39.44</td>
<td>0.0000</td>
</tr>
<tr>
<td>Substrate (S)</td>
<td>3</td>
<td>1.4287</td>
<td>0.4762</td>
<td>7.36</td>
<td>0.0002</td>
</tr>
<tr>
<td>L x ST</td>
<td>1</td>
<td>0.0095</td>
<td>0.0095</td>
<td>0.15</td>
<td>0.7033</td>
</tr>
<tr>
<td>L x S</td>
<td>3</td>
<td>0.0512</td>
<td>0.0171</td>
<td>0.26</td>
<td>0.8518</td>
</tr>
<tr>
<td>ST x S</td>
<td>3</td>
<td>0.5356</td>
<td>0.1785</td>
<td>2.76</td>
<td>0.0469</td>
</tr>
<tr>
<td>L x ST x S</td>
<td>3</td>
<td>0.0150</td>
<td>0.0050</td>
<td>0.08</td>
<td>0.9667</td>
</tr>
<tr>
<td>Residual</td>
<td>80</td>
<td>5.1776</td>
<td>0.0647</td>
<td>0.0150</td>
<td>0.9667</td>
</tr>
<tr>
<td>Total</td>
<td>95</td>
<td>9.9155</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2.5. Mean (± S.E.) proportional settlement of *M. capitata* larvae pre-exposed to antibiotic and FSW treatments in antibiotic and FSW substrate treatments (data for substrates within a treatment group combined).
Figure 2.6. Mean (± S.E.) proportional settlement of *M. capitata* larvae on substrates in antibiotic solution compared to substrates in FSW controls (CCA = crustose coralline algae; FA = filamentous algae covered coral skeleton).

GABA Treatments

No settlement or metamorphic responses (polyp balls) were observed in any treatment within three days following exposure to GABA. GABA at 10\(^{-2}\) M was toxic to *Montipora capitata* larvae, with only one of 50 larvae (2%) surviving after two days exposure. GABA also appeared to be toxic at 10\(^{-3}\) M to larvae over a three-week period. Qualitative behavioral responses appeared to differ between treatments within the first three days. Larvae in the 10\(^{-3}\) M treatment displayed little movement, those in the 10\(^{-4}\) M treatment were noticeably sluggish, while active swimming was observed in the 10\(^{-5}\) M, 10\(^{-6}\) M and control treatments. At the end of three weeks, all 10\(^{-2}\) M and 10\(^{-3}\) M exposed larvae were dead, two larvae each had settled and metamorphosed in the 10\(^{-4}\) M (mean survival = 46 ± 12 % S.E., n = 5) and 10\(^{-6}\) M (mean survival = 76 ± 19 % S.E., n = 5) treatments, no 10\(^{-5}\) M exposed larvae had settled (mean survival = 82 ± 6 % S.E., n = 5), and one control larvae had settled and metamorphosed (mean survival = 84 ± 13 % S.E.,
n = 5). No significant difference in settlement existed between $10^{-4}$ M GABA, $10^{-6}$ M GABA and 0.45 μm FSW control treatments (Kruskal-Wallis AOV, n = 15, $H = 0.56$, $P = 0.756$). Survival was not affected by GABA presence at tested concentrations below $10^{-3}$ M (ANOVA, n = 20, $F_{3,19} = 1.61$, $P = 0.226$).

**Settlement Substrates in the Field**

Settlement on plate sets was common on smooth “exposed” surfaces and in cryptic grooves and crevices of the tiles and encrusting communities. Settler surface distributions ranged from highly aggregated to well dispersed. Specific substrate types were recorded for 16% of the recent settlements observed (n = 3,321; South Fringing = 390 settlers, South Patch = 163, Central Fringing = 1,845, Central Patch = 711, North Fringing = 71, North Patch = 141). Substrates receiving greater than one percent of settlements at a site are shown in Figure 2.7. *Montipora capitata* larvae settled on a variety of encrusting community species as well as on conditioned tile surfaces. Various forms of crustose coralline algae hosted large percentages of larval settlement at North and Central Kāne‘ohe Bay sites, but were not the dominant supporting substrates at South Bay sites. Oyster shell surfaces created cryptic habitat and also supported large numbers of settlers, particularly in South and Central Kāne‘ohe Bay. Settlement on macroalgae (*Dictyosphaeria cavernosa*), solitary tunicates, dead coral skeleton, live and dead branching and live encrusting bryozoans, and slime mold surfaces was observed but was rare (<1%). Common substrates not observed to host settlement included all observed sponges, colonial tunicates, live corals, sedentary soft tube polychaetes, hydroids, chitons, fish eggs, various macroalgae (including *Caulerpa* sp. and *Bryopsis* sp.) and sediment.
Figure 2.7. Percent *M. capitata* settlement on recorded substrates at settlement survey sites in Kāneʻohe Bay (SF = South Bay Fringing reef; SP = South Bay Patch reef; CF = Central Bay Fringing reef; CP = Central Bay Patch reef; NF = North Bay Fringing reef; NP = North Bay Patch reef). Substrates include: Bk = blank tile with presumed biological film; CCA = crustose coralline algae; DCCA = dead CCA; DEB = dead encrusting bryozoan; DM = domed mollusk; Vm = vermetids; Oy = oyster; Doy = dead oyster shell; Fil = filamentous algae; Ht = *Hydroides* sp. tube, and; Mix = larval base in contact with more than one substrate type.
Settlement and Field Plate Conditioning

The mean settlement preference index was $-0.068 \pm 0.119 \text{ S.E.}$ for the 3.3 and 15.8 month comparison and $-0.040 \pm 0.071 \text{ S.E.}$ for the 15.8 and 28.3 month comparison. Neither index differed significantly from zero, and site indices did not differ significantly from each other, suggesting no statistically notable natural settlement preference for plates based on the levels of conditioning (2000 comparison, ANOVA, $n = 24$, $F_{3, 20} = 2.03$, $P = 0.142$; 2001 comparison, ANOVA, $n = 28$, $F_{3, 24} = 1.30$, $P = 0.298$). Post-hoc t-tests of individual sites in each year did not find significant differences from zero ($P > 0.05$) when corrected for making multiple comparisons.

Settlement and Surface Orientation in the Field

Percent summer settlement to plate surfaces averaged $0.04 \pm 0.03 \% \text{ S.E.}$ on plate tops; $25.01 \pm 4.09 \% \text{ S.E.}$ on plate sides, $42.30 \pm 9.91 \% \text{ S.E.}$ on inner surfaces, and $32.64 \pm 7.26 \% \text{ S.E.}$ on plate bottoms. Overall, the proportion of settlers on top surfaces was lower than that on each of the other surfaces (Figure 2.8), and significantly higher levels of settlers where identified on inner surfaces than sides (Table 2.4). Settlement preference for all but the top surfaces varied by site (Figure 2.8, Table 2.4).

Settlement Competency

Proportional Settlement Over Time

Although not quantified, large numbers (estimated in the hundreds) of larvae were observed attached to each of the plates three days following spawning. Settlement data at each census date are shown in Table 2.5. The mean number of new *Montipora capitata* settlers was highest in the initial census four days after spawning and declined substantially with time. Settlement rates (settlers day$^{-1}$) were significantly different over
Figure 2.8. Proportion of *M. capitata* summer settlers on plate surfaces (S = South; C = Central; F = Fringing reef; P = Patch reef).

Table 2.4. Factorial ANOVA of the proportion of *M. capitata* summer settlers (arcsine square-root transformed) on side, middle and bottom plate surfaces at South and Central Fringing and Patch reefs.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>3</td>
<td>0.0007</td>
<td>0.0002</td>
<td>0.0163</td>
<td>0.9970</td>
</tr>
<tr>
<td>Surface</td>
<td>2</td>
<td>0.1348</td>
<td>0.0674</td>
<td>4.4812</td>
<td>0.0352</td>
</tr>
<tr>
<td>Site*Surface</td>
<td>6</td>
<td>0.9701</td>
<td>0.1617</td>
<td>10.7520</td>
<td>0.0003</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>0.1805</td>
<td>0.0150</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

time, with rates at Time 1 > Time 2 > Time 3 (repeated measures ANOVA, n = 3, $F_{2,4} = 131.77, P = 0.0002$). Two larvae were observed attached to plate 2 on day 17, but could not be classified as settled.

The measured proportion of available larvae that cumulatively settled on all plates averaged 45.1 % (± 3.1 % S.E., n = 5). An additional 12 settlers were noted on clips (mean = 2.4 ± 2.2 S.E., n = 5) and 47 larvae were found settled on aquarium walls (mean = 9.4 ± 2.2 S.E., n = 5). Upon termination of the experiment, free-swimming larvae were recovered but were few in number (mean = 4.2 ± 1.9 S.E., n = 5).
Table 2.5. *Montipora capitata* aquaria settlement on plates by census date (days after spawning) under laboratory conditions (*new settlement on two plates could not be accurately measured due to high mortality of previously settled spat*).

<table>
<thead>
<tr>
<th>No. Days Post Spawning</th>
<th>Mean No. New Settlers (S.E.)</th>
<th>Range</th>
<th>Cumulative Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>363.2</td>
<td>39.9</td>
<td>228 - 473</td>
<td>5</td>
</tr>
<tr>
<td>7</td>
<td>74.4</td>
<td>9.3</td>
<td>47 - 103</td>
<td>5</td>
</tr>
<tr>
<td>12</td>
<td>23.0</td>
<td>3.2</td>
<td>18 - 29</td>
<td>*3</td>
</tr>
<tr>
<td>17</td>
<td>0</td>
<td>( - )</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>22</td>
<td>0</td>
<td>( - )</td>
<td>0</td>
<td>5</td>
</tr>
</tbody>
</table>

Long-term Settlement Competency

*Montipora capitata* larvae settled in proportionately high numbers (83 %) at 42 days post spawning. However, settlement was reduced at 56 plus days (settlement ≤11 %; Table 2.6). Although few in number, some *M. capitata* larvae displayed an ability to settle well beyond 120 days. Settlements at 191 to 197 and 207 to 213 days were monitored for an additional 109 days. These settlers metamorphosed into normal sized single polyps that survived throughout the monitoring period and maintained appearances consistent with those observed naturally in the field.

Field Settlement Over Time

Field settlement over time appeared to be highest within the spawning season (late May to August with peaks in June and July; Table 2.7; see Kolinski Chapter 3). The percentage of new *Montipora capitata* settlers identified during July and August censuses totaled 98.02 % over the two-year period. A total 1.86 % of new settlers were noted in the October censuses, and only 0.12 % of new settlers were noted in February and March in 2000 and March and April in 2001. Although these estimates cannot reliably be corrected for mortality of settlers not observed, consistent order of magnitude differences over time suggests proportionately high settlement soon after spawning, but there appears to be some potential for settlement delay.
Table 2.6. Settlement competency periods of *M. capitata* larvae under laboratory conditions (Note: two additional trials between 9-29-98 and 11-19-98 resulted in no settlement).

<table>
<thead>
<tr>
<th>Competency (days)</th>
<th>Spawning Date</th>
<th>Settlement Date</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>9 to 16</td>
<td>7-26-98</td>
<td>8-5-98 to 8-12-98</td>
<td>89% (179 of 201) settlement. Ten larvae placed in each of twenty cells, five with filamentous algae covered coral skeleton, five with CCA2, five with CCA6 and five with CCA8. No settlement differences between substrates. No settlement in controls. Seven day exposure of larvae to substrates.</td>
</tr>
<tr>
<td>42 to 45</td>
<td>7-26-98</td>
<td>9-7-98 to 9-10-98</td>
<td>83% (33 of 40) settlement. Eight larvae placed in each of five cells with filamentous algae covered coral skeleton. No settlement in controls. Seven day exposure to substrates.</td>
</tr>
<tr>
<td>56 to 64</td>
<td>7-26-98</td>
<td>9-21-98 to 9-29-98</td>
<td>11% (1 of 9) settlement. Three larvae placed in each of three cells with CCA8. No settlement in controls. Eight day exposure to substrates.</td>
</tr>
<tr>
<td>145 to 164</td>
<td>6-26-98</td>
<td>11-19-98 to 12-8-98</td>
<td>7% (1 of 15) settlement. Five larvae placed in each of three cells with filamentous algae covered coral skeleton and CCA6 and CCA8. No controls. Thirty-two day exposure to substrates.</td>
</tr>
<tr>
<td>207 to 213</td>
<td>6-26-98</td>
<td>1-20-99 to 1-26-99</td>
<td>7% (1 of 15) settlement. Five larvae placed in each of three cells with filamentous algae covered coral skeleton and CCA6 and CCA8. No controls. Eighty-one day exposure to substrates.</td>
</tr>
<tr>
<td>191 to 197</td>
<td>7-26-98</td>
<td>2-3-99 to 2-9-99</td>
<td>3% (1 of 30) settlement. Ten larvae placed in each of three cells with filamentous algae covered coral skeleton and CCA6 and CCA8. No controls. Ninety-five day exposure to substrates.</td>
</tr>
</tbody>
</table>

Table 2.7. Natural settlement of *M. capitata* larvae observed over time at settlement survey sites in Kane‘ohe Bay. Estimates extrapolated to mean number m$^{-2}$ of colonizable reef over time.

<table>
<thead>
<tr>
<th>Census Date</th>
<th>No. New Settlers Observed</th>
<th>No. Plate Sets</th>
<th>Estimated Mean No. New Settlers m$^{-2}$ colonizable substrate</th>
<th>% Two-Year Total of Estimated Mean No. New Settlers m$^{-2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct 1999</td>
<td>41</td>
<td>33</td>
<td>131</td>
<td>1.19</td>
</tr>
<tr>
<td>Feb/Mar 2000</td>
<td>6</td>
<td>84</td>
<td>8</td>
<td>0.07</td>
</tr>
<tr>
<td>Jul 2000</td>
<td>6374</td>
<td>168</td>
<td>3994</td>
<td>36.23</td>
</tr>
<tr>
<td>Oct 2000</td>
<td>118</td>
<td>168</td>
<td>74</td>
<td>0.67</td>
</tr>
<tr>
<td>Mar/Apr 2001</td>
<td>9</td>
<td>168</td>
<td>6</td>
<td>0.05</td>
</tr>
<tr>
<td>Jul/Aug 2001</td>
<td>10872</td>
<td>168</td>
<td>6812</td>
<td>61.79</td>
</tr>
</tbody>
</table>
Discussion

Settlement Preference

The complete absence of larval settlement in control cells lacking substrates in all but one of the laboratory experiments (one larvae settled in the GABA experiments after an extended period of time), in comparison to the generally high settlement levels in cells with substrates, strongly suggests that an external cue(s) stimulates settlement and metamorphosis of *Montipora capitata* larvae. However, laboratory and field observations failed to demonstrate *M. capitata* settlement preference for a single macroscopic biological substrate, as has been shown/suggested for various Atlantic and Pacific coral species (including members of the family Acroporidae; Morse et al. 1988, 1994, Morse and Morse 1991, Morse et al. 1996; Table 2.8). *Montipora capitata* larvae did show preference for some hard substrate types over others, with at least two encrusting species of crustose coralline algae (CCA6, CCA8) being favored over unconditioned rubble and branching coralline algae (CCA1) in laboratory experiments. In addition, recently broken settlement plate fragments tended to be less favored than select species of CCA and filamentous algae covered dead coral substrate, despite length of parent plate conditioning. However, it should be noted that the plate fragments in Figures 2.3 and 2.4 were created one day prior to preference experiments. Given the nonporous structure of the parent plates, the level of plate fragment surface conditioning varied tremendously within a sample (see Negri et al. 2001 settlement results related to unconditioned tiles). Proportional settlement of larvae on plate fragments created six days prior to preference testing was high for fragments not exposed to antibiotics, and did not differ from that on comparable CCA substrates (Figure 2.6). In the field, *M. capitata* larvae settled on a
variety of encrusting community species as well as conditioned, uncolonized tile surfaces. Identification of settlement substrate types by itself cannot verify a specific chemical inducer community, as settlement may occur on alternate substrates after larval contact with inducer organisms (Morse et al. 1988, Morse et al. 1996, Heyward and Negri 1999, Negri et al. 2001). However, the distribution of *M. capitata* across a wide range of habitats (Maragos 1972, 1977, Kolinski and Jokiel 2002) and the absence of observations of any specific preference in the laboratory and field suggests that, if *M. capitata* settlement is chemically induced, the biological community(s) producing the chemical inducer(s) is likely to be diverse and/or fairly ubiquitous in nature.

Marine bacteria have been noted as inducers of larvae settlement in a variety of marine invertebrate species (reviewed by Johnson et al. 1997, Leitz 1997, and Unabia and Hadfield 1999, Negri et al. 2001) including at least one species of scleractinian coral (Negri et al. 2001, see also Harrigan 1972 and Golbuu 1996). In some cases, associations between larval settlers and specific encrusting macroscopic organisms have been found to depend on the presence of surface bacteria (Johnson et al. 1991, 1997, Johnson and Sutton 1994, see also Negri et al. 2001). Laboratory experiments involving the antibiotic chloramphenical strongly supported the hypothesis of a role for bacteria in the induction of *M. capitata* larvae settlement. The experiments suggested the antibiotic directly affected the prokaryotic community and had no direct negative effect on larval ability to settle and metamorphose. Antibiotic effects on settlement likely resulted from a reduction in the entire prokaryotic community including community members that induce *M. capitata* settlement. Alternatively, antibiotics may have acted to change the natural bacterial community structure in a manner that allowed for a subsequent disproportionate...
increase in bacteria that inhibited settlement (see Johnson et al. 1997). This alternative is based on the premise that antibiotics never completely eradicate bacterial populations, which may recover as antibiotic concentrations decline. Nevertheless, differences associated with settlement levels at particular sites (Kolinski Chapter 3) and orientations may reflect different bacterial compositions inhabiting substrate surfaces.

Experimentation on the efficacy of isolated strains of bacteria to induce settlement should help to further clarify the likelihood of the inducer hypothesis and would be the next logical step in isolating and identifying potentially active inducer molecules and associated community surface distributions.

Gamma aminobutyric acid (GABA) does not appear to play a stimulus role in the settlement of *M. capitata* larvae despite its production, release and/or uptake by some marine bacteria (Imhoff 1986, Mountfort and Pybus 1992a, 1992b, Kaspar and Mountfort 1995, Johnson et al. 1997). GABA has been shown to induce settlement in larvae of various marine invertebrates (Morse et al. 1979, Heslinga and Hillmann 1981, Morse 1990, Rumrill and Cameron 1983, Pearce and Scheibling 1988, Nadeau et al. 1989, Avila et al. 1996); however, other tested cnidarian larvae, including *Agaricia* spp. (Morse et al. 1988), *Alcyonium siderium* (Sebens 1983), and *Phialidium gregarium* (McCauley 1997), also failed to settle in response to GABA exposure. GABA concentrations at or above $10^{-3}$ M were found to be toxic to *M. capitata* larvae. Although controversy exists as to the mechanism by which GABA influences invertebrate larvae to settle (Pawlik 1990, 1992), it has been suggested that inducement results partially through inhibition of neural activity related to ciliary movement (Rumrill and Cameron 1983, Barlow 1990, Pawlik 1990, Mountfort and Pybus 1992a, 1992b). Qualitative observations suggested $10^{-3}$ M and
$10^{-4}$M GABA treatments reduced *M. capitata* larval swimming activity. If such action was the direct result of inhibition of cilia functioning, then cessation of cilia movement alone is not enough to stimulate settlement and metamorphosis in *M. capitata* larvae.

