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Biology, June 24, 1994.

Title: The Effects of Altered Salinity on Settlement and Metamorphosis of Coral
Planula Larvae

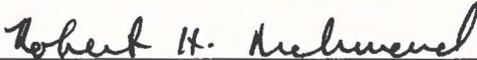
Approved: Robert H. Richmond
Robert H. Richmond, Chair, Thesis Committee

The effects of altered salinity on settlement and metamorphosis were tested on five species of coral larvae on Guam. Planulae were maintained under salinity levels of 38 ‰ to 25 ‰, and coral rubble was used as the settlement substratum. Larvae of spawning species and the brooding species had the highest rates of settlement and metamorphosis at 34 ‰. When salinity was decreased below normal levels, settlement and survivorship decreased significantly for *Acropora danai*, *A. digitifera*, *Goniastrea retiformis*, *Leptoria phrygia* and *Pocillopora damicornis*. Larvae of *P. damicornis* showed a 75 % decrease in settlement at 25 ‰; *A. danai* and *A. digitifera* showed a 100 % decrease in settlement at 25 ‰. In addition, larval mortality for the two Acroporids was more than 95 % at 25 ‰. *Goniastrea retiformis* larvae exhibited an increase in settlement from 15 % to 22 % when salinity levels were raised from 34 ‰ to 38 ‰ respectively. In contrast, *L. phrygia* larvae showed only a 2 % settlement rate when salinity was increased to 38 ‰. There appears to be a relationship between

site selection and salinity sensitivity for these species. For all species in this study, decreased salinity affects larval swimming behavior by influencing their ability to settle and metamorphose. Reduced salinity associated with heavy rains and runoff from land during low tides can significantly affect recruitment of corals.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Fernando Rivera presented June 24, 1994.


Robert H. Richmond, Chair

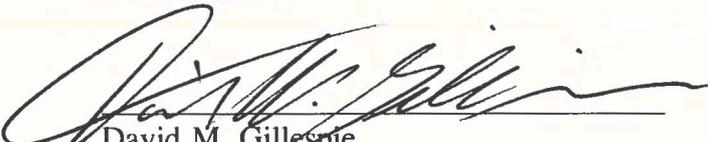

Gustav Paulay, member


Steven S. Amesbury, member


Michael T. Hamerly, member



ACCEPTED:


David M. Gillespie
Dean, Graduate School and Research

7-11-94
Date

THE EFFECT OF ALTERED SALINITY ON SETTLEMENT AND
METAMORPHOSIS OF CORAL PLANULA LARVAE

BY

FERNANDO E. RIVERA

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INTRODUCTION

The processes responsible for the persistence of coral reefs are reproduction and recruitment. While it has been demonstrated that salinity can affect fertilization success in corals (Richmond 1993), it is not known how variations in salinity affect settlement and metamorphosis. This study investigates how altered salinity affects success in settlement and metamorphosis of larvae of five species of corals.

Reproduction in corals can occur both sexually and asexually. Sexual reproduction involves the process of gametogenesis which culminates in the production of mature gametes for fertilization (Harrison and Wallace 1990). The fusion of these gametes results in the formation of a planula larva that will disperse, settle, metamorphose, and develop into a new colony. Larvae can arise as a result of internal fertilization (brooding), or via spawning with external fertilization and development.

Coral spawning events have been extensively studied on the Great Barrier Reef, where more than 130 scleractinian species have been recorded spawning together during a short, predictable annual mass-spawning period (Harrison et al. 1984, Willis et al. 1985, Wallace 1985, Babcock et al. 1986). The majority of reef corals are simultaneous hermaphrodites that release positively buoyant gamete clusters (eggs and sperm compressed into bundles) into the water column during spawning (Babcock et al. 1986, Veron 1986, Richmond and Hunter 1990, Harrison and Wallace 1990). These gamete clusters float to the surface where they break apart with subsequent external fertilization.

Synchronous coral spawning has also been observed in other parts of the Pacific and the Caribbean (see review in Richmond and Hunter 1990). The

reproduction of only a few of the 230 species of reef corals that inhabit Guam's reefs (Randall and Myers 1983) has been studied to date (Heyward 1989, Richmond and Hunter 1990). Many corals on Guam also participate in synchronous spawning events, during July and August (Heyward 1989, Richmond and Hunter 1990 and pers. obs.). The spawning takes place at night, during the rainy season, commencing the fifth or sixth day after the July full moon, and lasting for five to six days. Observations of colonies collected from Tumon Bay and Apra Harbor on the west side of Guam, and from the Pago Bay area on the east side of the island, indicate that some species spawn only one night per year. Other species of coral continue spawning for several nights and may spawn during two or three subsequent months (pers. obs.).

After fertilization and larval development, a coral larva must settle and metamorphose in order to develop into a colony and form part of a coral reef. Before settling, planula larvae usually perform an intensive searching behavior of the substratum until they find a suitable place for attachment (Atoda 1951, Krupp 1983, Harrison and Wallace 1990). Planulae normally explore the substratum through contact with their epidermis prior to settlement. The aboral epidermis appears to have an important sensory role in the recognition of suitable settlement sites (Vandermeulen 1974). Searching may be followed by settlement and metamorphosis, or by temporary attachment.

Generally, competent larvae (those which are able to settle and metamorphose) cannot delay metamorphosis indefinitely (Pechenik 1987). Most or all scleractinian corals produce lecithotrophic or mixotrophic (provided with zooxanthellae) planulae.

Larvae of most marine invertebrate species spend some time developing in the plankton until they become competent to metamorphose (Hadfield 1978).

Changes in environmental conditions (temperature, salinity) can influence the total amount of time spent in the plankton by altering the rate of utilization of the energy reserves in lecithotrophic species (Pechenick 1987). Previous studies have shown that extremes of temperature, salinity, and sedimentation are detrimental to corals and coral larvae (Coles and Jokiel 1978, Birkeland 1981, Hoeg-Guldberg and Smith 1989, Hodgson 1990). Excessive rain, runoff, and storm floods during periods of low tide can markedly decrease the salinity on shallow reefs and thus can cause serious mortality in reef organisms (Rogers 1990, Jokiel et al. 1993).

Little is known about the lower limits of salinity tolerance for coral larvae. Coles and Jokiel (1992) suggested that most species of corals are killed if salinity drops from 34 ‰ to 15 ‰ or 20 ‰ for 24 hours or more. *Porites cylindrica* exposed to salinities of 18 ‰ for 24 h suffered 100 % mortality (Kato 1987). Harrison and Wallace (1990) reported that during a mass spawning in the Great Barrier Reef, a heavy rain fell and destroyed the floating gametes for that annual reproductive season. Altered salinity during coral spawning can affect reproduction by causing a decrease in fertilization rate. Richmond (1993) reported that fertilization was reduced by up to 86 % when the salinity of sea water was diluted 20 % by the addition of distilled water. Edmondson (1946) found that larvae of *Pocillopora damicornis*, *Cyphastrea ocellina*, and *Dendrophyllia manni* died after exposed to fresh water for 12 minutes.