Table 2.8 summarizes available information related to coral settlement induction and catalogues scleractinian species in terms of their reported larval settlement preference behavior as generalists or specialists, highlighting identified or presumed inducer chemicals and/or communities. The relevance of distinguishing these groups is at least three fold. First, such categorization may help elucidate individual species distributions and recruitment rates (Morse et al. 1988, Morse 1992, Carlon and Olson 1993, Morse and Morse 1996, Raimondi and Morse 2000, Heyward and Negri 1999). Second, limited or specialized preference highlights potential life-history vulnerability with regards to physical and/or chemical benthic anthropogenic impacts. Third, limitations in natural recovery of degraded reef areas and method options to artificially accelerate reef recovery may be better understood through clarification of the specifics of larval settlement-substrate dependence (Negri et al. 2001). Available information to date is extremely limited and includes reported species preferences that require more thorough investigation. Excluding those corals for which additional types of substrate need to be tested (Potential Preference in Table 2.8), an equal number of coral species are listed as generalists and specialists (note: the majority of specialists show weak settlement preferences, with variability in substrate selection evident). Given the apparent association of *M. capitata* larval settlement with marine bacteria and the propensity to settle on a wide variety of conditioned substrate types, *M. capitata* is categorized as a generalist. Such categorization does not disallow association with one particular species.
Table 2.8. Suggested classification of scleractinian species based on available information of observed larval settlement preferences. Generalist = no strong preference among different types of tested substrates. Specialist = significant preference for a limited number of substrate types. *= Additional types of substrate need to be tested.

<table>
<thead>
<tr>
<th>Species</th>
<th>Investigator</th>
<th>Preference/Inducer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Generalists</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora millepora</td>
<td>Heyward and Negri (1999)</td>
<td>- Variety of substrates induce settlement in laboratory experiments including seven species of crustose red algae, two species of branching coralline algae, bare rubble, CCA skeleton and Goniastrea skeleton.</td>
</tr>
<tr>
<td></td>
<td>Negri et al. 2001</td>
<td>- Pseudoalteromonas sp. isolated from CCA Hydrolithon onkodes induces partial metamorphosis in high percentage of larvae, but few attach to substrate (perhaps due to use of artificial seawater).</td>
</tr>
<tr>
<td>Agaricia danai</td>
<td>Morse et al. 1988.</td>
<td>- Settlement on mixed CCA species on coral rubble, microalgal and bacterial films on coral substrate, and on boiled coral substrate (microalgal and bacterial films present prior to boiling). Inducer(s) unknown.</td>
</tr>
<tr>
<td>Favia fragum</td>
<td>Carlon and Olson 1993 (but see Lewis 1974).</td>
<td>- No preference in field trials—bare coral rubble, filamentous algae coated rubble and coralline algae. Inducer(s) unknown.</td>
</tr>
<tr>
<td>Montipora capitata</td>
<td>This study.</td>
<td>- High levels of settlement on at least three species of crustose coralline algae and filamentous algae covered coral skeleton. Role of marine bacteria evident in laboratory experiments.</td>
</tr>
<tr>
<td>Pocillopora damicornis</td>
<td>Harrigan 1972.</td>
<td>- Most hard substrates tested in laboratory experiments. Suggested inducer a thin living diatomaceous-bacterial film, particularly in association with green filamentous algae.</td>
</tr>
<tr>
<td>Specialists</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Strong Preference</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricia humilis</td>
<td>Morse et al. 1988,</td>
<td>- Specific preference for three tested species of CCA, including Hydrolithon boeresenii and Peyssonella sp. Sulfonated lipoglycosaminoglycon (polysaccharide) isolated from walls of CCA Hydrolithon boergensenii induces 100% metamorphosis of larvae. Pacific CCA Hydrolithon reinboldii also induces settlement. Induction by specific receptor recognition proposed.</td>
</tr>
<tr>
<td></td>
<td>Morse and Morse 1991 (see also Morse et al. 1994), Morse et al. 1996, Morse and Morse 1996, Raimondi and Morse 2000</td>
<td></td>
</tr>
<tr>
<td>- Weak Preference</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricia agaricites</td>
<td>Carlon and Olson 1993.</td>
<td>- Suggestive preference for rubble coated with CCA Paragoniolithon typica and Spongites sp. 2. Minor settlement on bare rubble.</td>
</tr>
<tr>
<td>A. tenuifolia</td>
<td>Morse et al. 1988</td>
<td>- Significant preference for mixed CCA species on coral rubble compared to microalgal and bacterial films on coral substrate, and boiled coral substrate (CCA present prior to boiling). No settlement in seawater only treatments. Non-stringent CCA preference suggested.</td>
</tr>
</tbody>
</table>

(continued)
<table>
<thead>
<tr>
<th>Species</th>
<th>Investigator</th>
<th>Preference/Inducer</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Specialists</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>- <strong>Weak Preference</strong></td>
</tr>
<tr>
<td>A. tenuifolia</td>
<td>Morse and Morse</td>
<td>- Sulfonated lipoglycosaminoglycon (polysaccharide) isolated from walls of CCA <em>Hydrolithon boergensis</em> induces high level of settlement on polystyrene container.</td>
</tr>
<tr>
<td></td>
<td>1991, Morse et al.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1994.</td>
<td></td>
</tr>
<tr>
<td>retiformis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stylaraea</td>
<td>Golbuu 1996.</td>
<td>- Significant preference for rocks covered with microbial reef films with limited settlement on CCA <em>Hydrolithon reinboldii</em>, <em>Peysonelia</em> sp. and reef rock devoid of CCA and reef microbial films.</td>
</tr>
<tr>
<td>punctata</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Potential Preference</em></td>
<td></td>
</tr>
<tr>
<td>Acropora</td>
<td>Morse et al. 1996.</td>
<td>- <em>Acropora digitifera</em> and <em>A. nasuta</em> preference for CCA <em>Hydrolithon reinboldi</em> with no settlement in brown algae <em>Lobophora variegata</em> or seawater only treatments. Settlement only on CCA in single tank experiment of all listed species given choice of CCA, live corals, inert reef collected substrata, fouled panels and inert settlement plate materials. Suggest strict requirement for contact with CCA. Limited alternative substrates tested in first experiment. Identification of CCA settlers in second experiment not reported (larvae identified, but not settlers).</td>
</tr>
<tr>
<td>digitifera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. hyacinthus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. florida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. formosa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. gemmifera</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. nasuta</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. tenuis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. sp. 1, 2 &amp; 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora</td>
<td>Negri et al. 2001.</td>
<td>- High levels of settlement in presence of CCA <em>Lithophyllum</em> sp (no settlement on sterile tile or <em>Porites</em> skeleton). <em>Pseudoalteromonas</em> sp. bacteria isolated from CCA <em>Hydrolithon onkodes</em> induces metamorphosis in high percentage of larvae in presence of tile (mostly unattached) and <em>Porites</em> skeleton TPA (see below) has no effect. Limited alternative substrates tested.</td>
</tr>
<tr>
<td>willisae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyphastrea</td>
<td>Morse et al. 1996.</td>
<td>- Preference for CCA <em>Hydrolithon reinboldi</em> with no settlement on dead coral branches, the brown algae <em>Lobophora variegata</em> or in seawater only. Molecule isolated from <em>Hydrolithon reinboldi</em> and <em>Peysonelia</em> induces metamorphosis. Suggest strict requirement for contact with CCA. Method description lacking and alternative substrates limited.</td>
</tr>
<tr>
<td>sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Favia favus</td>
<td>Morse et al. 1996.</td>
<td>- Limited laboratory tests found preference for CCA <em>Peysonelia</em> sp. with no settlement in the brown algae <em>Lobophora variegata</em> or seawater only treatments. Suggested stringent requirement for CCA inducer found in <em>Hydrolithon reinboldi</em> and <em>Peysonelia</em> sp. Limited alternative substrates tested.</td>
</tr>
<tr>
<td>Goniastrea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>retiformis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pistillata</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
or strain of bacteria. However, the evidence to date suggests that whatever the nature of
the relationship, substrate association does not appear confined to any recognizably
discrete type or member of the macroscopic biotic community.

No significant difference in levels of settlement existed between 3.3 month and
15.8 month field conditioned plates or 15.8 month and 28.3 month plates suggesting the
level of substrate conditioning required for *M. capitata* larval settlement is reached
relatively rapidly and can be maintained over time. This finding supports the tentative
conclusion that marine bacteria serve an inductive role in *M. capitata* settlement, as
bacteria are a fundamental part of early marine successional substrate communities that
persist in some form on exposed surfaces. These results also support Fitzhardinge’s
(1993) contention that *M. capitata* can be among the early scleractinian colonizers of
recently created substrates, although recruits may be difficult to detect without
magnification for some time due to relatively slow rates of growth (Fitzhardinge 1993,
Kolinski Chapter 3). Settlement association with an early successional organism has
advantages for an initially slow growing coral by providing footholds on newly created
surfaces. However, the fact that the inducing community may be widespread and
potentially ubiquitous suggests a generalist’s strategy for achieving recruitment. Such a
pattern corresponds well with the high larval dispersal potential and tolerance of adults
for a wide range of habitat conditions (Maragos 1972, Kolinski and Jokiel 2002). In
Hawai‘i, adult *M. capitata* rank relatively high in their ability to compete for space.
These characteristics apparently allow for relative spatial prominence in the species
depauperate Hawaiian coral community. However, in other areas of the Pacific where
species numbers are high and competition for space is strong, the generalist settlement
strategy may be the most important means by which *M. capitata* is able to maintain a presence.

**Settlement Competency**

Laboratory and field observations indicate that the majority of larvae of *Montipora capitata* can and will settle soon after completing embryogenesis if they encounter a suitable settlement substrate. The ability to settle remains high for a period approaching six weeks. Small numbers of *M. capitata* larvae may maintain and/or delay the onset of settlement competency for periods of time extending up to and potentially beyond seven months. Other studies have shown variation in settlement rates of coral larvae, with most settlement occurring soon after embryogenesis and development (Harrison and Wallace 1990, Carlon and Olson 1993, Morse et al. 1996, Zaslow and Benayahu 1996, Wilson and Harrison 1998, Heyward and Negri 1999, Ayre and Hughes 2000, Harii et al. 2001, Miller and Mundy 2003). Estimates on scleractinian coral capacity for long-term larval dispersal are few, with previously reported maximum values for a brooding species reaching 120 days for *Alveopora japonica* (Harii et al. 2001) and 105 days for the broadcast spawning species *Platygyra daedalea* (Nozawa and Harrison 2003; see also Tranter et al. 1982, Richmond 1987a, 1988, Wilson and Harrison 1998).

The observed settlement of an *M. capitata* larvae 207 – 213 days following parental release provides the longest duration of larval competency for a scleractinian coral. Given that direct long-term assessments can only, as yet, be made under laboratory conditions, the extent to which maximum reported periods are realized under natural conditions remains unknown.
Montipora capitata in Hawai‘i has a shorter pre-competent phase of larval development compared to some broadcast spawning species in Hawai‘i and other parts of the world (Kojis and Quinn 1981, Shlesinger and Loya 1985, Babcock and Heyward 1986, Harrison and Wallace 1990, Morse et al. 1996, Hayashibara et al. 1997, Wilson and Harrison 1998, Schwarz et al. 1999). Larvae in embryonic and early development stages presumably lack control over their vertical position within the water column and thus disperse wherever currents may take them. A short period of dispersal enhances potential for some local retention, especially in protected areas influenced mainly by tidal currents. However, the capacity of M. capitata larvae to maintain competency for up to six weeks allows for reef connectivity among both near and distant shorelines within the Hawaiian island chain (see Grigg 1983). High population densities of M. capitata (in bays, inlets and along naturally protected shorelines) enhance probabilities of fertilization and may be critical to long-term species persistence in more exposed areas by providing sources of larvae. Hodgson (1986) identified large concentrations of M. capitata larvae in tow samples within, and to some extent outside, Kāne‘ohe Bay and proposed an overall mass efflux of coral larvae from Kāne‘ohe Bay on the order of 90,000 larvae per day within the coral spawning season.

Planktonic survival and competency of larvae will be affected by numerous factors including temperature, food availability and predation (Thorson 1950, Pechenik 1987, 1999, Hoegh-Guldberg and Pearse 1995, Morgan 1995, Zaslow and Benayahu 1996, Pratchett et al. 2001, see also Jackson and Strathmann 1981). Measured daytime water temperatures in this study ranged between 28.1 to 21.4°C over the seven-month period. Pre-competent and/or competence periods may be less in warmer waters.
Unlike many other coral species, corals in the genus *Montipora* receive maternally derived zooxanthellae (Richmond 1997). It is likely that photosynthetically fixed carbohydrates help maintain metabolic activities in these larvae over time (see Richmond 1981, 1987a, 1988). Additional mechanisms of acquiring nutrition may include uptake of dissolved organic matter and direct feeding (Boidron-Metairon 1995). Larval feeding has not been examined in this species, however buoyant polyp balls (Richmond 1985a, Zaslow and Benayahu 1996) with apparently functioning tentacles have been noted in rearing bottles (Kolinski pers. obs.). Predation probabilities are based on predator abundance, predator preferences, larval abundance, larval behavior, availability of alternative prey, and time of exposure. Virtually nothing is known about natural rates of predation on larvae of *M. capitata*.

Although only low numbers of *M. capitata* larvae appear capable of maintaining an ability to settle after extended periods of time, the long-term results of this study provide a mechanism for coral connectivity between distant islands and archipelagos. Maragos and Jokiel (1986) estimated surface water transport times from Johnston Atoll (800 km southwest of Hawai‘i) to Hawai‘i to range between 21 and 50 days (well within the competency period of high proportions of *M. capitata* larvae) and 40 to 50 days from Hawai‘i to Johnston. *Montipora capitata* is common to low water motion areas at Johnston Atoll (Jokiel and Tyler 1993). Grigg (1981) estimated a surface water drift time of 187 days from Wake Island to Hawai‘i (2700 km). Jokiel (1984) noted that a small boat lost off the island of Hawai‘i was recovered 202 days later 7500 km distant in the Philippines (see Honolulu Advertiser, May 1, 1982) and suggested this direction for long
distance reef connectivity (Jokiel and Martinelli 1992). Larval connections between Hawai‘i and southwest Pacific Island regions are thus reasonable for this species, especially if viewed over geologic timescales. Connectivity may also occur via the rafting of settled corals on floating debris (Jokiel 1984, 1990a). Such means of transport greatly extends the potential period and breadth of dispersal as recruits may grow to reproductive size while remaining buoyant (Jokiel 1990a). The generalist settlement behavior of *M. capitata* makes rafting a feasible mechanism of transport for this species over geologic time. Unidentified species of *Montipora* have been found attached to pumice within the present geographic range of *M. capitata* (Jokiel 1990b).

Long distance larval drift has been used to account for coral species connections and/or founding events across the east Pacific Barrier (Dana 1975, Richmond 1987a, 1990), and may help maintain populations of various broadcast spawning species at certain high latitude locations (Veron 1995, Wilson and Harrison 1997, 1998). Although *M. capitata* has an extensive larval competency period, displays generalist settlement tendencies, and, following Veron (2000b), is widespread throughout much of the Indo-Pacific, it presently appears to be absent west of Indonesia, east of Hawai‘i, and reaches its eastern south Pacific extreme just past Fiji (Veron 2000b). Maragos (1995) suggests an even more restricted range, limited to the Hawaiian, Johnston and Line Islands. The Hawaiian-Line Islands region does have a high proportion of coral endemics (Maragos 1995, Maragos et al. in press), which suggests isolating mechanisms that may be related to distance from other island regions. Either way, the absence of *M. capitata* beyond stated boundaries may result from a combination of factors such as species age and origin (Stehli and Wells 1971), environmental suitability for recruits and adults (Dana 1975),
composition of competing benthic communities, current dynamics from likely source areas, and rarity of introduction due to low larval probabilities of reaching competency extremes and suitable destinations (see Jackson and Strathmann 1981). The biogeography and associated systematics of scleractinian corals are contentious issues not easily resolved. Additional research is needed.

Pechenik (1990) noted variability in periods of metamorphic competence is common to laboratory cultures of most marine invertebrates and suggested relevance in distinguishing delayed onset of competence from post-competent delays in metamorphosis. Either mechanism implies the capacity for dispersal, but variation in timing suggests slightly different strategies for affecting dispersion scale. Competent larvae that delay metamorphosis possess ability to settle as soon as a suitable substrate is encountered. Variation in settlement is likely substrate driven, and the scale of dispersal may be best explained by suitable substrate availability. However, variation in the delay of the onset of competency implies a potentially inherent forcing mechanism for wide scale dispersion (see Harper 1977, Raimondi and Keough 1990). Such variation is likely to be genetically/developmentally driven, and may not negate the possibility for further post-competent, substrate dependent, metamorphic delay. Wilson and Harrison (1998) observed variation in delay of settlement and metamorphosis in the presence of substrate for larvae of three scleractinian species ranging 26 to 78 days after first recorded settlement. In all above experiments involving *M. capitata* larvae, variation in timing of settlement was evident and at least a few larvae remained motile. The longest-term larvae were exposed to substrates 32 to 95 days prior to their settling. Early onset of competency does appear to be proportionately high in *M. capitata* larvae, and variability in settlement
rates may be due to variation in the degree or type of larval cue specificity (Raimondi and Keough 1990), or a host of other factors. However, anecdotal evidence suggesting potential pre-competent period variation cannot be ignored and should be fully investigated. Given the prolific reproductive nature of both broadcast spawning and planulating coral species, variation in periods of pre-competence may be an ecologically advantageous and relatively inexpensive means by which to enhance wide-scale offspring dispersion.
CHAPTER 3
SETTLEMENT, SURVIVAL AND EARLY GROWTH RELATIVE TO OTHER
COMMON HAWAIIAN SCLERACTINIAN

Introduction

Coral reefs are dynamic ecosystems that are subject to disturbances of both
can and anthropogenic origin at a variety of spatial and temporal scales (Connell
Disturbance provides potential to disrupt an existing balance of competitors, in many
cases creating habitats or conditions suitable to the arrival and survival of new settlers
disperse via planktonic larvae that are capable of establishing individuals in areas with
suitable substrate and conditions. The (re)establishment, long-term maintenance, and/or
continued dynamics of many of the species members of any coral community will be
dependent to a large extent on larval influxes and the early life history success of

Natural settlement and recruitment of various coral genera has been monitored
intermittently throughout the Pacific (Harrison and Wallace 1990 and cited references,
2000, Gleason 1996, Harriott and Banks 1995, Banks and Harriott 1996, Baird and

47
and Harriott 1999, Hughes et al. 1999, 2000, 2002, Kojis and Quinn 2001). However, characteristics of settlement, survival and early growth are not well documented for most Indo-Pacific scleractinian coral species. Previous efforts in Hawaiian waters have provided insights on early life history characteristics of a few of the more common corals (Dollar 1975, Polacheck 1978, Fitzhardinge and Bailey-Brock 1989, Fitzhardinge 1993, Deemers 1996). Such insights, however, have been limited and/or remain somewhat speculative due to either the short-term nature of the studies, an absence of focus on “invisible recruits” (sensu Wallace 1983), and/or an inability to track the fate of individuals across observation periods. Overall, there is a general deficiency of information on coral recruitment dynamics in Hawaiian waters (Kolinski and Cox 2003).