It is probable that coral larvae, at times, come into contact with waters of low salinity, especially on shallow reefs after heavy rains. As coral spawning occurs during the rainy season on Guam, and as most spawned larvae have a short competency period, coral larvae may encounter water of lowered salinities that may influence their abilities to settle and metamorphose. The purpose of this study is to test the ability of several species of coral planulae to settle and metamorphose, and hence recruit, under conditions of altered salinity.

MATERIALS AND METHODS

Collection of corals, gametes and larvae

Spawning species

The corals *Acropora danai* (of Wallace and Veron 1984 = *A. irregularis* of Randall and Myers 1983), *Acropora digitifera*, and *Goniastrea retiformis* are usually restricted to shallow reef environments on Guam (Figure. 1). These species were chosen because at times they can come in to contact with waters of low salinity following heavy rains. *Leptoria phrygia* was selected in contrast to these shallow water species, since this coral is commonly found on upper reef slopes where salinities can be more stable. From previous studies on Guam (Richmond and Hunter 1990), coral spawning was found to occur five to six days after the July full moon. Colonies of the above species were checked for mature oocytes a week before predicted spawning in July 1993, and marked for later collection.

Selected ripe colonies were collected from Tumon Bay, Pago Bay and Apra Harbor. *Acropora danai* and *A. digitifera* were collected from the reef front of Pago Bay at 3 and 1.5 m depths respectively. Depth range for these two species is 1 to 6 m (pers. obs.). *Goniastrea retiformis* was collected from the reef front of Tumon Bay and Pago Bay at a depth of 2 m. Depth range for this species is 1 to 12 m. *Leptoria phrygia* was collected from Pago Bay and Apra Harbor at a depth of 10 m. Depth range for this species is 1.5 to 17 m. Specimens of spawning corals were transferred to tanks with flowing sea water three days before expected spawning. Corals were

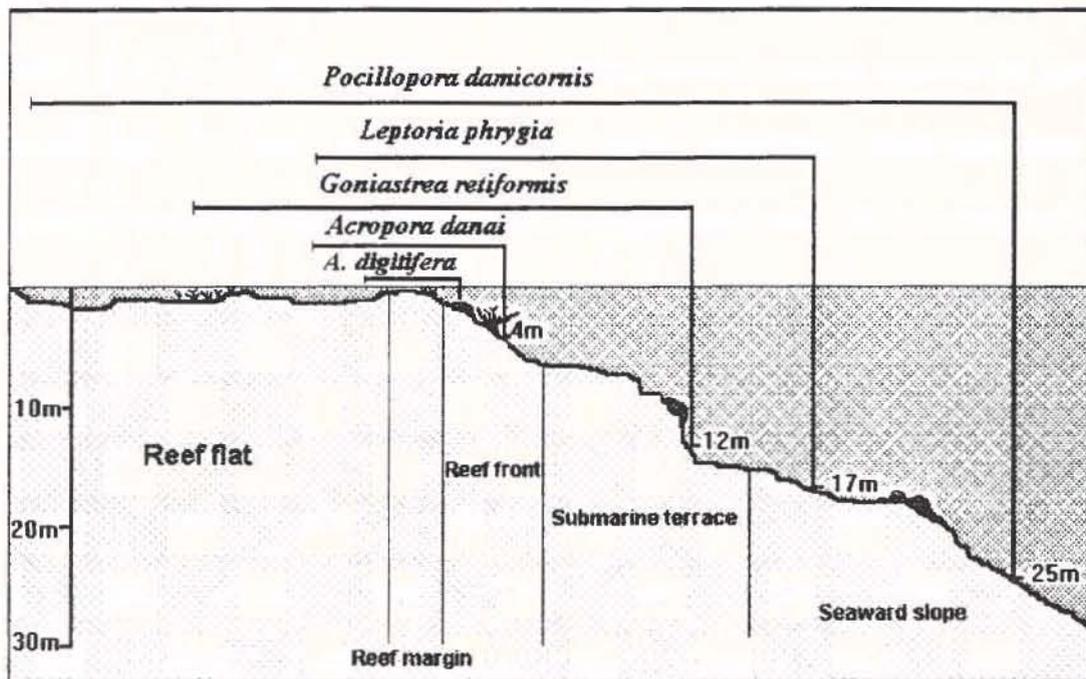


Figure 1. Depth distribution of the study corals.

monitored from the fifth to the eleventh day after the July full moon from 8:00 p.m. to 1:00 a.m. or until the corals began releasing gamete clusters. Just before colonies released their gamete bundles, corals were moved to 20-liter aquaria containing seawater. The released egg/sperm clusters are positively buoyant and floated to the surface, where they were immediately collected. The bundles were washed with UV treated filtered (0.45 μ m) sea water in a plastic beaker with 80- μ m nitex screen attached to the base. This procedure was repeated several times to separate the sperm from the eggs. The sperm were collected in a beaker, while the washed eggs were transferred to another beaker with UV treated filtered sea water. This procedure took from five to ten minutes depending on the species.

Fertilization

Eggs from one colony were fertilized with sperm from a different colony of the same species. Eggs were fertilized in a 1-liter plastic container of UV-filtered sea water, with five drops of dilute sperm solution. Sperm density was based on previous experiments (Richmond, Rivera pers. obs.). The fertilized eggs were checked the next day under a dissecting microscope to determine whether fertilization had occurred and whether embryos were developing. Healthy embryos were separated and transferred to a 3-liter bowl containing fresh filtered sea water until swimming planulae developed. Experiments began one day after active swimming larvae developed (see Table 1).

Table 1. Reproductive pattern of the study corals. Sex: H, Hermaphroditic. Mode: S, spawner; B, brooder. Timing: lunar day and month of spawning (month is divide into phases: 1 for full moon, 11 last quarter) yr, year-round

Species	Sex	Mode	Timing	Time to planula stage	Mean egg diameter (um)
ACROPORIDAE					
<i>Acropora danai</i>	H	S	Jul/Aug/Sep 10	55-60 hrs.	682
<i>Acropora digitifera</i>	H	S	Jul 9	65-70 hrs.	
FAVIIDAE					
<i>Goniastrea retiformis</i>	H	S	Jul 10-11	16-18 hrs.	317
<i>Leptoria phrygia</i>	H	S	Jul 10-11	16-18 hrs.	321
POCILLOPORIDAE					
<i>Pocillopora damicornis</i>	H	B	yr/1st quarter		

Brooding species

Pocillopora damicornis occurs in a wide variety of shallow and deep-water habitats (Richmond and Jokiel 1984, Veron 1986) (Figure 1). Since *P. damicornis* is a brooder, fertilization is internal. This species planulates monthly throughout the year on Guam. Colonies were collected from the inner reef flat of Agana Bay at 40 cm to 1 m depth, five days prior to predicted planulation, which occurs between new moon and first quarter. Colonies were placed in 4-liter containers with running sea water. The containers overflowed into planula collectors made from plastic beaker bases with walls of 125- μ m nitex screen (Richmond and Jokiel 1984). Planulae were placed in 2-liter containers in UV-filtered sea water with aeration and were used in salinity experiments one day after their release.

Salinity experiments

Salinity tests were run in 400-ml glass jars at salinity levels ranging from 38 ‰ to 25 ‰, with five replicates per treatment. Twenty to 40 planulae were placed in each jar. Salinity was reduced using distilled water, and measured with a refractometer calibrated against a chloridometer (HaakeBuchler chloridometer). Planulae were placed in each container together with a piece of coral rubble ca. 1.5 \times 5.5 cm to serve as a substratum for settlement. Coral rubble pieces covered with the crustose coralline alga *Hydrolithon* were selected. The containers were aerated, placed in a shaded area, covered with plastic wrap to prevent evaporation, and suspended in floating trays within the sea water tanks to maintain a constant temperature. Water

was changed daily. The number of successfully settled juveniles, judged on the basis of deposition of the primary corallite skeleton, was determined every day for 10 days. Settlement orientation (top, sides, bottom of coral rubble or glass) on the substratum was also recorded.

Two transects were established to measure salinity across the Pago Bay reef flat, to determine natural variations of salinity in relation to tide levels. The transects were located at 210 and 700 meters south of the Marine Laboratory respectively. Salinity measurements were made using a refractometer calibrated against a chloridometer. Eighteen pairs of samples were taken on each transect, one at the surface and one at the bottom, each during high and low tide. These measurements were taken on the 29th and 30th of March, which corresponded to the lowest and the highest tides of that month. No precipitation was registered during these days.

Settlement success over time, mortality, time of settlement, and larval behavior at all salinities were recorded. ANOVA and Tukey's tests were used to determine significance of differences among treatments.

RESULTS

Settlement

All four spawning species exhibited a significant decrease in settlement rates at salinities lower than 34 ‰ (Fig. 2 - 5). However, at higher than ambient salinity (38 ‰) larvae of *Goniastrea retiformis* did not show a decline in settlement relative to normal salinity (Fig. 4), but larvae of *Leptoria phrygia* did (Fig. 5, $p = 0.0019$).

A mean of 39 % of the *Pocillopora damicornis* larvae settled at the normal salinity, 34 ‰. This rate of settlement was significantly higher ($p = 0.0052$) than that obtained at lower salinities levels of 27 ‰ and 25 ‰ (Fig. 6).

Larval mortality

Larval mortality generally increased as salinity decreased below the control level (34 ‰). For *Pocillopora damicornis*, *Acropora danai*, and *Acropora digitifera*, mortality was significantly greater at the lowest salinity level tested than at normal salinity (Fig. 7 A, B, C). Larval mortality for *Goniastrea retiformis* was significantly higher ($p = 0.0079$) at 30 ‰ than at normal salinity (Fig. 7 D). The two species of *Acropora* suffered the highest mortality rates (more than 95 %) at a salinity of 25 ‰ (Fig. 6 B, 7 C). *Leptoria phrygia* larvae did not show any significant differences in mortality ($p = 0.184$) among treatments (Fig. 7 E).

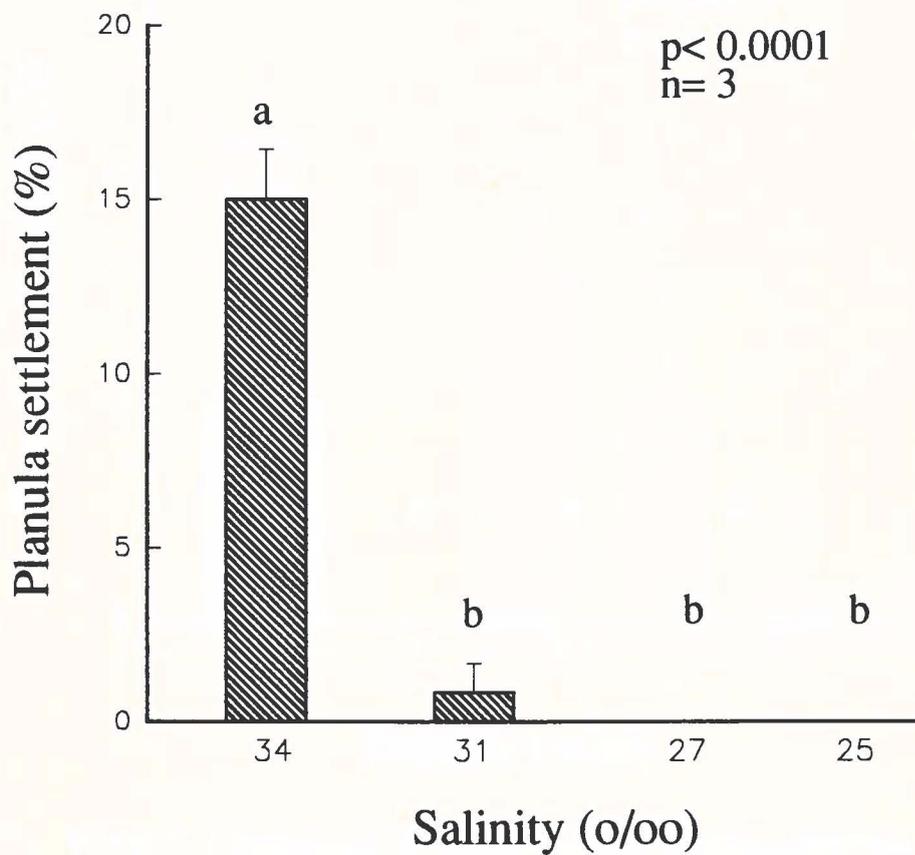


Figure 2. Effects of salinity on settlement of *Acropora danai*. Means with different letters are significantly different ($p < 0.05$) by Tukey's Test. Data were arcsin-square root transformed for ANOVA analysis. Error bars = 1SE.