_Montipora capitata_ is a coral common to a variety of Hawaiian reef habitats (Maragos 1972, 1977, Kolinski and Jokie1 2002, Maragos et al. in press). This species is a highly synchronized summertime spawner with buoyant egg-sperm bundles, surface fertilization (Heyward 1986, Kolinski and Cox 2003), a two to three day embryonic period (Mate et al. 1998, pers. obs.), and a propensity for settlement soon after embryogenesis is complete (Kolinski Chapter 2). Similar to a number of other coral species, _M. capitata_ is a generalist in terms of its preference for settlement on various hard substrates (Kolinski Chapter 2). _Montipora capitata_ is the only coral species within Kāne‘ohe Bay that gives rise to large, very obvious, summertime surface slicks of gametes and developing embryos on the nights and mornings following synchronized spawning. Plankton tows within the bay found _M. capitata_ larvae to be at least an order of magnitude more concentrated than larvae of any other coral species following respective species spawning events (Hodgson 1986). Early studies, however, have
suggested relatively low levels of settlement and/or survival at monitored sites within the bay (Polacheck 1978, Fitzhardinge and Bailey-Brock 1989, Fitzhardinge 1993).

This study focused on settlement and early life history characteristics of *M. capitata* in the shallow waters of Kāne‘ohe Bay in an effort to elucidate the enigma of high levels of larval production and low levels of recruitment. Settled individuals were tracked and measured on artificial plates over a two-year period. Specific comparisons of early life history characteristics of *M. capitata* were made relative to other common, naturally settling Hawaiian scleractinian species as a means to understand potential similarities and differences in early life history strategies.

**Methods**

The term “settler” was used in this study to refer to an individual coral that settled, as a larva, on a settlement plate apparatus. This terminology encompassed metamorphosed individuals and was used for settled corals throughout the duration of the study.

**Settlement Plates**

Field observations of scleractinian coral settlement were made on settlement plate sets established at six shallow water (depths 1.5 to 3.5 meters) sites, including one fringing (F) and patch (P) reef each in north (N), central (C) and south (S) Kāne‘ohe Bay (Kolinski Chapter 2, Figure 2.1). Plate sets are described and diagramed in Chapter 2 (Figure 2.2). Initial plate sets (two to a post, seven posts at a site) were installed in March, three months prior to the 1999 *Montipora capitata* summer spawning, with replicate sets being added three months prior to the 2000 summer spawning. Plate sets removed for analysis were always kept submerged in individual containers and were
transferred by boat to the Hawai‘i Institute of Marine Biology (HIMB) for settler identification, measurement and mapping using a Wild Heerbrugg dissecting microscope (with the aid of a 10 x 10 cm monofilament sectioned quadrat). In all cases, half of the sets on each post at a site were collected at one time and analyzed, with collection schedules rotated among sites to ensure equivalent time-related proportionate sampling. Plates were held in individual containers in a shaded flow-through seawater table while in the laboratory. Container seawater was filtered (40 μm) and changed regularly. These procedures ensured that plates were not contaminated with larvae entering with seawater at the lab. All plate sets were returned to their respective posts within one to two days. Examination of all plate sets at each census was conducted in less than one month.

In June 1999, roughly half of the plate sets (one from each of five to six posts at a site) were inspected and then seeded with cultured *M. capitata* larvae (Kolinski Chapter 2) for related experiments. These sets were enclosed within individual Glad™ brand plastic transparent disposable containers (739 ml) modified with 40 μm Nitex screen on all but the top surface to allow for adequate water exchange (Kolinski Chapter 2, Figure 2.2). The PVC clips ensured that chambers (including screens) did not touch the plates. Five hundred 6-day-old larvae were injected into each chamber in the field. Chambered sets were collected and settlers mapped and scored after 6 days. These seeded plates were returned (without the chambers) to the field and were inspected with the other plates the following fall, winter-spring and summer through summer 2001.

**Settlement Among Sites**

Adult colonies of various coral species were placed in separate flow-through seawater tables at HIMB for observation of spawning times (see Kolinski and Cox 2003)
and collection of gametes for larval culturing and settlement. Larvae of known species were allowed to settle on seawater conditioned (three months) unglazed terracotta tiles, and these laboratory settlers acted as references in the species identification of field settlers. Notes on species characteristics, digital photos and measurements were taken of laboratory settlers over time. Successful settlement and survival occurred for larvae of *Montipora capitata, M. patula, Porites compressa, P. lobata, Fungia scutaria, Pocillopora damicornis, Cyphastrea ocellina, and Tubastraea coccinea*. Photos of settlers provided in Fitzhardinge (1993) and English et al. (1997), and live polyps of adult colony fragments, were also referenced to aid in species identifications.

Cumulative counts of all field settlers for each species at each site were made for general comparison. A factorial ANOVA (with Tukey HSD means comparisons, \( \alpha = 0.05 \)), involving only species with observed settlers at all sites, was used to examine differences between mean numbers of settlers m\(^{-2}\) (log\(_{10}\) transformed) observed over two one-year monitoring periods. The comparison was limited to two-way interactions due to a restrictive number of degrees of freedom.

**Settlement Over Time**

Seasonal settlement was examined for those species having enough settlers at multiple sites to allow gross patterns in settlement timing to be discerned. Mean numbers of settlers m\(^{-2}\) (+1 log\(_{10}\) transformed) of each species in each season of observation (summer = July to early August, fall = October, winter-spring = February to April) over a two-year monitoring period were determined for graphical comparison. Large site variability between species within and across seasons prohibited direct inclusion of all species in a single factorial ANOVA. Thus, each species was analyzed using separate
mixed factorial ANOVAs (with Tukey HSD means comparisons, \( \alpha = 0.05 \)), analyzing the mean number of settlers m\(^{-2}\). The results were considered in relation to the reproductive mode and observed spawning patterns of each species.

**Settler Survival**

*Montipora capitata*

Proportional survival of one to two-week old seeded (1999) and natural (2000) summer *Montipora capitata* settlers was plotted against time to assess general trends in survivorship (Deevey 1947). Three survivorship curves were constructed; one for seeded larvae (1999), and one each for larvae that naturally settled on three month and 15.8 month (2000) field conditioned plates. Individual comparisons of proportional survival at three, nine and 12 months post-settlement were made between the groups. Initially, seasonal survival of natural summer 2000 settlers on three and 15.8 month conditioned plates was compared using paired t-tests on arcsine square-root transformed proportional survivorship values pooled for each site at three, nine and 12 months (only sites with > 20 individuals per category were analyzed). The findings allowed for all natural 2000 summer settlers at each site to be pooled for similar comparative analyses with seeded 1999 survivorship estimates. Survival was calculated as the proportion of initial summer settlers remaining alive at each census. Settlers on clips and wing-nuts were not included in any of the survival analyses as these areas were used for plate handling.

**Comparison with Other Species**

Comparison of survivorship of *Montipora capitata* to that of *Porites compressa* and *Pocillopora damicornis* was difficult to express due to protracted settlement times across seasons for the latter two species. Individuals entered into observation
progressively over the course of the two-year monitoring period and thus were monitored for varying periods of times. Unfortunately, variation in timing between censuses resulted in the data not being amenable for curve construction and analysis in available survival analysis statistical packages. A survival analysis framework was, thus, constructed in Microsoft Excel, accumulating all that was known concerning each individual’s fate over time. Time zero was set for each individual at the time it was first observed. Cumulative counts of each species at each site were calculated for each of 21 months beginning at month 4, and included total number of individuals for which information existed, total known number of survivors, and total number of right censored individuals (i.e., individuals surviving beyond the end of the monitoring period, Lee 1992). The first three months were not included in the analysis due to a lack of information concerning mortality and, thus, a bias towards high survivorship for some species. Months 22 to 25 were also not included, as proportions appeared to become biased by a lack of knowledge concerning fates of right censored individuals. Only sites with > 20 individuals were included for the construction of each species mean survivorship curve. Seeded \( M. \) capitata settlers were pooled with natural settlers for analysis.

Statistical comparisons of proportionate survival were made separately at four, 12 and 21 months using one-way ANOVAs and Tukey HDS tests \((\alpha = 0.05)\) on square-root arcsine square-root transformed data. A single outlier was omitted from the 21-month analysis for \( P. \) compressa to meet model assumptions (note: test results were similar with and without the outlier). An additional analysis comparing proportional survival of four-month survivors at 12 and 21 months was made to examine whether potential differences between species in numbers of very recent settlers at times of first observation could be
biasing long-term survival comparisons. The data were arcsine square-root transformed and analyzed using separate one-way ANOVA and Tukey HDS ($\alpha = 0.05$) tests.

**Settler Growth**

Measurements of individual settlers at each census were made using a Wild Herbrugg dissecting microscope with a lens micrometer and included counts of polyps (when possible), longest measured length, perpendicular width and, for *Pocillopora damicornis* when appropriate, height. Projected area of each settler at each census was calculated as $\pi ab$ (area of an ellipse; $a = \frac{1}{2}$ longest measured length; $b = \frac{1}{2}$ perpendicular width). Surface areas were not estimated for growth comparisons due to differences in growth forms and patterns as settlers grew larger (consistent 2 dimensional increases for *Montipora capitata* and *Porites compressa* versus initial 2 followed by 3 dimensional branching growth for *P. damicornis*). Settlements on clips and wing-nuts were not included in any of the growth analyses as these areas were used for plate handling.

Growth was estimated for select individuals as the change in polyp numbers over time. Only individuals with zero and/or positive increases in numbers of polyps in three or more consecutive counts were selected for analysis, with one set of zero and/or positive consecutive measurements and corresponding times being included for each individual. Polyp counts were standardized by dividing each count by the initial number of polyps in each set (as each polyp in a small colony had an ability to divide, this conversion standardized growth to an individual polyp for comparison). All standardized counts were $\log_{10}$ transformed. Slopes were estimated using regression analysis (Statistix 1.0). Growth estimates from all sites were pooled for interspecific comparisons using a one-way ANOVA. Consistency in growth was assessed between sites having replicate
M. capitata, P. compressa and P. damicornis slope estimates (Central Fringing, Central Patch and North Patch reefs) using a mixed factorial ANOVA. Post-hoc comparisons were made using Tukey HDS tests with $\alpha = 0.05$.

The relationship between settler growth and survival was examined for M. capitata, P. compressa and P. damicornis by comparing slope estimates of growth as determined above (pooled across all sites) between right-censored “survivors” (i.e., individuals that survived beyond the end of the monitoring period) and similar aged (nine months plus) settlers known to have died over the course of the monitoring period. A factorial ANOVA, with growth as the dependent variable, and a binomial logit homogeneity of slopes model, with survival as the dependent variable, were used to assess the relationship. Within species contrasts were made using Bonferroni corrected P-values.

Mean and minimum time estimates for M. capitata, P. compressa and P. damicornis settlers to reach 1 cm$^2$ projected area in the field were made using the mean and maximum growth slope estimates for right-censored individuals of each species. Regression analysis was used to predict the mean number of polyps for a 1 cm$^2$ projected area for each species. The polyp values were log$_{10}$ transformed and placed in respective mean growth regression models, which were then solved for time.

**Habitat Characteristics**

**Water Quality**

Water motion, total suspended solids, sedimentation rates, salinity and temperature were measured at center and end settlement plate posts ($n = 3$) at each site from July 1999 through October 2000. With the exception of salinity and temperature,
times between consecutive measurements always exceeded one month, with dates selected in advance on a haphazard basis. Water motion was determined using Plaster of Paris “clod cards” (Doty 1971, Jokiel and Morrissey 1993), with two clod cards being anchored to each of three bricks at each site per trial for a total of nine 24-hour trials. Control cards were placed in a five-gallon (18.92 l) bucket of seawater in a shaded, wind protected area on land. The cards were briefly rinsed in still fresh water, air-dried in an air-conditioned, dehumidified building for a month and then weighed on a Mettler P160 balance. Three one-liter water samples were collected at each site a total of eight times for measurement of total suspended solids (TSS). The water was collected adjacent to each of three posts in clear one-liter Nalgene polyethylene bottles. Sample volumes were vacuum filtered onto pre-weighed, 500°C pre-ashed GFF filters, with ample rinsing using de-ionized water. The TSS samples were placed in a 60°C drying oven for 24 hours prior to being weighed on a Mettler AB104 electronic microbalance. Rates of sedimentation were measured over 10 separate 24-hour periods using 15.24 cm deep, 5.45 cm wide, bottom-capped polyvinyl chloride (PVC) pipe traps. One trap was clip-tied to each of three posts at each site with openings level to plate top surfaces. The traps were plugged prior to removal from the posts and were vacuum filtered onto individual pre-weighed, 500°C pre-ashed GFC (8 months) and Whatman filters (2 months), with ample rinsing using de-ionized water. The sediments were dried at 60°C for 24 hours and then weighed on a Mettler AB104 electronic microbalance. Samples of water adjacent to three posts per site were collected in 125 ml clear Nalgene bottles and rapidly measured for salinity and temperature in the field using either a YSI Model 30 conductivity meter or refractometer and thermometer. Salinity was measured on 15, and temperature on 9 occasions.
Values of all measured water quality parameters were averaged across trials for inclusion in a Pearson’s correlation matrix for exploratory analysis against measurements of Montipora capitata, Porites compressa and Pocillopora damicornis mean yearly settlement, growth and 12-month survival using the following transformations: number of settlers m$^{-2}$ and water motion log$_{10}$ transformed; growth = slopes of log$_{10}$ standardized polyp increase per month; percent survival and percent adult cover m$^{-2}$ arcsine square-root transformed; total suspended solids and sediment +1 log$_{10}$ transformed.

**Benthic Cover**

Benthic composition was assessed along four 10 m transects placed within a 10 m x 50 m settlement plate zone (nearest transects roughly 15 m distant). One square meter quadrats delineated into 10 dm$^2$ grid cells were used to make 10 contiguous measurements along the length of each transect. The measurements were visual estimates of percent cover within each quadrat of sand, rubble, un-colonized hard substrate, coral and algae by species, sponges, and other space consuming macro-invertebrates. The mean percent cover of Montipora capitata, Porites compressa and Pocillopora damicornis (arcsine square-root transformed) at each site was included in a Pearson’s correlation matrix for exploratory analysis against measurements of these species mean yearly settlement m$^{-2}$ (log$_{10}$ transformed), mean rates of growth (slopes of log$_{10}$ standardized polyp increase per month) and 12-month survival (arcsine square-root transformed).

**Site Projection Example**

Mean values of settlement, survival and colonizable substrate were used to project and compare large-scale levels of settlement and the four, 12 and 21 month fate of summer 2000 Montipora capitata, Porites compressa and Pocillopora damicornis settlers.
throughout each 500 m² study area. Numbers of survivors at 12 and 21 months were based on estimates of proportionate survival of four-month survivors so as to limit potential long-term bias arising from differences in proportions of very recent settlers while accounting for right-censored individuals. These species have been observed to settle on rubble (Kolinski pers. obs.); thus, substrate suitable for colonization was defined as hard and rubble structure not covered by sand, live coral, macroalgae, sponges, colonial tunicates, or other space limiting macro-invertebrates.

Results

Settlement Among Sites

Nine identifiable species of scleractinian corals were observed on settlement plates over the two-year period (Table 3.1). *Montipora capitata* cumulatively accounted for 91% of all noted plate settlers and dominated (82 to 96%) at all but the North Bay sites (roughly 2% at each site). *Porites compressa* dominated cumulative counts at North Patch reef (60% of noted settlers), and *Pocillopora damicornis* at North Fringing reef (61%). Remaining identified species accounted for less than one percent of noted cumulative site settlers with the exception of *Culicia tenella* at North Fringing reef (4% of noted settlers) and *Cyphastrea ocellina* at North Patch reef (3%). *Montipora capitata*, *P. compressa* and *P. damicornis* were the only species observed on plates at all monitored sites. *Culicia tenella* was observed on plates at all sites with the exception of South Patch reef (Table 3.1).

Statistical comparison of number of observed settlers of the three main species, *M. capitata*, *P. compressa* and *P. damicornis*, over two consecutive one-year monitoring periods identified significantly higher levels of overall settlement at Central Bay sites,
Table 3.1. Cumulative numbers of scleractinian corals observed on settlement plates at six sites in Kāne‘ohe Bay from summer 1999 to summer 2001 (C = Central; N = North; S = South; F = Fringing reef; P = Patch reef).

<table>
<thead>
<tr>
<th>Species</th>
<th>NP</th>
<th>NF</th>
<th>CP</th>
<th>CF</th>
<th>SP</th>
<th>SF</th>
<th>Total settlers</th>
<th>% of all noted settlers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Montipora capitata</td>
<td>7</td>
<td>6</td>
<td>1982</td>
<td>14974</td>
<td>260</td>
<td>421</td>
<td>17650</td>
<td>90.87</td>
</tr>
<tr>
<td>Porites compressa</td>
<td>276</td>
<td>108</td>
<td>92</td>
<td>352</td>
<td>46</td>
<td>59</td>
<td>933</td>
<td>4.80</td>
</tr>
<tr>
<td>Pocillopora damicornis</td>
<td>140</td>
<td>224</td>
<td>137</td>
<td>171</td>
<td>6</td>
<td>10</td>
<td>688</td>
<td>3.54</td>
</tr>
<tr>
<td>Culicia tenella</td>
<td>3</td>
<td>15</td>
<td>17</td>
<td>25</td>
<td>-</td>
<td>1</td>
<td>61</td>
<td>0.31</td>
</tr>
<tr>
<td>Cyphastrea ocellina</td>
<td>13</td>
<td>-</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>16</td>
<td>0.08</td>
</tr>
<tr>
<td>Montipora patula</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>0.01</td>
</tr>
<tr>
<td>Fungia scutaria</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Leptastrea bottae</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Tubastraea coccinea</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>0.01</td>
</tr>
<tr>
<td>Unknown</td>
<td>23</td>
<td>15</td>
<td>10</td>
<td>15</td>
<td>4</td>
<td>4</td>
<td>71</td>
<td>0.37</td>
</tr>
</tbody>
</table>

Total: 463 369 2242 15539 316 495 19424
% of Total: 2.38 1.90 11.54 80.00 1.63 2.55

which was mainly the result of high numbers of *M. capitata* settlers. Although, overall mean numbers of *M. capitata* and *P. compressa* settlers were significantly greater than *P. damicornis*, this varied among individual sites (Table 3.2, Figure 3.1). Only *P. compressa* displayed statistically similar levels of cumulative settlement across all sites over the course of the two-year monitoring period (Table 3.2).

Table 3.2. Factorial ANOVA (with Tukey HSD means comparisons, \( \alpha = 0.05 \)) of *M. capitata*, *P. compressa* and *P. damicornis* settlers (log\(_{10}\) mean number settlers m\(^{-2}\) colonizable reef) observed over two one-year monitoring periods (C = Central; N = North; S = South; F = Fringing reef; P = Patch reef; Mcap = *M. capitata*; Pcom = *P. compressa*; Pdam = *P. damicornis*).