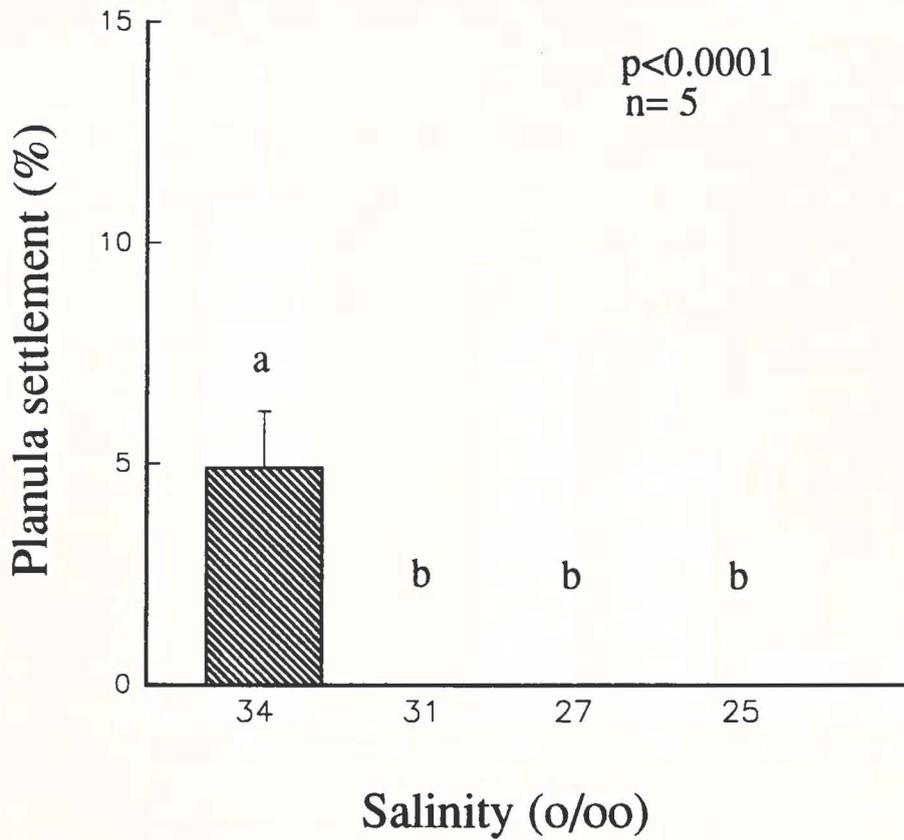


Figure 3. Effects of salinity on settlement of *Acropora digitifera* planulae. Means with different letters are significantly different ($p < 0.05$) by Tukey's Test. Data were arcsin-square root transformed for ANOVA analysis. Error bars = 1SE.

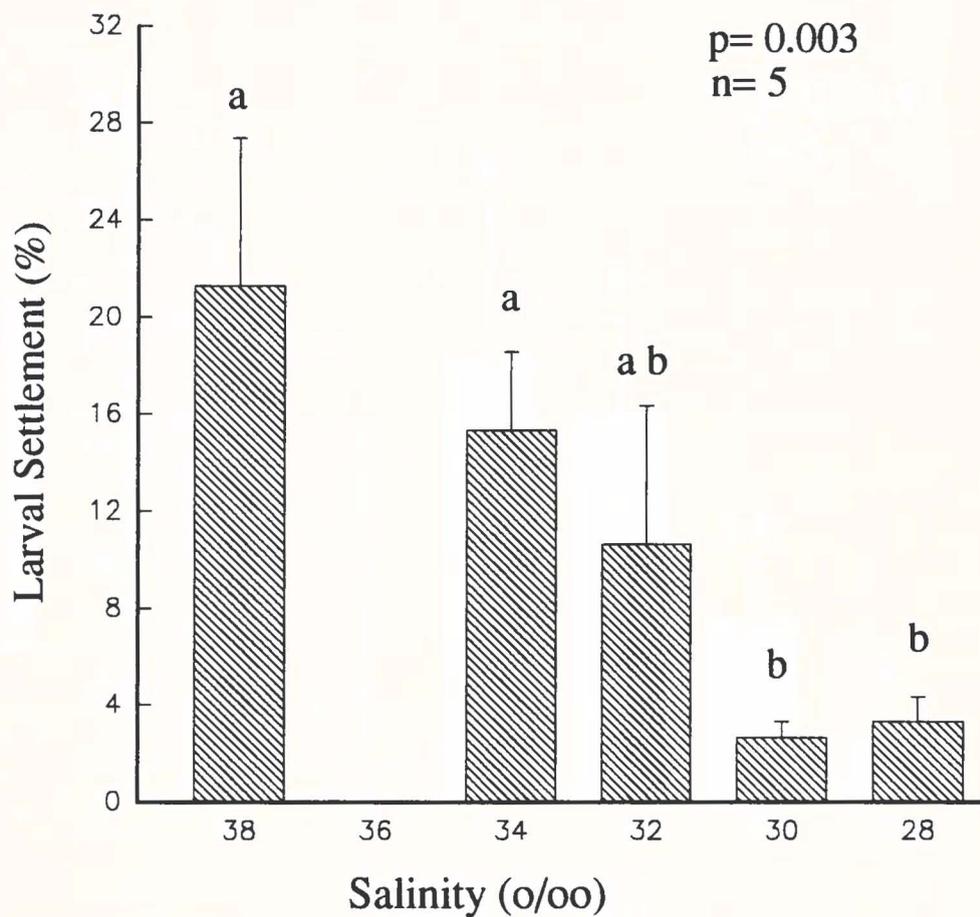


Figure.4. Effects of salinity on settlement of *Goniastrea retiformis* planulae. Means with different letters are significantly different ($p < 0.05$) by Tukey's Test. Data were arcsin-square root transformed for ANOVA analysis. Error bars = 1SE.