<table>
<thead>
<tr>
<th>Df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>198.1377</td>
<td>198.1377</td>
<td>3508.940</td>
<td>0.0000</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>0.1622</td>
<td>0.1622</td>
<td>2.872</td>
<td>0.1210</td>
</tr>
<tr>
<td>Site</td>
<td>5</td>
<td>9.5887</td>
<td>1.9177</td>
<td>33.962</td>
<td>0.0000</td>
</tr>
<tr>
<td>Species</td>
<td>2</td>
<td>1.9663</td>
<td>0.9832</td>
<td>17.412</td>
<td>0.0006</td>
</tr>
<tr>
<td>Year*Site</td>
<td>5</td>
<td>1.7095</td>
<td>0.3419</td>
<td>6.055</td>
<td>0.0078</td>
</tr>
<tr>
<td>Year*Species</td>
<td>2</td>
<td>0.2096</td>
<td>0.1048</td>
<td>1.856</td>
<td>0.2064</td>
</tr>
<tr>
<td>Site*Species</td>
<td>10</td>
<td>14.0030</td>
<td>1.4003</td>
<td>24.799</td>
<td>0.0000</td>
</tr>
<tr>
<td>Error</td>
<td>10</td>
<td>0.5647</td>
<td>0.0565</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Site*Species: NF Pdam Pcom > Mcap NP Pcom Pdam > Mcap CF Mcap > Pcom Pdam
CP Mcap > Pdam Pcom SF Mcap Pcom Pdam SP Mcap Pcom > Pdam

Mcap CF CP SF SP NF NF Pcom CF NF NP CP SF SP Pdam CF NF CP NP SF SP
Figure 3.1. Log$_{10}$ mean number $M.\ capitata,$ $P.\ compressa,$ and $P.\ damicornis$ settlers m$^{-2}$ colonizable reef (± S.E.) observed over two one-year monitoring periods at sites in Kāne‘ohe Bay ($C =\text{Central};\ N =\text{North};\ S =\text{South};\ F =\text{Fringing reef};\ P =\text{Patch reef}$).

Settlement Over Time

Seasonal patterns of settlement were discernable for $Montipora\ capitata,$ $Porites\ compressa,$ $Pocillopora\ damicornis,$ and $Culicia\ tenella$ at multiple sites within Kāne‘ohe Bay where overall settlement levels were relatively high (Figure 3.2). Although direct statistical comparisons among species could not be made due to tremendous site variability within and across seasons, statistical evaluation of temporal trends for each species allowed for an indirect comparison (Table 3.3). Three patterns of settlement were apparent. Pulsed settlement was evident soon after peak summer spawning periods in June and July for the broadcast spawning hermaphrodite $M.\ capitata,$ with the vast majority of settlers ($> 70\%$) appearing to have recently settled. Observed settlement was significantly higher in the summer, followed by fall and then winter/spring (Table 3.3).
Summer settlement of *P. compressa*, a gonochoric broadcast spawning species with variable reproductive release from June through September, did not differ significantly from monitored settlement in fall, although settlement in summer and fall was significantly higher than that noted in winter/spring (Table 3.3). *Pocillopora damicornis*, a brooding species with year round reproduction, did not display statistically significant seasonal differences in settlement. Observed settlement for *C. tenella* did not differ statistically between seasons. The reproductive mode of *C. tenella* is presently unknown. There was no evidence of large discrete settlement pulses within a season for *P. compressa, P. damicornis* or *C. tenella* during the two-year monitoring period.

**Figure 3.2.** Temporal settlement (log$_{10}$ mean number of settlers m$^{-2}$ colonizable substrate +1, ± S.E.) of select species of scleractinian corals at sites in Kāne‘ohe Bay (*M. capitata* at CF, CP, SF and SP; *P. compressa* at all bay sites; *P. damicornis* at NF, NP, CF and CP; and *C. tenella* at NF, CF and CP. Fal = Fall, W/S = Winter–Spring, and Sum = Summer).
Table 3.3. Mixed model ANOVAs (with Tukey HSD mean comparisons, \( \alpha = 0.05 \)) examining temporal differences in mean estimated settlement \( m^2 \) of colonizable substrate at select sites in Kāne‘ohe Bay for individual scleractinian coral species (C = Central; N = North; S = South; F = Fringing reef; P = Patch reef).

**Montipora capitata**

<table>
<thead>
<tr>
<th>Source</th>
<th>(F/R)</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>Fixed</td>
<td>2</td>
<td>26.3740</td>
<td>13.1870</td>
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<td>6.4749</td>
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<tr>
<td>Error</td>
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<td>1.5223</td>
<td>0.1269</td>
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<td></td>
</tr>
</tbody>
</table>

Summer > Fall > Winter-Spring; CF CP > SF SP

**Porites compressa**

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<tr>
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<th>(F/R)</th>
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<td>Season</td>
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<td>3.6938</td>
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</tr>
</tbody>
</table>

Fall Summer > Winter-Spring; CF NP NF CP SF SP

**Pocillopora damicornis**

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<th>P</th>
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</thead>
<tbody>
<tr>
<td>Season</td>
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<td>0.8623</td>
<td>0.4312</td>
<td>3.6108</td>
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</tr>
<tr>
<td>Site</td>
<td>Random</td>
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<td>0.3929</td>
<td>0.1310</td>
<td>1.0967</td>
<td>0.4202</td>
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<tr>
<td>Season*Site</td>
<td>Random</td>
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<td>0.7164</td>
<td>0.1194</td>
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<tr>
<td>Error</td>
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<td>12</td>
<td>2.8276</td>
<td>0.2356</td>
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<td></td>
</tr>
</tbody>
</table>

Fall Summer Winter-Spring; CF CP NF NP

**Culicia tenella**

<table>
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<tr>
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<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>Fixed</td>
<td>2</td>
<td>0.5909</td>
<td>0.2955</td>
<td>1.2453</td>
<td>0.3798</td>
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<tr>
<td>Site</td>
<td>Random</td>
<td>2</td>
<td>0.4601</td>
<td>0.2301</td>
<td>0.9696</td>
<td>0.4536</td>
</tr>
<tr>
<td>Season*Site</td>
<td>Random</td>
<td>4</td>
<td>0.9490</td>
<td>0.2373</td>
<td>0.6247</td>
<td>0.6567</td>
</tr>
<tr>
<td>Error</td>
<td>Fixed</td>
<td>9</td>
<td>3.4185</td>
<td>0.3798</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Summer Fall Winter-Spring; CF CP NF

**Settler Survival**

**Montipora capitata**

Summer settlers of *Montipora capitata* in Kāne‘ohe Bay cumulatively displayed type III survivorship (Deevey 1947) as shown in Figure 3.3. The number of monitored surviving summer settlers declined roughly an order of magnitude from initial settlement levels in an approximately three month period for both seeded and naturally settled larvae, and declined an additional order of magnitude over the remainder of a year. Mean proportional survivorship of natural (summer 2000) settlers on new and old plates did not
Figure 3.3. Survivorship of newly settled *M. capitata* larvae over time on three month conditioned plates seeded with larvae (1999) and three (new) and 15.8 (old) month conditioned plates with natural settlers (2000). Data combined for all Kāne‘ohe Bay sites.

differ significantly at any monitoring period over the course of a year (Paired t-test on arcsine square-root transformed proportional survivorship at Central Fringing, Central Patch and South Fringing reefs: fall 2000, n = 3, T = 0.37, P = 0.749; spring 2001, n = 3, T = 1.03, P = 0.413; summer 2001, n = 3, T = 1.43, P = 0.288). Although mean proportional survivorship of the natural summer 2000 settlers was significantly greater than that of the 1999 seeded settlers at three months post-settlement (Paired t-test on arcsine square-root transformed proportional survivorship at Central Fringing, Central Patch, South Fringing and South Patch reefs: n = 4, T = 3.25, P = 0.048), no significant difference was evident at the nine (n = 4, T = 1.33, P = 0.276) or 12 month (n = 4, T = 1.90, P = 0.153) monitoring periods between the two years. Overall survival of natural settlers from summer 2000 averaged 2.56 % (± 1.13 S.E., n = 4) by summer 2001.
Survival of summer 1999 seeded settlers averaged 0.15 % (± 0.08 S.E., n = 6) by summer 2000. The number of seeded settlers continued to decline to one survivor two years post settlement, with mean survivorship equal to 0.03 % (± 0.03 S.E.; note that an additional seeded settler on a plate wing-nut also survived the duration of the monitoring period, but wing-nut settlers were excluded from analysis due to unavoidable mortality caused by removal of nuts for plate examination). One of 134 (0.74 %) settlers first noted in fall 1999 also survived over the course of the monitoring period. None of six (0 %) 2000 winter/spring settlers survived to summer 2001.

Comparison with Other Species

Survivorship curves for Porites compressa and Pocillopora damicornis relative to Montipora capitata settlers from time of first observation are shown for months four through 21 (limits for determination) in Figure 3.4. Similar to M. capitata, P. compressa and P. damicornis displayed Type III survivorship. However, their mean short and long-term survivorships were significantly greater than that of M. capitata (Table 3.4). A species comparison of proportional survival of surviving four-month old settlers at 12 and 21 months was made to examine whether potential differences in numbers of very recent settlers at times of first observation could be biasing long-term survival comparisons. Mean proportionate survival of four-month old P. compressa settlers was significantly higher than M. capitata at 12 and 21 months (one-way ANOVA of arcsine square-root transformed data: 12 months, n = 16, $F_{2,15} = 4.86, P = 0.027$; 21 months, n = 15, $F_{2,14} = 8.39, P = 0.005$), but neither P. compressa nor M. capitata differed from P. damicornis at either time interval.
Figure 3.4. Mean proportional survivorship (± S.E.) of *M. capitata* (all sites), *P. compressa* (all sites) and *P. damicornis* (Central and North Bay Fringing and Patch reef sites) settlers observed in Kane‘ohe Bay.

Table 3.4. Species comparison of proportionate survival at 4, 12 and 21 months (one-way ANOVA of square-root arcsine square-root transformed data with Tukey HSD mean comparisons, $\alpha = 0.05$; one outlier eliminated from *P. compressa* data set at month 21).

<table>
<thead>
<tr>
<th>Time</th>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 months</td>
<td>Species</td>
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<td>1.0257</td>
<td>0.5129</td>
<td>51.49</td>
<td>0.0000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>13</td>
<td>0.1295</td>
<td>0.0100</td>
<td></td>
<td></td>
<td>P_com = P_dam &gt; Meap</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>15</td>
<td>1.1552</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 months</td>
<td>Species</td>
<td>2</td>
<td>0.5428</td>
<td>0.2714</td>
<td>25.91</td>
<td>0.0000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Within</td>
<td>13</td>
<td>0.1362</td>
<td>0.0105</td>
<td></td>
<td></td>
<td>P_com = P_dam &gt; Meap</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>15</td>
<td>0.6790</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 months</td>
<td>Species</td>
<td>2</td>
<td>0.5996</td>
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</tr>
<tr>
<td></td>
<td>Within</td>
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<td></td>
<td></td>
<td>P_com = P_dam &gt; Meap</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>14</td>
<td>0.7247</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

Settler Growth

Species Comparisons

Mean linearized rates of standardized growth of *Montipora capitata*, *Porites compressa* and *Pocillopora damicornis* settlers pooled across all sites are shown in
Figure 3.5. *Montipora capitata* grew exceedingly slowly and displayed a significantly lower mean rate of polyp increase over time compared to *P. compressa* and *P. damicornis*, which did not differ. Rates of growth did not differ between sites where comparisons could be made (Table 3.5). The greatest number of polyps achieved for an individual settler within the two-year monitoring period was estimated to exceed 1000 for both *P. compressa* and *P. damicornis* but never reached higher than 18 for *M. capitata* (8.89 months). *Montipora capitata* settled and reared in the lab reached a maximum 53 polyps over a 41-month (3.4 year) period. However, mean field growth rates were roughly 2.5 times that of lab-reared settlers (Field = 0.0248 ± 0.0033 S.E.; Lab = 0.0101 ± 0.0017 S.E.; Two sample t-test of no difference, df = 127.4, T = 3.96, P = 0.0002).

![Figure 3.5](image.png)

**Figure 3.5.** Mean growth rates (slopes of log₁₀ standardized polyp increase per month) ± S.E. of *M. capitata*, *P. compressa* and *P. damicornis* settlers pooled across sites.
Table 3.5. Species comparisons of growth rates (slope of log₁₀ standardized polyp increase by month). One-way ANOVA used for pooled data all sites. Mixed factorial ANOVA using data from Central Fringing, Patch and North Patch reefs, where replicate estimates occurred for *M. capitata*, *P. compressa* and *P. damicornis*.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Source</th>
<th>(F/R)</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Comparison</th>
</tr>
</thead>
<tbody>
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<td>All</td>
<td>Intercept</td>
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<td>1.0707</td>
<td>1.0707</td>
<td>528.0246</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>2</td>
<td>0.2586</td>
<td>0.1293</td>
<td>63.7748</td>
<td>0.0000</td>
<td>Pdam, Pcom &gt;&gt; Mcap</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>262</td>
<td>0.5313</td>
<td>0.0020</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CF, CP, NP</td>
<td>Intercept</td>
<td>Fixed</td>
<td>1</td>
<td>0.4427</td>
<td>0.4427</td>
<td>584.3048</td>
<td>0.0000</td>
<td>Pdam, Pcom &gt;&gt; Mcap</td>
</tr>
<tr>
<td></td>
<td>Species</td>
<td>Fixed</td>
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<td>0.1122</td>
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<td>50.0877</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Species*Site</td>
<td>Random</td>
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<td>0.0038</td>
<td>0.0009</td>
<td>0.4719</td>
<td>0.7563</td>
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</tr>
<tr>
<td></td>
<td>Error</td>
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<td>0.3533</td>
<td>0.0020</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Projected mean time for settlers to reach 1 cm² (projected area) in the field was roughly 59 months (4.9 years) for *M. capitata*, 20 months (1.7 years) for *P. compressa* and 21 months (1.7 years) for *P. damicornis*. Minimum projected time to reach 1 cm² based on fastest recorded growth rate was 13 months for *M. capitata* and approximately 10 months for both *P. compressa* and *P. damicornis*. One-cm² *Porites compressa* and *P. damicornis* were observed at 12 month censuses. *Montipora capitata* was not observed to reach 1 cm² throughout the two-year monitoring period.

**Extended Single Polyp Status**

Large numbers of *Montipora capitata* field survivors never exceeded the one polyp stage throughout the monitoring period. The percentage of surviving plate settlers in a single polyp stage 12 months after first being observed totaled 61 % for *M. capitata*, 8 % for *Porites compressa* and 0 % for *Pocillopora damicornis*. Competitive interactions within respective one-year periods with other encrusting organisms were noted for 70 % of single polyp *M. capitata*, and 70 % of single polyp *P. compressa* survivors. A decline in polyp number was significantly related to prior competitive interactions for *P. compressa* (Chi-square = 9.12, df=1, P = 0.003), but not *M. capitata* (Chi-square = 0.05, df=1, P = 0.821; Table 3.6). One-year single polyp status was significantly related to
declines in polyp numbers in *P. compressa* (Chi-square = 8.55, df = 1, P = 0.004), but not *M. capitata* (Chi-square = 1.01, df = 1, P = 0.315).

**Table 3.6.** Survivors noted as single polyps 12 months after first observation.

<table>
<thead>
<tr>
<th>Category</th>
<th><em>M. capitata</em></th>
<th><em>P. compressa</em></th>
<th><em>P. damicornis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1-polyp stage at 12 months</td>
<td>23/38 60.5%</td>
<td>10/121 8.3%</td>
<td>0/41 0.0%</td>
</tr>
<tr>
<td>1-polyp survivors which experienced competitive interactions</td>
<td>16/23 69.6%</td>
<td>7/10 70.0%</td>
<td>0/0 0.0%</td>
</tr>
<tr>
<td>1-polyp survivors which experienced previous polyp declines</td>
<td>1/23 4.3%</td>
<td>8/10 80.0%</td>
<td>0/0 0.0%</td>
</tr>
</tbody>
</table>

**Growth and Settler Survival**

The relationship between growth rates and longer-term survival (indicated by right censorship of settlers ≥9 months of age) is shown in Figure 3.6. Although overall, settlers with higher growth rates displayed significantly higher probabilities of survival, this relationship was significant only for *Porites compressa* and *Pocillopora damicornis*, but not *Montipora capitata* (Table 3.7).

![Figure 3.6. Mean growth rates (slopes of log\(_{10}\) standardized polyp increase per month) ± S.E. of *M. capitata*, *P. compressa* and *P. damicornis* survivors (right censored individuals) and non-censored settlers.](image-url)
**Table 3.7.** a) Factorial ANOVA of growth rates (slope of log_{10} standardized polyp increase per month) of *M. capitata*, *P. compressa* and *P. damicornis* survivors (right censored individuals) and non-censored settlers; b) Binomial logit homogeneity of slopes model of survival (examines survival as the dependent variable and growth as an explanatory variable); c) Within species contrasts of growth rates between right censored and non-censored settlers.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.7784</td>
<td>0.7784</td>
<td>444.9728</td>
<td>0.0000</td>
</tr>
<tr>
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<td>0.0000</td>
</tr>
<tr>
<td>Rcen</td>
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<td>0.0536</td>
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</tr>
<tr>
<td>Species*Rcen</td>
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<td>0.0285</td>
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<td>0.0004</td>
</tr>
<tr>
<td>Error</td>
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<td>0.4513</td>
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</table>

**b) Source**

<table>
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<tbody>
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<td>7.8872</td>
<td>0.0050</td>
</tr>
<tr>
<td>Species</td>
<td>2.00</td>
<td>5.7070</td>
<td>0.0576</td>
</tr>
<tr>
<td>Growth</td>
<td>1.00</td>
<td>19.0507</td>
<td>0.0000</td>
</tr>
<tr>
<td>Species*growth</td>
<td>2.00</td>
<td>6.3552</td>
<td>0.0417</td>
</tr>
</tbody>
</table>

**c)**

<table>
<thead>
<tr>
<th>Live</th>
<th>Dead</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. capitata</em></td>
<td><em>P. compressa</em></td>
</tr>
<tr>
<td>M. capitata</td>
<td>1.0000</td>
</tr>
<tr>
<td>P. compressa</td>
<td>0.0000</td>
</tr>
<tr>
<td>P. damicornis</td>
<td></td>
</tr>
</tbody>
</table>

**Settlement, Survival, Growth and Habitat**

Exploratory analysis of general relationships between the means of measured habitat characteristics (water motion, total suspended solids, sedimentation rates, salinity, temperature, % adult coral cover; Table 3.8) and mean site settlement, early growth and survival of *Montipora capitata*, *Porites compressa* and *Pocillopora damicornis* was conducted using a Pearson’s correlation matrix (Table 3.9). The only significant correlation among habitat characteristics (not shown) was noted between mean water motion and mean rates of sedimentation (Pearson’s correlation, *r* = 0.9057, *n* = 6, *P* = 0.013). *Montipora capitata*, *P. compressa* and *P. damicornis* differed in the types of significant habitat correlations they displayed, with bay water clarity (total suspended solids) and salinity appearing potentially important to *M. capitata* settlement and survival, water motion and water clarity potentially important to *P. compressa* survival,
Table 3.8. Means (± S.E.) and ranges (in parentheses) of recorded habitat characteristics at monitored settlement sites in Kāne‘ohe Bay (C = Central Bay, N = North Bay, S = South Bay, F = Fringing reef, P = Patch reef)