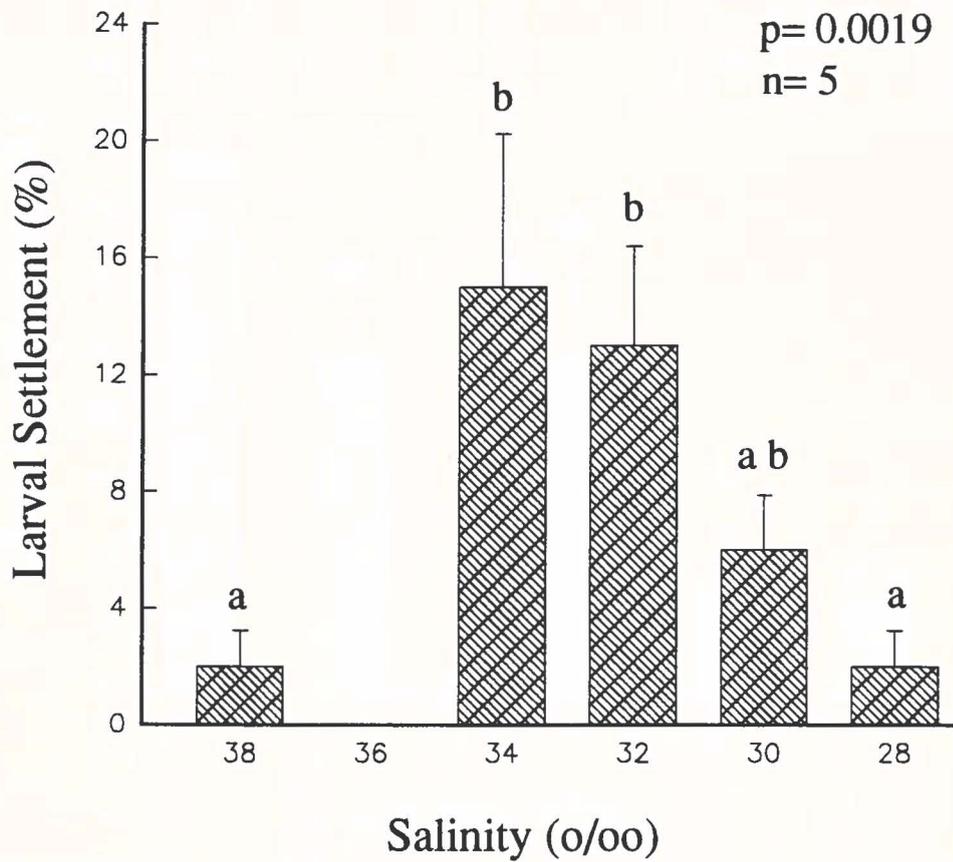


Figure 5. Effects of salinity on settlement of *Leptoria phrygia* planulae. Means with different letters are significantly different ($p < 0.05$) by Tukey's Test. Data was arcsin-square root transformed for ANOVA analysis. Error bars = 1SE.

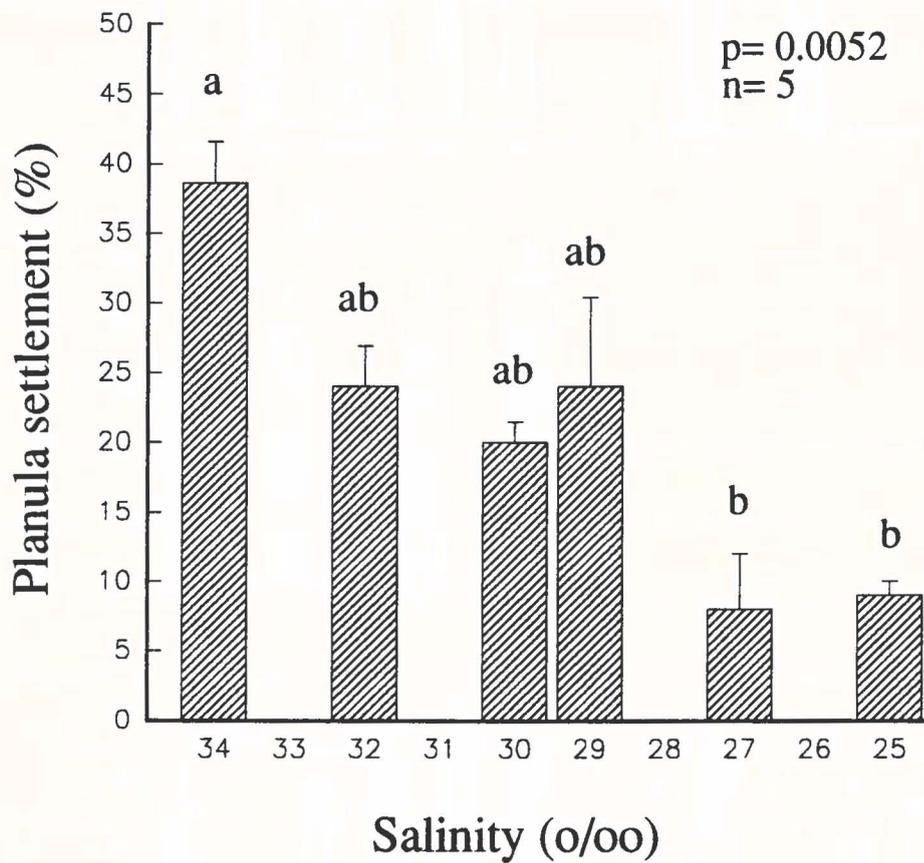


Figure 6. Effects of salinity on settlement of *Pocillopora damicornis* planulae. Means with different letters are significantly different ($p < 0.05$) by Tukey's test. Data were arcsin-square root transformed for ANOVA analysis. Error bars = 1SE.