<table>
<thead>
<tr>
<th>Site</th>
<th>Water Motion (DF)</th>
<th>Total Suspended Solids (mg/l)</th>
<th>Sediment Rate (mg/cm²/day)</th>
<th>Salinity (%/o)</th>
<th>Temperature (°C)</th>
<th>M. capitata</th>
<th>P. compressa</th>
<th>P. damicornis</th>
</tr>
</thead>
<tbody>
<tr>
<td>CF</td>
<td>10.72 ± 0.70</td>
<td>1.85 ± 0.22</td>
<td>5.25 ± 1.42</td>
<td>33.6 ± 0.4</td>
<td>26.0 ± 0.9</td>
<td>1.56 ± 0.43</td>
<td>10.21 ± 3.56</td>
<td>0.26 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>(8.74-13.92)</td>
<td>(0.86-2.64)</td>
<td>(2.01-16.49)</td>
<td>(31.5-35.9)</td>
<td>(22.9-27.8)</td>
<td>(0.65-2.45)</td>
<td>(3.65-16.55)</td>
<td>(0.08-0.67)</td>
</tr>
<tr>
<td>CP</td>
<td>13.47 ± 0.93</td>
<td>1.98 ± 0.29</td>
<td>10.36 ± 3.40</td>
<td>33.6 ± 0.4</td>
<td>26.3 ± 0.6</td>
<td>64.24 ± 7.70</td>
<td>8.77 ± 3.84</td>
<td>0.15 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>(10.03-18.06)</td>
<td>(0.97-3.75)</td>
<td>(2.77-33.28)</td>
<td>(31.8-36.0)</td>
<td>(24.7-28.0)</td>
<td>(42.73-78.44)</td>
<td>(2.55-19.93)</td>
<td>(0.00-0.45)</td>
</tr>
<tr>
<td>NF</td>
<td>19.84 ± 1.09</td>
<td>3.25 ± 0.68</td>
<td>7.54 ± 0.62</td>
<td>33.3 ± 0.5</td>
<td>26.4 ± 0.8</td>
<td>20.22 ± 8.74</td>
<td>18.13 ± 4.85</td>
<td>0.58 ± 0.20</td>
</tr>
<tr>
<td></td>
<td>(15.50-24.27)</td>
<td>(1.42-6.62)</td>
<td>(4.31-10.27)</td>
<td>(31.2-36.7)</td>
<td>(23.6-27.8)</td>
<td>(6.50-45.78)</td>
<td>(10.62-31.71)</td>
<td>(0.09-0.98)</td>
</tr>
<tr>
<td>NP</td>
<td>22.92 ± 1.32</td>
<td>4.22 ± 1.89</td>
<td>8.20 ± 4.34</td>
<td>33.6 ± 0.5</td>
<td>25.8 ± 0.8</td>
<td>12.35 ± 5.00</td>
<td>9.21 ± 3.66</td>
<td>0.14 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>(17.89-28.97)</td>
<td>(1.23-17.16)</td>
<td>(2.69-47.14)</td>
<td>(31.4-37.0)</td>
<td>(22.7-27.4)</td>
<td>(2.00-23.55)</td>
<td>(1.65-18.70)</td>
<td>(0.03-0.32)</td>
</tr>
<tr>
<td>SF</td>
<td>4.60 ± 0.36</td>
<td>1.92 ± 0.20</td>
<td>1.53 ± 0.19</td>
<td>33.6 ± 0.4</td>
<td>26.1 ± 0.8</td>
<td>32.26 ± 3.13</td>
<td>34.05 ± 4.85</td>
<td>0.14 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>(3.57-6.69)</td>
<td>(0.78-2.75)</td>
<td>(0.70-2.63)</td>
<td>(31.6-36.0)</td>
<td>(23.2-28.1)</td>
<td>(26.70-41.03)</td>
<td>(24.70-47.53)</td>
<td>(0.05-0.18)</td>
</tr>
<tr>
<td>SP</td>
<td>4.30 ± 0.37</td>
<td>1.71 ± 0.11</td>
<td>1.52 ± 0.12</td>
<td>33.6 ± 0.4</td>
<td>26.0 ± 0.6</td>
<td>39.35 ± 7.24</td>
<td>44.10 ± 9.59</td>
<td>0.07 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>(3.16-6.12)</td>
<td>(1.03-1.92)</td>
<td>(0.86-1.96)</td>
<td>(31.5-36.0)</td>
<td>(23.8-27.7)</td>
<td>(28.93-60.60)</td>
<td>(17.35-62.98)</td>
<td>(0.05-0.13)</td>
</tr>
</tbody>
</table>
Table 3.9. Pearson's correlations matrix of means of measured habitat characteristics and mean number of settlers, settler growth and percent survival for three species across six sites in Kane' ohe Bay. Correlation coefficients and associated P-values presented. (Number of settlers m$^{-2}$ and water motion log$_{10}$ transformed; growth = slope of log$_{10}$ standardized polyp increase per month; % 12 month survival and % adult cover m$^{-2}$ arcsine square-root transformed; total suspended solids and sediment log$_{10}$ +1 transformed).

<table>
<thead>
<tr>
<th>Species</th>
<th>Water Motion (DF)</th>
<th>Total Suspended Solids (mg/l)</th>
<th>Sediment (mg/cm² day)</th>
<th>Salinity (‰)</th>
<th>Temperature (°C)</th>
<th>% Adult Cover/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. capitata</td>
<td>-0.4451</td>
<td>-0.8671</td>
<td>-0.1969</td>
<td>0.5673</td>
<td>-0.0416</td>
<td>0.0359</td>
</tr>
<tr>
<td></td>
<td>0.3764</td>
<td>0.0253</td>
<td>0.7084</td>
<td>0.2404</td>
<td>0.9376</td>
<td>0.9462</td>
</tr>
<tr>
<td>P. compressa</td>
<td>0.6036</td>
<td>0.3353</td>
<td>0.4079</td>
<td>-0.0130</td>
<td>-0.4851</td>
<td>-0.7305</td>
</tr>
<tr>
<td></td>
<td>0.2046</td>
<td>0.5158</td>
<td>0.4221</td>
<td>0.9806</td>
<td>0.3295</td>
<td>0.0992</td>
</tr>
<tr>
<td>P. damicornis</td>
<td>0.8610</td>
<td>0.4627</td>
<td>0.8942</td>
<td>-0.4341</td>
<td>0.2489</td>
<td>0.4448</td>
</tr>
<tr>
<td></td>
<td>0.0276</td>
<td>0.3555</td>
<td>0.0162</td>
<td>0.3897</td>
<td>0.6344</td>
<td>0.3767</td>
</tr>
<tr>
<td>M. capitata</td>
<td>-0.3660</td>
<td>-0.0608</td>
<td>-0.4764</td>
<td>-0.3430</td>
<td>-0.3800</td>
<td>0.1476</td>
</tr>
<tr>
<td></td>
<td>0.5447</td>
<td>0.9227</td>
<td>0.4172</td>
<td>0.5720</td>
<td>0.5281</td>
<td>0.8128</td>
</tr>
<tr>
<td>P. compressa</td>
<td>0.7015</td>
<td>0.3866</td>
<td>0.6275</td>
<td>-0.2728</td>
<td>-0.2722</td>
<td>-0.6517</td>
</tr>
<tr>
<td></td>
<td>0.1203</td>
<td>0.4490</td>
<td>0.1823</td>
<td>0.6010</td>
<td>0.6018</td>
<td>0.1608</td>
</tr>
<tr>
<td>P. damicornis</td>
<td>-0.4927</td>
<td>-0.4752</td>
<td>-0.9306</td>
<td>0.7746</td>
<td>-0.7970</td>
<td>-0.4045</td>
</tr>
<tr>
<td></td>
<td>0.5073</td>
<td>0.5248</td>
<td>0.0694</td>
<td>0.2254</td>
<td>0.2030</td>
<td>0.5955</td>
</tr>
<tr>
<td>M. capitata</td>
<td>-0.6858</td>
<td>-0.7269</td>
<td>-0.6933</td>
<td>0.9616</td>
<td>-0.6186</td>
<td>0.1563</td>
</tr>
<tr>
<td></td>
<td>0.1326</td>
<td>0.1017</td>
<td>0.1267</td>
<td>0.0022</td>
<td>0.1904</td>
<td>0.7675</td>
</tr>
<tr>
<td>P. compressa</td>
<td>0.8150</td>
<td>0.9820</td>
<td>0.5615</td>
<td>-0.6614</td>
<td>0.0235</td>
<td>-0.4260</td>
</tr>
<tr>
<td></td>
<td><strong>0.0482</strong></td>
<td><strong>0.0005</strong></td>
<td>0.2463</td>
<td>0.1525</td>
<td>0.9648</td>
<td>0.3996</td>
</tr>
<tr>
<td>P. damicornis</td>
<td>0.0072</td>
<td>0.2142</td>
<td>-0.2014</td>
<td>-0.6924</td>
<td>0.2051</td>
<td>0.9325</td>
</tr>
<tr>
<td></td>
<td>0.9928</td>
<td>0.7858</td>
<td>0.7986</td>
<td>0.3076</td>
<td>0.7949</td>
<td>0.0675</td>
</tr>
</tbody>
</table>
and water motion and/or sedimentation rate potentially important to settlement of *P. damicornis*. Mean growth did not correlate significantly with means of any of the measured habitat characteristics. No significant relationship between a species’ mean number of settlers m\(^{-2}\), early growth or survival and corresponding adult distributions was found (Table 3.9).

**Site Projection Example**

A general projection of settlement and survival throughout each 500 m\(^2\) study area is shown for summer 2000 settlers of *Montipora capitata*, *Porites compressa* and *Pocillopora damicornis* in Table 3.10. Projected survivor numbers at four, 12 and 21 months were significantly positively correlated with initial settler numbers of *M. capitata* (Pearson’s correlations, *P* < 0.05), suggesting an overall influence of larvae availability on numbers of post-settlement survivors in this species. Significant positive correlations were also evident for *P. compressa* and *P. damicornis* at 4 months (Pearson’s correlations, *P* < 0.05), but were not present at 21 months (Pearson’s correlations, *P* > 0.05).

Interspecific variability in survival dramatically changed proportional settler representation over time at some sites (Table 3.10). *Montipora capitata* dominated initial counts at four of the six sites (67 %), but by 21 months remained the dominant representative species at one (17 %). *Porites compressa*, although dominant initially at only two sites (33 %), was projected to dominate survivor numbers at four of the six sites (83 %) within the 21-month period. The projection of zero survival in zones with known adult abundance (Table 3.10) suggests site-specific variation in settler survival over time.
Table 3.10. Projected numbers of settlers and survivors in 500 m$^2$ zones of measurement representing six sites in Kāne‘ohe Bay (C = Central Bay, N = North Bay, S = South Bay, F = Fringing Reef, P = Patch Reef)

<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Mean No. Settlers/m$^2$ Colonizable Substrate</th>
<th>Mean No. Initial Settlers</th>
<th>No. of 4 Month Survivors</th>
<th>No. of 12 Month Survivors</th>
<th>No. of 21 Month Survivors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(m$^2$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CF</td>
<td>M. capitata</td>
<td>21,553</td>
<td>6.168 x 10$^6$</td>
<td>81,999</td>
<td>28,700</td>
<td>3,417</td>
</tr>
<tr>
<td></td>
<td>P. compressa</td>
<td>338</td>
<td>96,834</td>
<td>38,956</td>
<td>24,932</td>
<td>11,986</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>79</td>
<td>22,595</td>
<td>12,980</td>
<td>5,079</td>
<td>2,049</td>
</tr>
<tr>
<td>CP</td>
<td>M. capitata</td>
<td>1,932</td>
<td>149,512</td>
<td>3,214</td>
<td>536</td>
<td>201</td>
</tr>
<tr>
<td></td>
<td>P. compressa</td>
<td>79</td>
<td>6,108</td>
<td>2,489</td>
<td>995</td>
<td>622</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>90</td>
<td>6,981</td>
<td>2,493</td>
<td>1,247</td>
<td>831</td>
</tr>
<tr>
<td>NF</td>
<td>M. capitata</td>
<td>4</td>
<td>637</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>P. compressa</td>
<td>79</td>
<td>13,376</td>
<td>10,744</td>
<td>6,208</td>
<td>4,356</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>26</td>
<td>4,459</td>
<td>3,358</td>
<td>1,099</td>
<td>488</td>
</tr>
<tr>
<td>NP</td>
<td>M. capitata</td>
<td>8</td>
<td>1,227</td>
<td>15</td>
<td>3</td>
<td>0</td>
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<tr>
<td></td>
<td>P. compressa</td>
<td>357</td>
<td>58,259</td>
<td>39,271</td>
<td>27,150</td>
<td>19,635</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>218</td>
<td>35,569</td>
<td>15,869</td>
<td>3,967</td>
<td>1,700</td>
</tr>
<tr>
<td>SF</td>
<td>M. capitata</td>
<td>338</td>
<td>16,875</td>
<td>271</td>
<td>135</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>P. compressa</td>
<td>94</td>
<td>4,688</td>
<td>1,875</td>
<td>852</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>8</td>
<td>375</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>SP</td>
<td>M. capitata</td>
<td>83</td>
<td>4,166</td>
<td>383</td>
<td>96</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>P. compressa</td>
<td>53</td>
<td>2,651</td>
<td>994</td>
<td>398</td>
<td>249</td>
</tr>
<tr>
<td></td>
<td>P. damicornis</td>
<td>4</td>
<td>189</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Discussion

Site and Seasonal Variation

Spatial and temporal variability in coral settlement and recruitment is a phenomenon common to many reef systems (Harrison and Wallace 1990 and cited references, Fisk and Harriott 1990, Samaroo 1991, Tomascik 1991, Smith 1992, 1997, Fitzhardinge 1993, Glynn et al. 1994, 1996, 2000, Gleason 1996, Baird and Hughes 1997, Connell et al. 1997, Dustan and Johnson 1998, Fairfull and Harriott 1999, Hughes et al. 1999, 2000, 2002, Carlon 2001, Kojis and Quinn 2001, Jinendradasa and Ekarantne 2003) and has been noted previously in Kane‘ohe Bay (Fitzhardinge 1993). In this study, overall settlement appeared highest at Central Bay sites, particularly Central Fringing reef, although the relative significance of settlement at this site varied among the most common coral species. Levels of Montipora capitata settlement at Central Bay sites were up to two orders of magnitude higher than South and North Bay sites. Porites compressa, however, did not differ in overall mean settlement between sites, and settlement at Central and North Bay sites was not significantly different for Pocillopora damicornis, although both were significantly higher than South Bay sites. These differences in distributional patterns of settlement did not correspond to site-specific adult abundances, and may be a consequence of differences in fertilization strategies (i.e., location of fertilization, see Kolinski and Cox 2003) and/or the level of synchronization in gamete/planulae release, in combination with water flow patterns within Kane‘ohe Bay and between bay and oceanic zones (Bathen 1968, Smith et al. 1981, Figure 3.7).

At a gross level of measurement, settlement over time corresponded well with observed spawning times of the major coral species. Montipora capitata was found to
settle mainly in the summer. This was the only species observed to display discrete settlement pulses soon after peaks in spawning. In contrast, *P. compressa* did not display discrete spawning peaks and exhibited greater temporal dispersion of settlement, which occurred mostly in summer and fall. *Pocillopora damicornis* is a year round brooder in Hawai‘i (Edmondson 1946, Harrigan 1972, Jokiel 1985, Jokiel et al. 1985). Although it has been suggested that significant *P. damicornis* settlement would be restricted to summer months in Hawaiian waters (Jokiel and Guinther 1978), such a pattern was not apparent when comparing levels of settlement across seasons in this study. The tendency to reproduce year round in corals is most often associated with brooding species (Harrison and Wallace 1990), suggesting that *C. tenella* is a brooder.

The apparent disassociation between levels of settlement and adult abundances suggests some separation of source and sink populations within Kāne‘ohe Bay (Holthus et al. 1989, Fitzhardinge 1993). Central Fringing reef, for example, appeared as a sink for *M. capitata* and *P. compressa* larvae despite relatively low site abundance of adult populations (particularly *M. capitata*). Water flow within this area is tidal, but is also influenced by wind driven long-shore currents originating in the South Bay (Bathen 1968, Smith et al. 1981, Figure 3.7). The residency time of South Bay waters is approximately 13 days (Smith et al. 1981). Embryonic development of *M. capitata* and *P. compressa* occurs within 2 to 3 days (Mate et al. 1998, Hunter 1988a, Kolinski Chapter 2 and unpublished data), and larvae of *M. capitata* are highly competent to settle from 3 to 42 days post fertilization (Kolinski Chapter 2). High density adult populations at South Bay sites, in combination with flow patterns, water residency times and timing for embryonic larval development, suggests there may be a connectivity corridor between
South Bay and the Central Fringing reef area, at least for *M. capitata*. Further investigation of connectivity within the bay using genetic analysis is currently underway (Kinzie et al. 2003).

**Figure 3.7.** Generalized seawater circulation pattern in Kāne‘ohe Bay. Modified from Bathen (1968) and Smith et al. (1981).
Settler Survival

Type III survivorship was strongly evident for *Montipora capitata*, and appeared also for *Porites compressa* and *Pocillopora damicornis* settlers at Kāne‘ohe Bay sites. Such a pattern of survival is common to marine invertebrates (reviewed by Gosselin and Qian 1997, Hunt and Scheibling 1997), including many scleractinian coral species for which settler survival has been examined (Babcock 1985, Sato 1985, Babcock and Mundy 1996, Mundy and Babcock 2000, Baird and Hughes 2000, Raimondi and Morse 2000). Numerous factors may influence early survival, including genetic unsuitability or abnormalities, low energy reserves, predation, accidental ingestion, bulldozing or trampling by mobile invertebrates, competition, disease, and a variety of abiotic disturbances (such as changes in water motion, water clarity, light exposure, sedimentation, salinity, etc.; Gosselin and Qian 1997, Hunt and Scheibling 1997). Field mortalities exceeding 99% have previously been reported for *M. capitata* in Kāne‘ohe Bay within a few months following settlement (Fitzhardinge and Bailey-Brock 1989). Assuming significant loss of gametes through failure to fertilize (Oliver and Willis 1987, Oliver and Babcock 1992, Levitan 1995, Lasker et al. 1996, Underwood and Keough 2001) and high mortality of embryos and larvae in the plankton and when settling (Underwood and Fairweather 1989, Morgan 1995, Pechenick 1999), such repeated loss of settled individuals suggests great investment of reproductive effort may be needed by individuals of *M. capitata* to increase the likelihood of eventual replacement with fecund offspring (note: high production may occur with a relatively minor cost, Kolinski Chapter 4). Spatial and temporal variation in habitat suitability is a likely driving force towards such reproductive “waste” (Underwood and Keough 2001). The dispersal of larvae

*Montipora capitata* settlers did not appear to be as suited for survival on shallow Kane‘ohe Bay reefs as *P. compressa* and *P. damicornis*. Initially this was assumed to be the result of species differences in proportions of very recent settlers observed across censuses. Although this assumption eventually needs to be tested, results of the analysis examining proportional survival of four-month survivors at 12 and 21 months tended to support the initial findings of survival differences. Variability in survival did exist among sites, and temporal variability must occur, as is evidenced by adult abundances at sites with zero settler survival. A better comparative test might involve the seeding and monitoring of multiple plates at multiple sites with similar aged larvae of each species repeatedly over a number of years.

The differences in survival of *M. capitata, P. compressa* and *P. damicornis* settlers can dramatically alter settler year-class representation at a site over time. This was most evident at Central Fringing reef, where roughly 6 million projected *M. capitata* setters ended up being outnumbered by 100,000 *P. compressa* settlers after 21 months had elapsed. The tendency for *P. compressa* to dominate settler survivorship numbers may partially explain this species success in occupying space in a number of environments. *Montipora capitata* success in gaining occupancy of space may partially depend on repetitive influxes of very large numbers of settlers. A significant positive correlation between initial numbers of *M. capitata* settlers and survivors over time was
found, and there was some suggestion that a minimum threshold density of settlers may
be needed to ensure long-term (21 months in this study) year class representation of this
species at a site.

**Settler Growth**

The mean standardized rate of growth of *Montipora capitata* was exceedingly
slow compared to *Porites compressa* and *Pocillopora damicornis*, although potential
growth rates (i.e., fastest recorded) were not too dissimilar. The three species differ in
larvae size, and thus presumably available energy at settlement. In this study, larval size
had no apparent influence on mean rates of overall settler growth, as was evidenced by *P.
compressa* (which has the smallest larvae) displaying a significantly higher mean growth
rate than the larger *M. capitata*, and a statistically similar rate of growth to that of *P.
damicornis* (largest larvae of the three species). Previous comparisons between broadcast
spawning and planulating species have suggested relatively faster early growth rates for
planulating species (Babcock 1985, Harrison and Wallace 1990). Clearly this was not the
case for *P. compressa* and *P. damicornis* in Kāneʻohe Bay. *Montipora capitata*, *P.
compressa* and *P. damicornis* all possess zooxanthellae upon parental release as eggs or
larvae. Thus, differences in mean early growth cannot be attributed to any apparent need
of any of these species to acquire and multiply zooxanthellae following settlement (see
Babcock 1985, Van Moorsel 1988). Internal factors other than those related to initial size,
available energy, and zooxanthellae acquisition ostensibly play a critical role(s) in the
growth determination of settlers of these three species. Although not detected in this
study, environmental factors also likely play a very important role.
A large proportion (61%) of the surviving *M. capitata* settlers displayed an ability to remain in a “dormant” one-polyp state for extended periods of time exceeding one year. This phenomenon was not observed in *P. compressa* or *P. damicornis* (small numbers of one-polyp, year old *P. compressa* settlers were observed; however, such status was associated with previous declines in polyp numbers), but may not be unique as similar delays in growth have been observed in *Goniastrea aspera* in Japan (Sakai 1998). Variable rates in growth and an ability to maintain “dormancy” across multiple breeding seasons have implications for appropriate assessment of age/year class representation and correlation to observed reproductive phenomena (Hughes and Connell 1987, Muko et al. 2001). New observations of numerous large visible recruits of *M. capitata* on a reef may say more about a particular year’s conditions affecting growth of cumulative settlers that arrived across a number of years than about any single reproductive event involving high reproductive output, fertilization success and/or levels of settlement. Age determinations of even small *M. capitata* recruits will be difficult to determine without direct monitoring from the period of initial settlement.

A relationship between rates of growth and longer-term (nine plus months) survival was not evident for *M. capitata*, but was significant for *P. compressa* and *P. damicornis*. Fast early growth leading to occupation of space is generally considered to be advantageous in competitive and/or frequently disturbed habitats (Jackson 1977, Birkeland 1977, Kojis and Quinn 1981, Jackson and Hughes 1985, Szmant 1986, Johnson 1992, Sakai 1998). Growth apparently is important for the persistence of *P. compressa* and *P. damicornis*, both of which displayed temporally scattered and somewhat lower overall levels of settlement. *Montipora capitata* may gain its advantage through high
settler numbers occupying a variety of spaces that, when given opportunity and appropriate conditions, grow and recruit into the community. The comparison may thus be one of quality versus quantity.

**A Comparison of Parameters and Suggested Recruitment Strategies**

A summary of reproduction and recruitment related findings for *Montipora capitata*, *Porites compressa* and *Pocillopora damicornis* in Kāneʻohe Bay are listed in Table 3.11 as a means to understand and compare early life history strategies. Various characteristics differ among the three species. As mentioned above, the early life history strategy of *M. capitata* appears to be heavily focused around quantity, based mainly on reproductive characteristics that lead to high levels of larval development and settlement. Discrete periods of spawning synchrony, hermaphroditism and surface water fertilization are all characteristics that increase potential for high levels of larval development. The larvae display a mainly generalist strategy in terms of settlement substrate preference (Kolinski Chapter 2). Although *M. capitata* larvae remain competent to settle for extended periods of time (Kolinski Chapter 2), the vast majority of recruitment occurs in pulses soon after spawning during the summer. High overall mortality of settlers is displayed (Fitzhardinge and Bailey-Brock 1989, Fitzhardinge 1993, this study), suggesting internal and/or external qualitative inadequacies. On average, growth is slow. Although *M. capitata* settlers appear to possess a potential for relatively rapid growth, such growth may be delayed until favorable conditions prevail. An ability of some settlers to survive in the absence of growth suggests that an accumulation of year classes may persist and recruit to the community together when conditions allow.
Table 3.11. Life history characteristics of *M. capitata*, *P. compressa* and *P. damicornis* in Kāne‘ohe Bay (\(^1\) = Hodgson 1986; \(^2\) = Krupp et al. 1992; \(^3\) = Polacheck 1978)

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>M. capitata</em></th>
<th><em>P. compressa</em></th>
<th><em>P. damicornis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>Hermaphrodite</td>
<td>Gonochoric</td>
<td>Hermaphrodite</td>
</tr>
<tr>
<td>Reproductive mode</td>
<td>Broadcast Spawner</td>
<td>Broadcast Spawner</td>
<td>Brooder</td>
</tr>
<tr>
<td>Reproductive Season</td>
<td>Summer - Fall</td>
<td>Summer - Fall</td>
<td>Year Round</td>
</tr>
<tr>
<td>Synchrony in Spawning/Planulation</td>
<td>Highly Synchronized</td>
<td>Extended</td>
<td>Extended</td>
</tr>
<tr>
<td>Location of Fertilization</td>
<td>Water Surface</td>
<td>Water Column</td>
<td>Polyps</td>
</tr>
<tr>
<td>Relative Larval Size</td>
<td>Mid Size - Large</td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>(^1) Peak Larval Numbers in Plankton Tows (per 100 m(^3))</td>
<td>16000</td>
<td>1000</td>
<td>108</td>
</tr>
<tr>
<td>Settlement Timing</td>
<td>Highly Pulsed</td>
<td>Extended</td>
<td>Extended</td>
</tr>
<tr>
<td>Settlement Preference</td>
<td>Generalist</td>
<td>Unknown</td>
<td>Generalist</td>
</tr>
<tr>
<td>Relative Mean Settler Growth Rate</td>
<td>Slow</td>
<td>Fast</td>
<td>Fast</td>
</tr>
<tr>
<td>Relative Potential Settler Growth Rate</td>
<td>Fast</td>
<td>Very Fast</td>
<td>Very Fast</td>
</tr>
<tr>
<td>Single Polyp “Dormancy”</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Settler Survivorship</td>
<td>Type III</td>
<td>Type III</td>
<td>Type III</td>
</tr>
<tr>
<td>Mean One-year Survival (%)</td>
<td>0.4 (± 0.1 S.E.)</td>
<td>16.7 (±4.8 S.E.)</td>
<td>8.7 (± 1.3 S.E.)</td>
</tr>
<tr>
<td>Significant Correlation: No. Initial Settlers vs. No. 21 Month Survivors</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Settler Growth-Survival Relationship</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>(^2) Maturation Size (Colony Diameter, cm)</td>
<td>9.5 (?)</td>
<td>3.5 (?)</td>
<td>2.5</td>
</tr>
<tr>
<td>Pheonix Effect(^3) in Settlers</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Adult Community Persistence</td>
<td>Long-Term</td>
<td>Long-term</td>
<td>Short-term</td>
</tr>
<tr>
<td>(^3) Maximum Diameter Commonly Observed</td>
<td>&gt; 1 m</td>
<td>&gt; 1 m</td>
<td>12 – 14 cm</td>
</tr>
</tbody>
</table>

In contrast to *M. capitata*, *P. compressa* and *P. damicornis* appear to place emphasis on certain qualitative characteristics in their early life histories. In *P. compressa*, separate sexes, extended, less synchronized periods of spawning, and fertilization within the three-dimensional water column potentially limit larval numbers (see Hodgson 1986) but leads to an extended settlement period over time. Type III
survivorship of settlers exists; however, known mortality levels relative to that of *M. capitata* are significantly lower. High relative rates of growth are evident within this species, which may be explained by the finding that survival is significantly related to growth. Several of the settlers, however, displayed an ability to "resurrect" from what appeared to be a state of death (Kolinski in prep.). Fast early growth and high levels of survival are qualitative characteristics likely influencing the persistence of this species. *Pocillopora damicornis* has growth and survival characteristics very similar to that of *P. compressa*. However, *P. damicornis* in Kane‘ohe Bay is a brooder, albeit with reported asexually derived larvae (Stoddart 1986), producing and releasing planulae year round (Jokiel 1985). Maximum colony size and total area coverage within Kane‘ohe Bay are much lower than that of *M. capitata* and *P. compressa*, and distributions are generally restricted to shallow water reef flats and margins (Maragos 1972, Polacheck 1978, Maragos et al. 1985, Holthus et al. 1989, Hunter and Evans 1995). Thus, the total number of larvae released can be expected to be much lower than that produced by *M. capitata* and *P. compressa* in a given year (see Hodgson 1986, Hunter and Evans 1995). The larvae are able to settle soon after release (Harrigan 1972) but remain competent for periods of at least 100 days (Richmond 1987a). *Pocillopora damicornis* larvae appear to be generalists in terms of settlement preference (see Kolinski Chapter 2). The settlers grow relatively rapidly and display relatively high proportional levels of survival. Their early survival does appear to be linked to growth. *Pocillopora damicornis* has been noted as an opportunistic species (Stoddart 1983, Richmond 1988, Endean and Cameron 1990, Jokiel 1998). It tends to be the first species observed on new substrates in Kane‘ohe Bay (Fitzhardinge 1993, this study), but is noted for determinate/size limited growth.
(Maragos, pers. comm.) and high rates of turnover within populations (Maragos 1972, Polacheck 1978, Richmond 1985b, 1987b, Jokiel 1998). Based on reported colony sizes at maturity (Polacheck 1978), surviving *P. damicornis* settlers are likely to be the first of the three species to begin gamete/larval production.
CHAPTER 4

ENERGY ALLOCATION TO REPRODUCTION

Introduction

Sexual reproduction in scleractinian corals involves the formation and dispersal of planktonic larvae in habitats that vary spatially and temporally. Corals are iteroparous, mainly modular organisms, with a potential to be reproductively prolific. The implications of large, repetitive reproductive output include increased probabilities of successful fertilization, dispersal, settlement and recruitment over time (Underwood and Fairweather 1989, Oliver and Babcock 1992, Levitan 1995, Hughes et al. 2000). Rates of mortality in the early life history of corals, however, tend to be high (Babcock 1985, Fitzhardinge and Bailey-Brock 1989, Fitzhardinge 1993, Babcock and Mundy 1996, Fairfull and Harriott 1999, Kolinski Chapter 3), bringing into question the magnitude and importance of parental investment and the costs associated with reproduction.

Lipids are energy rich molecules critical in a number of ways to various early life history strategies of corals. Lipids provide buoyancy to eggs-sperm bundles of numerous coral species for fertilization in the two-dimensional like environment of the waters surface (Babcock et al. 1986, Harrison 1988, Harrison and Wallace 1990, Arai et al. 1993, Richmond 1997). Development of coral larvae and lengths of competency and dispersal appear to be partially dependent on the energy derived from stored lipids (Richmond 1988, Arai et al. 1993, see also Wilson and Harrison 1998, Isomura and Nishihira 2001), which make up roughly 70 % of the composition of eggs and larvae in species investigated (Richmond 1987a, Arai et al. 1993). Lipids may influence the vertical migration of larvae through the water column, with lipid expulsion being used to

Direct examination of the energetic costs of reproduction in relation to energy uptake has only occurred for two brooding species, with projections restricted to sunny days (Edmunds and Davies 1986, Davies 1991, Jokiel 1998). This study examined energy allocation to reproduction in the broadcast spawning coral *Montipora capitata* in relation to energy derived from photosynthesis on an annual basis. *Montipora capitata* is a hermaphroditic coral that spawns annually during summer months. It releases buoyant, lipid-filled egg-sperm bundles that congregate and fertilize at the waters’ surface (Heyward 1986, Kolinski and Cox 2003). Although tending to settle soon after embryogenesis, larvae of this species can remain competent to settle for up to seven months (Kolinski Chapter 2). Large concentrations of larvae (Hodgson 1986) and settlers (Kolinski Chapter 3) have been observed in the field; however, settler survival is extremely low, even relative to other common species of scleractinian corals (Kolinski Chapter 3). These early life history traits of *M. capitata* are viewed from the perspective of energetic costs associated with reproduction in this species.

**Methods**

**Collection of Corals and Measurement of Environmental Parameters**

Colonies of *Montipora capitata* were collected from 1 m depth on the windward reef flat of Coconut Island and from 3 to 4 m depth off the windward reef slope of Kokokahi (close to the depth limits of *M. capitata* at this site), Kāneʻohe Bay, Oʻahu, Hawaiʻi (Figure 4.1). The colonies were tagged and placed in cleared areas at their respective collection sites and depths four months prior to monitoring for gamete release in 1997. A total of 14 of 18 colonies collected at Coconut Island and 17 of 18 colonies at
Figure 4.1. Coral collection sites in Kāneʻohe Bay, Oʻahu, Hawaiʻi. Kokokahi were successfully monitored. Maximum diameters were measured in May prior to spawning and ranged between 15 and 20 cm. Colony displacement volumes were measured in August following spawning and ranged between 162 and 833 cm$^3$. All selected colonies had greater than 95% live tissue cover. Additional colonies of various sizes were collected from these sites and depths in 1998 to increase sample sizes for various gamete measurements as described below.

Environmental parameters were measured on a monthly basis between August 1996 and July 1997 at three locations along a 50-meter transect at each colony collection site and depth. Light attenuation at depth was measured using two Li-Cor Inc. model LI-188B units with LI-1925B sensors (note: measurements occurred in only nine of the 12 months due to equipment malfunction). Sensors were equilibrated at the water’s surface,
and then one sensor was placed face up on the substrate at depth. Five measurements of mean photosynthetically active radiation (PAR; 400 to 700 nm) were made over 10 second intervals at each location. Mean values were used to determine mean percent PAR at depth and extinction coefficients for each month at each site. Three one-liter water samples were collected at monthly intervals in clear Nalgene™ polyethylene bottles at each site for measurement of total suspended solids (TSS). All water was collected 0.15 m above the substrate. The samples were vacuum filtered onto pre-weighed 500°C pre-ashed GC50 filters, with ample rinsing using de-ionized water. The TSS samples were placed in a 60°C drying oven for 24 hours prior to being weighed on a Mettler AB104 electronic microbalance. Rates of sedimentation were measured for 24-hour periods at monthly intervals using 15.24 cm deep, 5.45 cm wide, bottom-capped polyvinyl chloride (PVC) pipe traps. Two traps were clipped to PVC posts at each of the three locations at each site. The traps were plugged prior to removal from the posts and were vacuum filtered onto individual pre-weighed 500°C pre-ashed GC50 filters with ample rinsing using de-ionized water. The sediments were dried at 60°C for 24 hours and then weighed on a Mettler AB104 electronic microbalance. Oxygen concentrations were measured monthly using a YSI model 55. Oxygen flux on reefs is known to increase throughout the day (Kohn and Helfrich 1957, Kinsey 1985), which complicated comparisons between sites, as measurements could not be made simultaneously at both Coconut Island and Kokokahi. Data exploration showed oxygen concentrations at Coconut Island to be consistently higher than Kokokahi despite measurement time, thus only those values obtained when Coconut Island was measured first where used in a pair-wise analysis (one-sided, paired by month). Salinity and temperature were measured monthly using a
YSI model 30 conductivity meter. Water motion was determined using Plaster of Paris “clod cards” (Doty 1971, Jokiel and Morrissey 1993), with two clod cards being anchored to each of three bricks at each site per trial for a period of 24-hours. Control cards were placed in a five-gallon (19 l) bucket of seawater in a shaded, wind protected area on land. The cards were briefly rinsed in still fresh water, air-dried for a month (in an air-conditioned, dehumidified room) and then weighed on a Mettler P160 balance. The values of each measured parameter were averaged for each month at each site for parametric or non-parametric pair-wise comparisons.

Reproductive Output

Spawning of Montipora capitata is a predictable event, occurring between the months of May and September during new and first quarter moons between 20:45 and 22:30 (Hunter 1988b, Kolinski and Cox 2003). Colonies were transferred to flow-through sea water tables covered with 15 % shade-cloth at the Hawai‘i Institute of Marine Biology two to three days prior to each new moon from May through September 1997. At 18:00 each evening, colonies were placed in submerged, individually sized black plastic flowerpots with pot upper-lips maintained slightly above the water level of each table such that each pot contained the buoyant gamete bundles of a single colony once released. Open ports in pot bottoms allowed for water exchange without loss of gametes. Water exchange was enhanced by the presence of large aerators placed in the seawater tables. The colonies were carefully returned to the tables each night after 22:45, and were returned to the field after each month’s predicted/observed lunar associated spawning period. Colonies remained submerged during all transfers between field and lab and into/out of pots.
Surface waters within pots were examined for gamete presence under low, usually red, light conditions. Gametes, upon spawning, were collected with disposable plastic pipettes and were counted individually and/or collectively measured for volume in 10 ml and 25 ml graduated cylinders. Volume measurements never exceeded 2.3 ml for any sample, and all measurements occurred prior to significant bundle breakup. A colony volume to gamete bundle number relationship ($\text{No. Bundles} = 843.6 \times \text{Volume} - 26.3; n = 30, R^2 = 0.95$) was determined for colonies monitored in 1997 and 1998, using one representative sample from each colony in regression analysis, satisfying appropriate model assumptions. Collective measurements for each 1997 colony were scored throughout the spawning season, with measured volumes being converted to bundle numbers using the regression.