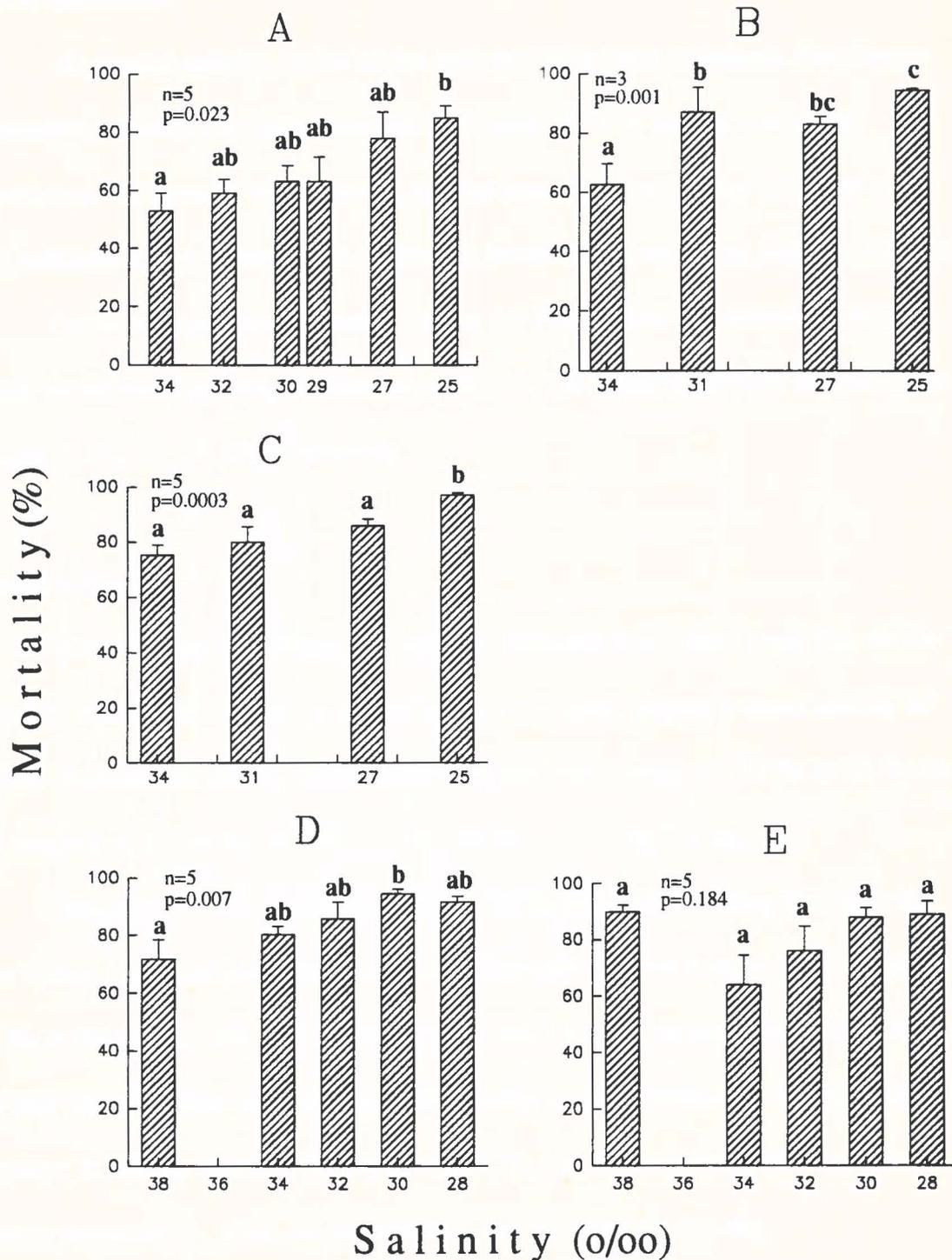


Figure 7. Larval mortality at different salinities. Means with different letters are significantly different ($p < 0.05$) by Tukey test. Data were arcsin-square root transformed for ANOVA analysis. Error bar = 1SE.

A: *Pocillopora damicornis* B: *Acropora danai* C: *Acropora digitifera*
 D: *Goniastrea retiformis* E: *Leptoria phrygia*

Age at settlement

At normal salinity, larvae of the only brooding coral examined, *Pocillopora damicornis*, showed the highest percent settlement of 33 % on day one of the experiment. In contrast, the spawning species began settling on day two with only 1 % settlement, and reached peak settlement levels during days four and five (Fig. 8).

Cumulative percent settlement figures for *Pocillopora damicornis*, *Acropora danai*, *Acropora digitifera*, *Goniastrea retiformis*, and *Leptoria phrygia* are shown in Figures 9, 10, 11, 12, 13 respectively.

Natural salinity

Water salinity measurements from two transects taken from Pago Bay on the 29th and 30th of March, during both high and low tides, showed a mean salinity of 33 ‰. Surface and bottom salinity measurements had a range of 32 ‰ to 35 ‰ for the transect at 210 m and 31 ‰ to 35 ‰ for the transect at 700 m.

Matson (1991) reported that water samples collected at Tumon Bay near the Leo Palace Hotel, on April 20, 1988 during high tide showed a mean of 30 ‰ and 31 ‰ at the surface and at the bottom respectively another transect was taken along the reef flat. Samples taken the same day during low tide revealed a considerable decrease in salinity levels, with a mean of 25 ‰ and 29 ‰ at the surface and at the bottom respectively. Also, no precipitation was recorded on this day.

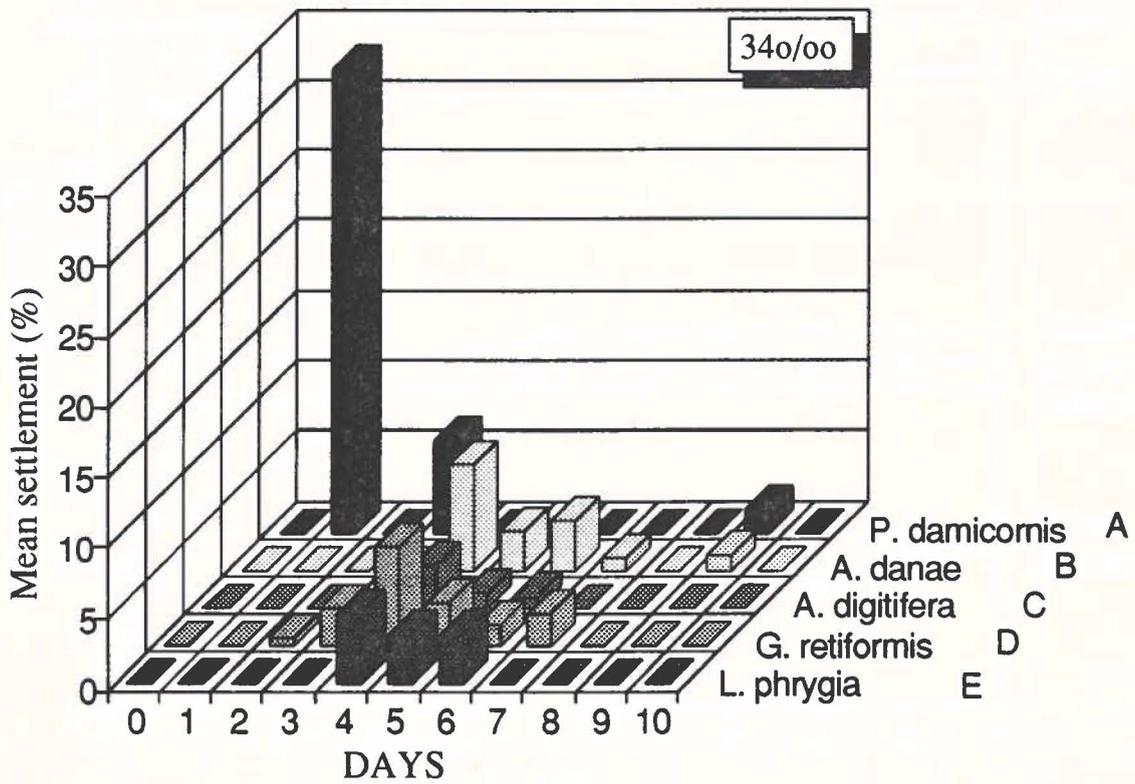


Figure 8. Time of larval settlement among a brooding and several spawning corals. A: brooder. B-E: spawners. n=5 for A, C, D, E, n=3 for B.

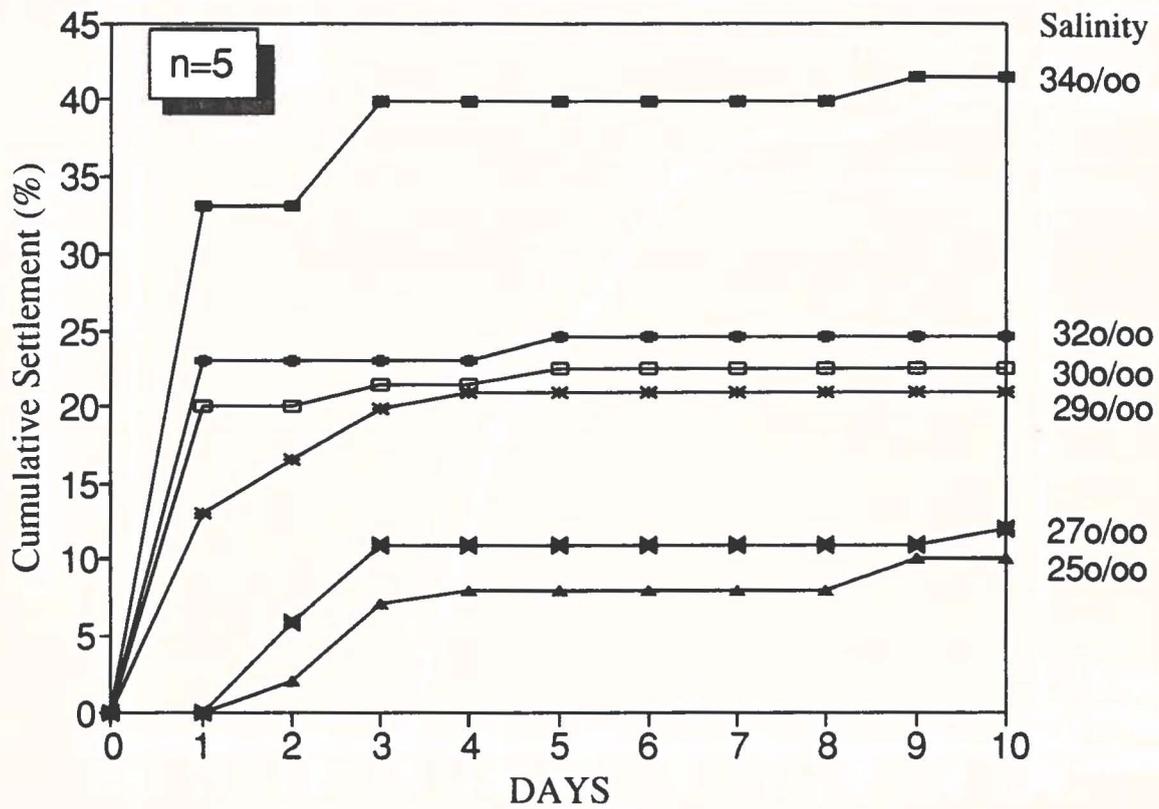


Figure 9. Cumulative settlement of *Pocillopora damicornis* larvae during a 10-day period.

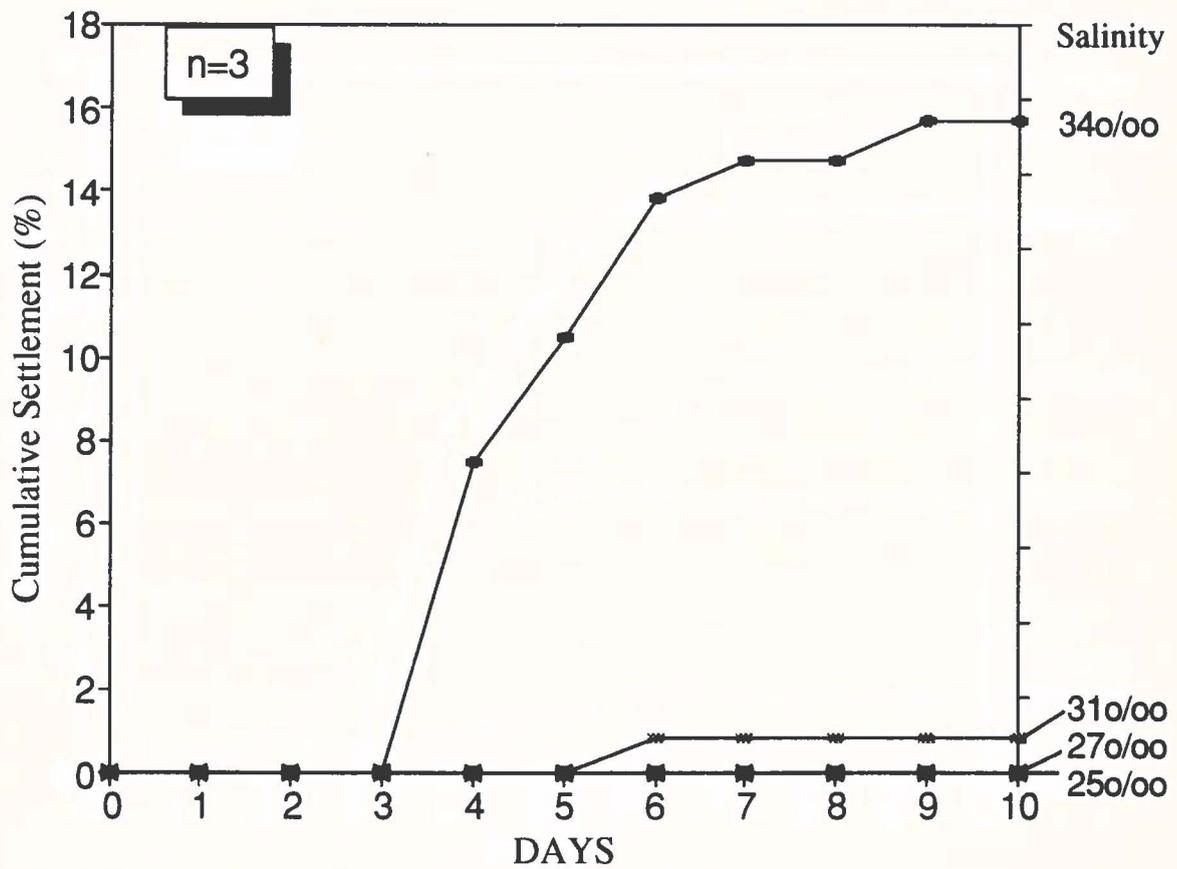


Figure 10. Cumulative settlement of *Acropora danai* larvae during a 10-day period