**Energy Estimates**

Gamete bundles were collected from 11 Coconut Island (five in 1997 and six in 1998) and 11 Kokokahi colonies (six in 1997 and five in 1998) and were pipetted directly onto individual screens of 100 μm Nitex mesh, quickly rinsed with de-ionized water to remove salts (bundles and eggs did not lyse), placed in plastic Gelman petri-dishes, frozen at $-50^\circ\text{C}$, and then lyophilized for 12 to 16 hours. Bundle samples between 8.59 and 10.88 mg from each container were molded into small balls using clean stainless steel spatulas. Samples were weighed on an Ohaus Analytical Plus electronic balance. Energy content was determined using a Phillipson microbomb calorimeter (see Phillipson 1964). Multiple samples from each colony were measured, and caloric contents were calculated utilizing the mean of three benzoic acid standards. Additional samples were burned on pre-ashed and weighed GC50 filters at $500^\circ\text{C}$ to determine ash content (Paine 1991).
Mean bundle mass was determined for known numbers of gamete bundles from 18 colonies (four 1997, and five 1998 Coconut Island colonies and three 1997, and six 1998 Kokokahi colonies) on an Ohaus Analytical Plus electronic balance. Comparisons of energy content per mg gametes and of bundle weights were made between sites and times using factorial ANOVA, meeting all model assumptions. Estimates of energy content of the total reproductive output of corals monitored in 1997 were determined by multiplying mean gamete values of joules per mg x mg per bundle x total bundles per colony.

**Photosynthesis versus Irradiance Measurements**

In November 2001, five *Montipora capitata* colonies each were collected from Coconut Island and Kokokahi for measurement of photosynthesis versus irradiance (*P-I*) at the Hawai‘i Institute of Marine Biology. These colonies were to act as surrogates for estimating annual productivity in the monitored 1997 colonies. Collection sites and depths were the same as those in 1997 and 1998. Colonies were selected such that the sizes spanned the range for colonies monitored for reproductive output in 1997. Maximum colony diameters were between 15 and 20 cm, and all colonies had greater than 95 % live tissue cover. Colony size measurements included volume (water displacement), buoyant weight (see Jokiel et al. 1978) and projected area (area of an ellipse = \( \pi \times 0.5 \text{ length} \times 0.5 \text{ width} \)).

Oxygen production of *M. capitata* colonies was measured over three clear days in four open-topped Plexiglas containers placed in two white flow-through seawater tables such that the containers were in unobstructed sunlight. Each container received seawater pumped directly from the Coconut Island reef flat such that water volumes were replaced
every two to three minutes. When oxygen measurements were being made, water was re-circulated using Little Giant centrifugal pumps, maintaining vigorous water motion similar to that at colony collection sites. Water pumped through the flow-through seawater tables ensured temperatures similar to the reef flat environment were maintained in each container throughout the course of the study. Water temperatures during incubations remained at 26.02 °C (± 0.01 S.E.).

Photosynthetically active radiation (between 400 and 700 nm) was measured as μEinsteins m⁻² sec⁻¹ using a Li-Cor Inc. model LI-1400, with a LI-192SB underwater sensor submerged adjacent to containers in each flow-through seawater table. Oxygen concentration was measured in mg min⁻¹ using two YSI model 600XLM. Oxygen measurements were made in the following fashion: The YSI sensors were placed in a bucket of fresh water. The external seawater source to two of the four containers (one in each table) was shut off, and the pumps were used to lower water in the containers to predetermined levels corresponding to colony size. The pumps were reconnected such that water in each container was re-circulated, and a YSI sensor was placed in the corner of each container for a period of 10 minutes (note: calibration trials found no difference in oxygen readings between units or between positions within the containers). The YSI sensors were then transferred to the fresh water bucket (salinity changes allowed for easy data recognition of an individual trial), outside flow was returned to the two containers, and the process was repeated for the other two containers. Measurements were made in a staggered fashion between 04:30 and 16:30 on each of the three days. The colonies were placed in the containers with external seawater flow roughly six hours prior to first measurements to ensure colony stress would not occur. The colonies did not appear to be
stressed throughout the procedure. In darkness, polyps were extended, and mucus production was minimal throughout the course of the experiment.

Rates of oxygen production and consumption (mg min\(^{-1}\)) were calculated as the slope of 20 oxygen measurements made (one every 30 seconds) over each 10-minute period, correcting values for the total water volume. Gas exchange across the water surface was assumed to be inconsequential due to the short incubation times and extremely low wind stress on the measurement days in the sheltered containers (see Jokiel and Morrissey 1986).

Hyperbolic tangent (tanh) function curves (see Jassby and Platt 1976, Chalker 1981) were fitted to the \(P-I\) data using the computer program SigmaPlot. All \(P-I\) relationships were expressed by the equation

\[
P = (P_m-R) \tanh \left( \frac{I}{I_k} \right) + R
\]

(Jokiel and Morrissey 1986), where \(P\) is the net oxygen flux between the coral and the surrounding water, \(P_m\) is the maximum photosynthetic rate (horizontal asymptote of the curve), \(R\) is respiration (determined as negative oxygen flux in darkness), \(I\) is the measured irradiance (PAR), and \(I_k\) is the saturation constant (irradiance at which the initial slope of curve intercepts the horizontal asymptote).

**Estimates of Colony Productivity**

Estimates of total primary productivity from 1 June 1996 through 31 May 1997 were made by applying depth corrected irradiance (I) measurements averaged on an hourly basis over the relevant time period to the hyperbolic tangent functions and solving for \(P\). Photosynthetically active radiation has been measured every 10 seconds (averaged for each hour) at the Hawai‘i Institute of Marine Biology for the past 20 years using a
Cambell Scientific data logging system with a Li-Cor model LI-190SB sensor. Irradiance values were corrected using site and depth specific mean extinction coefficients determined for Coconut Island reef flat and Kokokahi reef slope waters from August 1996 through July 1997 (n = 9) using two Li-Cor Inc. model LI-188B with LI-1925B sensors. Hourly values of mg oxygen were added to obtain integrated estimates of net daily photosynthesis, which were then summed over the 365 days for each colony. Total oxygen values were converted to energy units (joules) using the assumption that the main carbon fixation product is lipid and the pathway is via glyceraldehydes 3-phosphate to glycerol (Davies 1991), or, as expressed in Jokiel (1998):

$$\text{CO}_2 + \text{H}_2\text{O} + 489,000 \text{J} \rightarrow \frac{1}{3}(\text{glyceraldehyde 3-phosphate}) + \text{O}_2.$$  

Values of annual respiration were determined by assuming oxygen flux per unit time was equivalent during daylight and darkness (Chalker et al. 1988, Falkowski et al. 1990, but see Edmunds and Davies 1988) and across seasons. Hourly estimates of oxygen flux determined during dark hours (negative values) were multiplied by 24 and then 365 to obtain annual respiration values. The addition of respiration and net productivity values provided estimates of gross photosynthetic productivity, which were converted to joules. All measured P-I parameters were assumed to remain stable throughout the applied period.

**Estimates of Annual Energy Allocation to Sexual Reproduction**

Correlations of colony size and gross and net colony productivity were insignificant (Pearson's correlations, $P > 0.05$) or inconsistent between sites for the surrogate colonies, thus average productivity values (joules) were used as a baseline for estimating the percent of annual gross and net productivity allocated to reproductive
products for the 1997 colonies. This procedure slightly increased the estimated percentages compared to values determined using size-standardized productivity. The estimates of energy content of the total reproductive output for each coral monitored in 1997 were divided by the site and time specific average annual gross and net energy values of productivity determined for the 2001 surrogate colonies as a means of estimating percent energy allocation to sexual reproduction.

**Results**

**Environmental Parameters**

Despite significantly higher TSS values at Kokokahi (mean difference = 0.93 ± 0.21 S.E. mg l⁻¹, Paired t-test, n = 12, df = 11, T = -4.34, P = 0.001), extinction coefficients (CI mean = 0.37 ± 0.02 S.E. m⁻¹, KK mean = 0.37 ± 0.03 S.E. m⁻¹) did not differ significantly between sites (Paired t-test n = 9, df = 8, T = -0.07, P = 0.947). Percent light at sample depths, however, was significantly higher at Coconut Island (mean = 77 ± 2 S.E. %) than Kokokahi (mean = 33 ± 3 S.E. %; Paired t-test of arcsine square-root transformed data, n = 9, df = 8, T = 11.56, P = 0.000) due to depth differences between sites (0.7 m versus 3.1 m depth). Water motion was significantly higher on the Coconut Island reef flat (mean difference = 4.91 ± 0.55 S.E. DF, Paired t-test, n = 12, df = 11, T = 8.91, P = 0.000). Sedimentation rates did not differ (Sign test, n = 12, P = 0.387).

Oxygen concentrations were significantly higher at Coconut Island than Kokokahi (Paired t-test, n = 3, df = 2, T = -15.53, P = 0.002), despite the fact that all Coconut Island values assessed were obtained earlier in the day than those at Kokokahi. Mean temperature was slightly but significantly higher at Coconut Island (mean difference =
0.3 ± 0.1 S.E. °C, Wilcoxon signed rank test, n = 12, P = 0.047). No difference in salinity was observed (Wilcoxon signed rank test, n = 12, P = 0.879).

In addition to measured water quality differences between the two sites, qualitatively, the Kokokahi site appeared degraded compared to the Coconut Island site. Coral cover was less than 3 % at Kokokahi (greater than 30 % at Coconut Island). Substrate at Kokokahi was mainly fine, black sediment that was anoxic just below the surface, compared to white, medium grained carbonate reef flat sands at Coconut Island. Filter feeding invertebrates, such as polychaetes and sponges, were observed to be more prevalent at Kokokahi.

**Reproductive Output**

Colony spawning in 1997 occurred in June, July and August. No spawning was noted in May or September. Seventy-four percent of the colonies spawned in both June and July, with two of the colonies spawning again in August. The percent of gamete bundles released from each colony averaged 42.24 (± 0.07) % in June, 57.73 (± 0.07 S.E.) % in July and 0.003 (± 0.003 S.E.) % in August.

Although seven of the 31 colonies (23 %; two from Coconut Island and five from Kokokahi) released less than 100 gamete bundles, all but one (97 %) of the monitored colonies released gametes. The average fecundity of colonies (standardized by colony volume) from Coconut Island (mean = 6.19 ± 1.04 S.E. bundles cm⁻³) and Kokokahi (mean = 5.35 ± 1.45 S.E. bundles cm⁻³) did not differ significantly (Two sample t-test with equal variance, n = 31, P = 0.654). The number of gamete bundles released ranged from 0 to 7834 and averaged 2962 (± 466 S.E.) bundles per colony. Colonies that released greater than 100 bundles (n = 24) averaged 3820 (± 473 S.E.) bundles per
colony. Colony volumes ranged from 162 to 833 cm$^3$ (mean = 489 ± 33 S.E. cm$^3$). A significant relationship between colony size and fecundity was found (Table 4.1).

**Table 4.1.** Regression analysis of colony reproductive output (bundles) versus colony size (cm$^3$)

<table>
<thead>
<tr>
<th>Predictor Variables</th>
<th>Coefficient</th>
<th>Std. Error</th>
<th>Student’s T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-484.159</td>
<td>1165.08</td>
<td>-0.42</td>
<td>0.6808</td>
</tr>
<tr>
<td>Colony Size (cm$^3$)</td>
<td>7.05117</td>
<td>2.23212</td>
<td>3.16</td>
<td>0.0037</td>
</tr>
</tbody>
</table>

**R$^2$**

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
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</thead>
<tbody>
<tr>
<td>Regression</td>
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<td>5.172E+07</td>
<td>5.172E+07</td>
<td>9.98</td>
<td>0.0037</td>
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<tr>
<td>Residual</td>
<td>29</td>
<td>1.503E+08</td>
<td>5182646</td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
<td>30</td>
<td>2.020E+08</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Energy Content of Reproductive Products**

The average energy content of gametes in bundles from Coconut Island (32.16 ± 0.32 S.E. J mg$^{-1}$; 7.68 ± 0.08 S.E. cal mg$^{-1}$) and Kokokahi colonies (32.17 ± 0.30 J mg$^{-1}$; 7.68 ± 0.07 S.E. cal mg$^{-1}$) did not differ significantly between sites or years (Table 4.2). Pooled energy values of gamete bundles averaged 32.17 ± 0.21 S.E. J mg$^{-1}$ (7.68 ± 0.05 S.E. cal mg$^{-1}$; n = 21 colonies). The average percent ash was 2.79 ± 0.15 S.E. Mean bundle weights did not differ significantly between sites or years (Table 4.3). The estimated energetic content of an individual gamete bundle ranged from 5.39 joules (1.28 cal) to 13.34 joules (3.19 cal), with a mean value of 8.69 ± 0.44 S.E. joules (2.08 ± 0.11 S.E. cal; n = 18).

**Table 4.2.** Factorial ANOVA of energy content (joules) per mg of Coconut Island and Kokokahi gametes collected in 1997 and 1998.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>1</td>
<td>2.316</td>
<td>2.3160</td>
<td>0.0339</td>
<td>0.8560</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>3.314</td>
<td>3.3138</td>
<td>0.0485</td>
<td>0.8282</td>
</tr>
<tr>
<td>Site*Year</td>
<td>1</td>
<td>2.316</td>
<td>2.3160</td>
<td>0.0339</td>
<td>0.8560</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>1230.598</td>
<td>68.367</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3. Factorial ANOVA of mean bundle weights (mg) of Coconut Island and Kokokahi gametes collected in 1997 and 1998.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>1</td>
<td>0.0009</td>
<td>0.0009</td>
<td>0.0111</td>
<td>0.9173</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>0.0772</td>
<td>0.0772</td>
<td>0.9320</td>
<td>0.3496</td>
</tr>
<tr>
<td>Site*Year</td>
<td>1</td>
<td>0.0521</td>
<td>0.0521</td>
<td>0.6289</td>
<td>0.4401</td>
</tr>
<tr>
<td>Error</td>
<td>15</td>
<td>1.2428</td>
<td>0.0829</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Applying the mean value of gamete bundle energy content, the average energy value of total gametes released per colony during the 1997 reproductive season was 25,740 ± 4050 S.E. J colony⁻¹ (6160 ± 969 S.E. cal colony⁻¹), and ranged from 0 to 6.81 x 10⁴ joules. The mean was 33,200 ± 4114 S.E. J colony⁻¹ (7950 ± 984 S.E. cal colony⁻¹) for colonies (n = 24) releasing greater than 100 gamete bundles (range = 2940 to 6.81 x 10⁴ joules).

**Photosynthesis versus Irradiance Measurements and Estimates of Productivity**

Correlations between measurements of colony size (projected area, volume, buoyant weight) and estimates of Iₖ, R, Pₘ, projected gross annual O₂ production, net annual O₂ production and gross and net photosynthetic productivity were not significant (Pearson’s correlations, P > 0.05) or were not consistent between groups within the measured size range. Although Pₘ values tended to be higher for colonies from Coconut Island than Kokokahi, these differences were not significant at α = 0.05 (mean difference = 0.2206 ± 0.1131 S.E. mg O₂ min⁻¹, Paired t-test, one-sided, n = 4, df = 3, T = 1.95, P = 0.073; only corals of similar sizes compared). Coconut Island colonies displayed significantly higher Iₖ values (mean difference = 77.275 ± 32.110 S.E. μE s⁻¹ m⁻², Paired t-test, one-sided, n = 4, df = 3, T = 2.41, P = 0.048) and rates of respiration (mean difference = -0.0841 mg O₂ min⁻¹, Paired t-test, one-sided, n = 4, df = 3, T = -2.74, P = 0.036) than similarly sized Kokokahi colonies. Hyperbolic tangent parameter values and projected values of respiration, gross and net O₂ production, and gross and net
photosynthetic productivity at depth are shown in Table 4.4. Despite higher respiration rates and $I_k$ values in Coconut Island colonies, differences in available light at depth led to significantly greater mean values of projected annual gross (Two-sample t-test, $n = 10$, $df = 8$, $T = 2.44$, $P = 0.041$) and net (Two-sample t-test for unequal variance, $n = 10$, $df = 8$, $T = 3.07$, $P = 0.015$) photosynthetic energy production for Coconut Island colonies.

Projected gross productivity from photosynthesis between June 1996 and May 1997 averaged $3.12 \times 10^6 \pm 5.12 \times 10^5$ S.E. joules ($7.44 \times 10^5 \pm 1.22 \times 10^5$ S.E. cal) for colonies from Coconut Island and $1.61 \times 10^6 \pm 1.65 \times 10^5$ S.E. joules ($3.84 \times 10^5 \pm 3.94 \times 10^4$ S.E. cal) for colonies from Kokokahi. Projected net productivity from photosynthesis averaged $14.64 \times 10^5 \pm 2.96 \times 10^5$ S.E. joules ($3.49 \times 10^5 \pm 7.06 \times 10^4$ S.E. cal) for colonies from Coconut Island and $6.04 \times 10^5 \pm 1.55 \times 10^5$ S.E. joules ($1.44 \times 10^5 \pm 3.71 \times 10^4$ S.E. cal) for colonies from Kokokahi.

**Estimates of Annual Energy Allocation to Sexual Reproduction**

Applying the mean site values for annual photosynthetic productivity determined above, colonies monitored for reproductive output invested between 0.003 and 1.95 % (mean = $1.00 \pm 0.18$ S.E. %) of their gross productivity from photosynthesis to reproduction at Coconut Island, and between 0.00 and 4.23 % (mean = $1.32 \pm 0.36$ S.E. %) at Kokokahi. Percent investment of net productivity was estimated to range from 0.003 and 4.16 % (mean = $2.13 \pm 0.38$ S.E. %) for Coconut Island colonies and 0.00 to 11.26 % (mean = $3.50 \pm 0.95$ S.E. %) for Kokokahi colonies. Considering only colonies that released greater than 100 gamete bundles, mean percentages of gross and net values increased to $1.16 \pm 0.16$ S.E. % gross and $2.49 \pm 0.34$ S.E. % net for Coconut Island colonies, and $1.86 \pm 0.41$ S.E. % gross and $4.95 \pm 1.09$ S.E. % net for colonies from...
Table 4.4. Photosynthesis versus irradiance hyperbolic tangent parameters, projected O\textsubscript{2} production values and photosynthetic productivity estimates for Coconut Island (CI) and Kokokahi (KK) colonies between June 1996 and May 1997 at depth.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Volume (cm\textsuperscript{3})</th>
<th>R (mg O\textsubscript{2} min\textsuperscript{-1})</th>
<th>I\textsubscript{m} (\mu E s\textsuperscript{-1} m\textsuperscript{2})</th>
<th>P\textsubscript{m} (mg O\textsubscript{2} min\textsuperscript{-1})</th>
<th>Gross O\textsubscript{2} (mg yr\textsuperscript{-1})</th>
<th>O\textsubscript{2} Respired (mg yr\textsuperscript{-1})</th>
<th>Net O\textsubscript{2} (mg yr\textsuperscript{-1})</th>
<th>Gross 1\textdegree Productivity (joules yr\textsuperscript{-1})</th>
<th>Net 1\textdegree Productivity (joules yr\textsuperscript{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>CI-1</td>
<td>346</td>
<td>-0.1397</td>
<td>251.79</td>
<td>0.4940</td>
<td>12.98</td>
<td>7.34</td>
<td>5.64</td>
<td>1.98</td>
<td>8.62</td>
</tr>
<tr>
<td>CI-2</td>
<td>433</td>
<td>-0.1570</td>
<td>210.58</td>
<td>0.4899</td>
<td>13.80</td>
<td>8.25</td>
<td>5.55</td>
<td>2.11</td>
<td>8.49</td>
</tr>
<tr>
<td>CI-3</td>
<td>591</td>
<td>-0.2165</td>
<td>360.92</td>
<td>0.8813</td>
<td>22.07</td>
<td>11.38</td>
<td>8.89</td>
<td>3.10</td>
<td>13.58</td>
</tr>
<tr>
<td>CI-4</td>
<td>834</td>
<td>-0.2957</td>
<td>312.01</td>
<td>1.3109</td>
<td>31.06</td>
<td>15.54</td>
<td>15.52</td>
<td>4.75</td>
<td>23.71</td>
</tr>
<tr>
<td>CI-5</td>
<td>1138</td>
<td>-0.2221</td>
<td>389.51</td>
<td>1.1114</td>
<td>23.97</td>
<td>11.67</td>
<td>12.29</td>
<td>3.66</td>
<td>18.79</td>
</tr>
<tr>
<td>Mean</td>
<td>668</td>
<td>-0.2062</td>
<td>304.96</td>
<td>0.8575</td>
<td>20.42</td>
<td>10.84</td>
<td>9.58</td>
<td>3.12</td>
<td>14.64</td>
</tr>
<tr>
<td>KK-1</td>
<td>232</td>
<td>-0.0938</td>
<td>108.05</td>
<td>0.2476</td>
<td>6.94</td>
<td>4.93</td>
<td>2.01</td>
<td>1.06</td>
<td>3.08</td>
</tr>
<tr>
<td>KK-2</td>
<td>437</td>
<td>-0.1296</td>
<td>138.85</td>
<td>0.5087</td>
<td>12.09</td>
<td>6.81</td>
<td>5.28</td>
<td>1.85</td>
<td>8.07</td>
</tr>
<tr>
<td>KK-3</td>
<td>498</td>
<td>-0.1522</td>
<td>194.53</td>
<td>0.3916</td>
<td>9.10</td>
<td>8.00</td>
<td>1.10</td>
<td>1.39</td>
<td>1.68</td>
</tr>
<tr>
<td>KK-4</td>
<td>608</td>
<td>-0.1174</td>
<td>259.02</td>
<td>0.7446</td>
<td>12.57</td>
<td>6.17</td>
<td>6.40</td>
<td>1.92</td>
<td>9.77</td>
</tr>
<tr>
<td>KK-5</td>
<td>804</td>
<td>-0.1317</td>
<td>320.28</td>
<td>0.7927</td>
<td>11.91</td>
<td>6.92</td>
<td>4.98</td>
<td>1.82</td>
<td>7.62</td>
</tr>
<tr>
<td>Mean</td>
<td>516</td>
<td>-0.1249</td>
<td>204.14</td>
<td>0.5370</td>
<td>10.52</td>
<td>6.57</td>
<td>3.95</td>
<td>1.61</td>
<td>6.04</td>
</tr>
</tbody>
</table>
Kokokahi. No significant differences between sites were found for any of the percent allocation estimates (all comparisons using Analysis of Covariance of arcsine square-root transformed percentages with colony size as the covariate, \( P >> 0.05 \)). All estimates apply only to colonies within the measured size range.

**Discussion**

**Site Comparisons**

Results of the comparative analyses of parameter estimates derived from the hyperbolic tangent functions for Coconut Island and Kokokahi colonies were consistent with findings of other depth and shade related studies involving corals (Wethey and Porter 1976, Davies 1980, Zvalinskii et al. 1980, Falkowski and Dubinsky 1981, Chalker et al. 1983, Porter et al. 1984, Haramaty et al. 1997, Villinski 2003), including *Montipora capitata* (Kinzie and Hunter 1987). Although collection sites differed in depth by only two to three meters, the difference in irradiance was large and significant due to the relatively large extinction coefficients. The \( P-I \) parameters differed in a manner that suggested divergence in photo-adaptive responses to site-specific irradiances (see Jokiel 1988, Chalker et al. 1988). Respiration and \( I_k \) were significantly higher for the shallow Coconut Island colonies. \( P_m \) values also tended to be higher for the Coconut Island colonies. Although the latter difference was not significant at \( \alpha = 0.05 \) (\( P = 0.074 \)), small sample size may be reason. Gross and net primary productivity of colonies within the measured size range were significantly lower at Kokokahi, the deeper, more shaded site. Overall, the comparisons of \( P-I \) parameters met general expectations for colonies in different light regimes, which supported the methodology.
The lack of difference between mean percent energy allocation to reproduction between corals from the two sites is interesting given significantly different mean values of primary productivity and the lack of a significant difference in mean number of gamete bundles released. Reproduction, however, was highly variable for colonies at both sites, thus affecting the statistical comparison. The range in estimates of percent energy allocation was much greater for Kokokahi colonies, reaching a maximum of 11.26 % (of net primary productivity) compared to 4.26 % for Coconut Island colonies. Percent energy allocation to reproduction was nearly twice as high for Kokokahi than Coconut Island colonies when considering only those colonies that released greater than 100 bundles. Site-specific variation in colony fecundities may result from a number of factors including differences in colony size, morphology, age, reproductive history, genetics, and microhabitat (see Harrison and Wallace 1990, Hall and Hughes 1996, Villinski 2003). Tests of homogeneity of variances between sites suggest site-specific variation in fecundity is a feature common to this species.

**Comparisons Between Species and Colony Processes**

Mean percent energy allocation to reproduction in *Montipora capitata* is similar to that reported for *Pocillopora damicornis* (4.1 % of net, and 1.6 to 3 % of gross primary production in 10 cm diameter colonies; Davies 1991, Jokiel 1998), but is larger than the estimate for *Porites porites* (0.8 % of net, and 0.4 % of gross primary productivity in small nubbins; Edmunds and Davies 1986). Although these values seem extremely low, some perspective may be gained through comparison with estimates of relative energy investments made to other colony processes, such as growth, mucus release and storage. Davies (1991) estimated a partial energy budget for *M. capitata* and *P. damicornis* using
small nubbins from the Coconut Island reef slope. Growth was measured over seven
“normal” days (i.e., neither cloudless or overcast). The tissue energy content Davies
(1991) used in these calculations was that for *Pocillopora eydouxi* (18.05 J mg⁻¹, Davies
1984). I substituted the value of 27.5 J mg⁻¹ for *M. capitata* and 25.4 J mg⁻¹ for *P.
damicornis* based on measurements of colony tissue from Coconut Island and Kokokahi
sites (Kolinski, unpublished data; the *P. damicornis* value came from Coconut Island
colonies and was adjusted down 5 % to account for the potential presence of reproductive
estimates for “normal” days were recalculated as 21 % for *M. capitata* and 37 % for *P.
damicornis*, or roughly 6 to 10 times the mean percent annual energy allocation to
reproduction in these species. Percent net energy allocation to growth was 14 % for *P.
porites* (Edmunds and Davies 1986), roughly 16 times that allocated to reproduction
(based on sunny day estimates).

Although studies for a few corals suggest that large percentages of excess
photosynthetically fixed energy are released as mucus and dissolved organic carbon-lipid
Edmunds and Davies 1986, Crossland 1987), direct measurements are few. Crossland et
al. (1980) found 40 % of the ¹⁴C bicarbonate incorporated into *Acropora acuminata* to be
released as mucus and mucus-lipid over a 24-hour period. Mucus and dissolved organic
carbon-lipid released from *Stylophora pistillata* represented roughly 20 % of the
photosynthetically fixed carbon, and overall levels of release were similar for *Acropora
variabilis* (Crossland 1987). No measurements of energy lost in the form of mucus or
dissolved organic lipid have been made for *M. capitata, Pocillopora damicornis* or
Porites porites; however, *M. capitata* and *P. damicornis* have been observed to release large amounts of mucus when stressed (Kolinski, pers. obs.). Stimson (1987, referring to Ducklow and Mitchell 1979) suggested that mucus may be released to attract bacteria for ingestion by coral colonies. Others suggest that shallow water corals are just getting rid of excess photosynthate (Davies 1984, Falkowski et al. 1984, Muscatine 1990). Based on data from Crossland (1987), Davies (1991) projected that the minimum excess energy released as mucus and/or dissolved organic carbon-lipid on any given day from *M. capitata* and *P. damicornis* would be 47 % of that remaining on an ideal day after budgeting for colony respiration and growth. This translates to 48 % of net energy from primary productivity for *M. capitata* and 58 % for *P. damicornis* on a “normal” day, or roughly 14 to 23 times the mean percent energy allocation to reproduction in these species.

*Montipora capitata* stores large amounts of lipid relative to other common Hawaiian scleractinian corals (Stimson 1987, Davies 1991). Although no direct comparison of pre- and post-spawning lipid levels has been made for *M. capitata*, Stimson (1987) and Davies (1991) showed tissue composition to be above 40 % lipid by weight, with a roughly five percent difference between samples from spawning and non-spawning months (Stimson 1987). Similarly, the lipid composition in *P. damicornis* runs from 30 to 40 % by weight, with a roughly 5 % reduction following planulation (Stimson 1987, Davies 1991, Ward 1995a and b). Davies (1991) estimated lipid reserves could support *M. capitata* colonies for 114 overcast days during which respiration exceeded productivity. In *P. damicornis*, the estimate was 28 days. Appropriate data were not available for *P. porites*. Many corals appear to have the ability to reabsorb their
reproductive products (Rinkevich and Loya 1979, Szmant-Froelich et al. 1980, Harriott 1983, Wyers 1985, Kojis 1986, Szmant and Gassmann 1990, Harrison and Wallace 1990, Glynn et al. 1994, Bassim 1998); thus, gametes and planulae are in a sense a secondary storage source of energy for coral colonies, at least for some period of time during gamete formation. In Hawaiian *M. capitata*, summertime release of gametes correlates with rising and peak annual levels of irradiance; thus, energy lost from reproductive "storage" can quickly be replaced. Estimates for *M. capitata* based on 1997 depth irradiance measurements suggest it would take approximately 14 July days to replace the average energy of released gamete bundles for measured Coconut Island colonies, and 30 days for Kokokahi colonies after compensating for colony respiration, 21 % energy allocation to growth and 48 % expenditure as released mucus. These estimates increase by month post-spawning, averaging 15 and 33 August days for Coconut Island and Kokokahi colonies, and 18 and 39 September days for site colonies respectively. Thus, average energy lost to reproductive release could be replaced within two to three weeks for the shallow Coconut Island colonies, and four to six weeks for the colonies at Kokokahi. This advantage to reproduction in summer months deserves further attention.

**Limitations of Methodology**

There are a number of different methodologies that can be applied to estimate energy allocation to reproduction in corals (Richmond 1987b, Edmunds and Davies 1986, Jokiel 1998, Rose and Bradley 1998, Leuzinger et al. 2003, Villinski 2003, this study). None, however, is without limitations, as certain components of the coral energy budget are presently difficult to quantify. At least two factors in this study potentially bias percent reproductive allocation estimates upwards. These include a lack of accounting for
heterotrophic sources of energy (see Coma et al. 1998, Anthony and Fabricius 2000) and evidence that daylight respiration rates may be higher than those determined in darkness (this underestimates gross productivity and thus overestimates percent of gross energy allocation to reproduction, Edmunds and Davies 1988). In contrast, other factors may have led to underestimating percent reproductive energy allocation. There was no accounting for the energy used in gamete formation or energy associated with materials lost and utilized in repair of somatic tissue following spawning (Leuzinger et al. 2003). The effects of change in colony size, morphology, and thus, photosynthetic efficiency (Jokiel and Morrissey 1986) over time have not been accounted for in any studies. In addition, *Pocillopora damicornis* and *Porites porites* percent reproductive allocation estimates were restricted to productivity values for clear, sunny days (Edmunds and Davies 1986, Jokiel 1998). Extrapolation to longer time periods requires compensating for irradiance fluctuations due to variable cloud cover (Davies 1991). The extent to which these factors offset each other in each of these species is unknown, but estimates of percent energy allocation to reproduction would remain low.

Application of the $P-I$ models for *M. capitata* did not incorporate the potential for seasonal variation in $P-I$ parameters. Respiration, $I_k$ and $P_m$ vary as a function of light (Wethey and Porter 1976, Davies 1980, Zvalinskii et al. 1980, Falkowski and Dubinsky 1981, Chalker et al. 1983, Porter et al. 1984, Kinzie and Hunter 1987, Haramaty et al. 1997, Villinski 2003), which varies seasonally. Monthly irradiance in November 2001 was higher than that for each month from June 1996 through March 1997. Use of the November derived models thus, may have overestimated colony values of respiration, $I_k$ and $P_m$ for 10 of the 12 months considered. Overestimation of respiration and $I_k$ would
lead to conservative values of annual net productivity. High $P_m$ values would overestimate productivity. Although *M. capitata* are known to respond to 80% differences in light availability through shifts in $P_m$ (Kinzie and Hunter 1987), the $P_m$ estimates for colonies naturally exposed to irradiances differing by roughly 45% at Coconut Island and Kokokahi did not differ significantly. Monthly irradiance from June 1996 through May 1997 ranged from $-15$ to $+11\%$ that of November 2001. Application of the November 2001 *P-I* models may thus, overall, have resulted in conservative estimates of annual productivity.

**Conclusions**

Although *Montipora capitata* can be reproducively prolific, this study suggests the overall average energetic cost of reproduction to colonies within the measured colony size range is minimal. This makes sense for a species with high fertilization and settlement potential but very low settler survivorship (Kolinski Chapter 3). Large repetitive reproductive efforts at little cost increase the probability of eventually producing reproductive offspring while minimizing the impact of reproduction on the long-term survivorship of parent colonies. Other factors, such as nitrogen, phosphorus and/or stem cells may limit overall fecundity in coral colonies that divert resources to preset hierarchical processes (Harrison and Wallace 1990, Rinkevich 1996). The costs related to these factors, in terms of reproduction, have yet to be determined for any coral species. However, energy in shallow water environments does not, in general, appear limiting.
SUMMARY

Sexual reproduction and the early life history of the scleractinian coral, *Montipora capitata*, was assessed in Kāneʻohe Bay, Oʻahu, Hawaiʻi. *Montipora capitata* is the only species in Kāneʻohe Bay that gives rise to large, very obvious, summertime surface-water slicks of gametes and developing embryos on nights and mornings following synchronized spawning. Spawning occurs between 20:45 and 22:30 hrs during new and first quarter moons between May and September, with the majority of egg-sperm bundles being released in June and/or July. Gamete bundles float to the water’s surface where fertilization takes place. Fertilization success is likely affected by the genotypic diversity and densities of spawning adults.

The larvae develop within 2.5 to 3 days, and are competent to settle 3 days following spawning. Ability to settle remains high (83% proportional settlement) at six weeks post spawning, but becomes reduced (≤11% proportional settlement) at 56 plus days. A few surviving larvae may remain competent to settle for 207 plus days. Patterns of settlement in the laboratory and field suggest major settlement pulses within days of summer spawning if substrate is encountered, with minor settlement occurring through fall and winter months. Water circulation likely determines larval retention, transport and settlement patterns. High population densities of *M. capitata* in bays, inlets and along naturally protected shorelines, enhance probabilities of fertilization and may be critical to long-term species persistence in more exposed areas by providing sources of larvae. Long-term competency to settle may partially explain the presence of *M. capitata* across the Hawaiian Archipelago and possibly throughout surrounding regions.
Montipora capitata larvae are stimulated to settle and metamorphose by external, substrate associated, cues. The larvae discriminate between substrates for settlement, but display overall generalist settlement tendencies in that they settle equally well on a variety of different substrates including various crustose coralline algae species and filamentous algae covered rubble. This finding corresponds with the high tolerance of adults for a wide range of habitat conditions. Treatments with antibiotics suggest bacteria play a role in inducing M. capitata larval settlement. Gamma aminobutyric acid did not induce settlement. The level of substrate conditioning required by M. capacitata larvae for settlement is reached relatively rapidly, suggesting M. capitata may be among the early settlers on newly created, disturbed or introduced substrates.

Larvae of three common shallow water coral species, Montipora capitata (a hermaphroditic broadcast spawner), Porites compressa (a gonochoric broadcast spawner) and Pocillopora damicornis (a brooder) settled in high enough numbers on settlement plates to allow monitoring and comparison of their early life history attributes. Montipora capitata accounted for 91% of roughly 20,000 observed settlers at six sites across Kāne‘ohe Bay over a two-year period. Average annual settler numbers were greatest at monitored Central Bay sites, and reached 2.8 x 10^4 settlers m^-2 for M. capitata (Central Fringing reef), compared to 788 settlers m^-2 for P. compressa (Central Fringing reef), and 680 settlers m^-2 for P. damicornis (North Fringing reef). Type III survivorship was evident for M. capitata, P. compressa and P. damicornis, but survival was significantly lower for M. capitata (mean 12-month post-settlement survivorship < 1 %, compared to 17 % for P. compressa and 9 % for P. damicornis). Although significant for P. compressa and P. damicornis, a relationship between settler growth and survival was not
evident for *M. capitata*. The mean estimated time for settlers to reach 1 cm² projected area in the field was 4.9 years for *M. capitata* and 1.7 years for *P. compressa* and *P. damicornis*. A large proportion (61%) of surviving *M. capitata* settlers displayed an ability to remain in a “dormant” one-polyp state for extended periods of time exceeding one year. This phenomenon was not observed in the other species. These patterns of settlement, survival and early growth in *Montipora capitata* suggest a reproductive strategy based on larval quantity as opposed to quality, more so than observed in the other two species.

The apparent need for large reproductive output given high settler mortality brought into question the magnitude and importance of parental investment and costs associated with reproduction in *Montipora capitata*. This was assessed for colonies from two sites in Kāne‘ohe Bay in terms of energetic costs. Average fecundity in colonies at Coconut island and Kokokahi did not differ despite a roughly 45% difference in available irradiance between these sites. Fecundity was related to colony size. The mean percent of annual net photosynthetic productivity allocated to reproduction was estimated to be 2.13% for Coconut Island colonies and 3.50% for Kokokahi colonies. These values are low compared to estimates of 21% energy allocation to growth and a minimum 48% energy allocation to mucus production. The summertime release of gametes in *M. capitata* correlates with rising and peak annual levels of irradiance. It was estimated the energy released in gamete bundles could be replaced within two to three weeks for Coconut Island colonies and four to six weeks for colonies at Kokokahi when considering growth and mucus production.
Montipora capitata, a broadcast spawning scleractinian coral, may gain its early life history advantage through large repetitive, low cost, influxes of larvae settling in a variety of habitats. When given opportunity and appropriate conditions, the collection of multiple year-class survivors, although relatively few, grow and recruit into the community. Such a strategy puts emphasis on high adult survivorship and reproductive output. Adult *M. capitata* have a high tolerance for survival in a variety of habitats and frequently attain sizes greater than 1 m. A susceptibility to fragmentation (data collected but not addressed in this study) offers a mechanism that may augment genotypic longevity, allowing for localized dispersal that may enhance fertilization success amongst new neighbors.

The results of this investigation are applicable to emerging management issues including coral reef connectivity, recovery and restoration. *Montipora capitata* has great potential for reef connectivity within and among archipelagos. However, large repetitive inputs of larvae may be needed for successful recruitment. Larval settlers may not be visible for years due to low survival, slow growth and growth “dormancy”. Efforts should be made to determine whether certain habitat factors accelerate settler growth and increase survival. Although *M. capitata* is not a good candidate for larval seeding efforts in reef restoration, it is a species tolerant of a wide range of habitat conditions. Methods of reef restoration involving adult transplantation and fragment seeding are more suitable for this species (data collected but not addressed in this study).
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