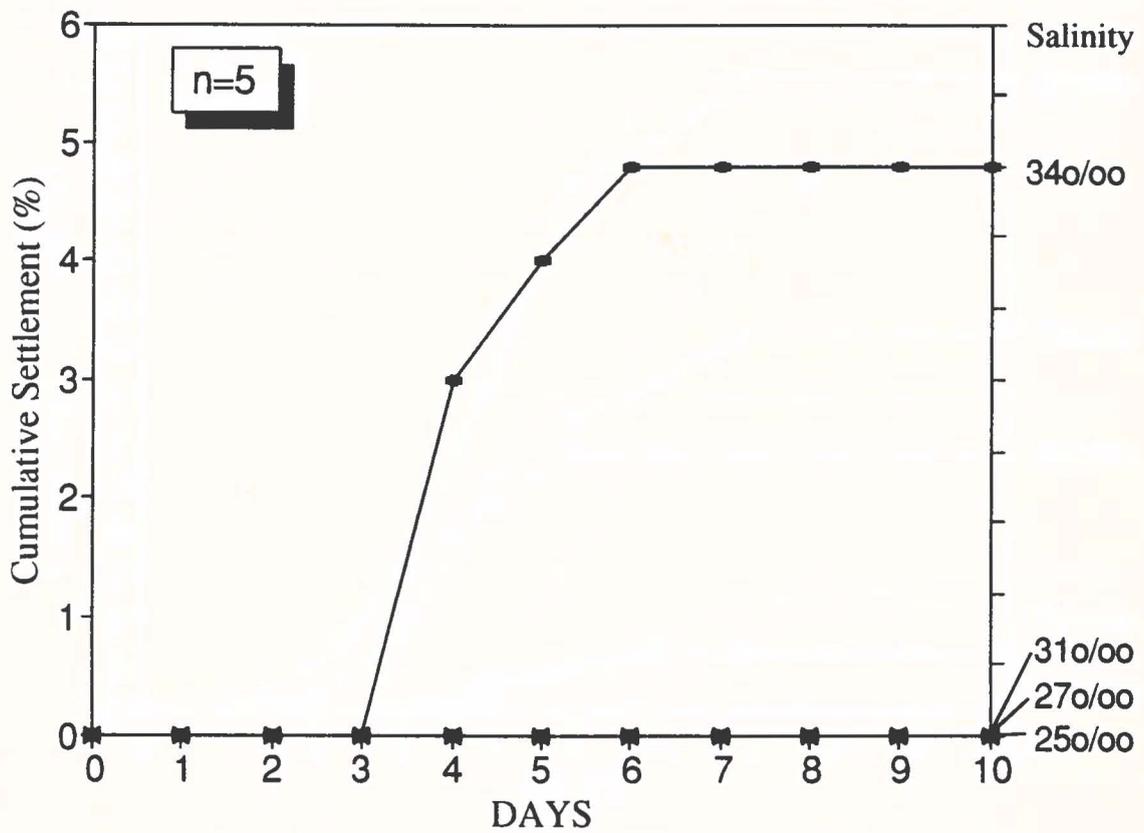


Figure 11. Cumulative settlement of *Acropora digitifera* larvae during a 10-day period

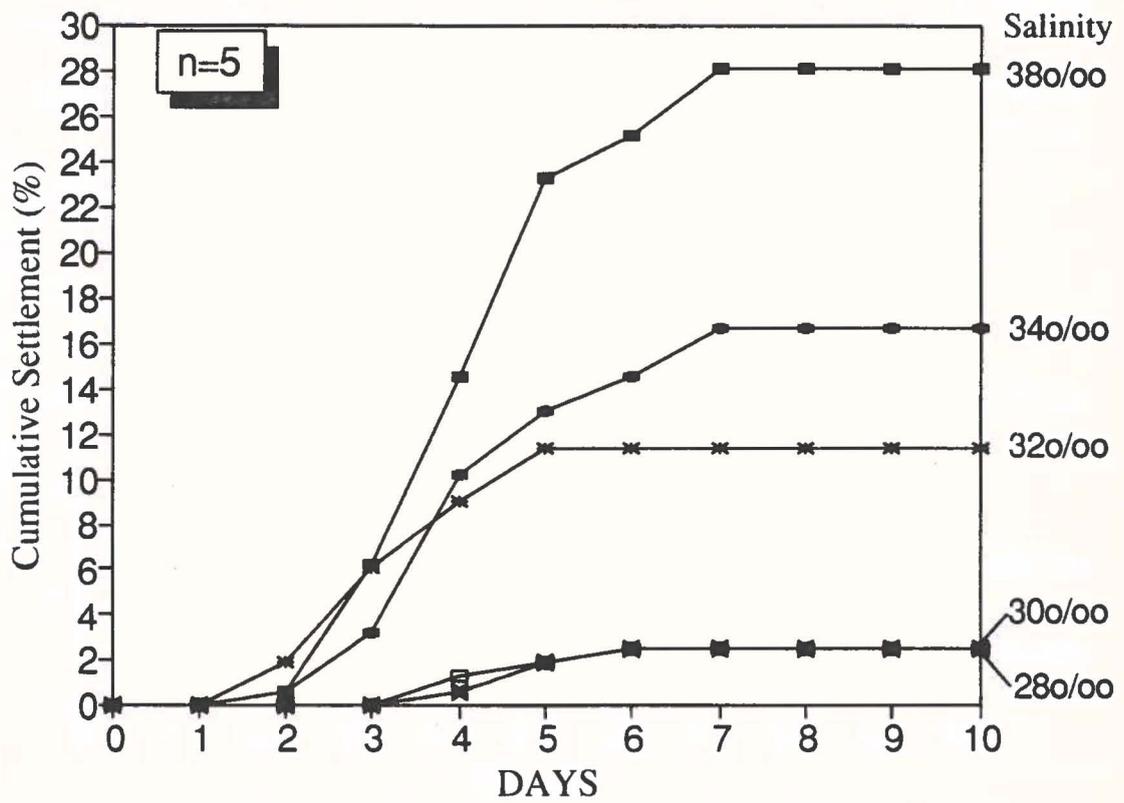


Figure 12. Cumulative settlement of *Goniastrea retiformis* larvae during a 10-day period.

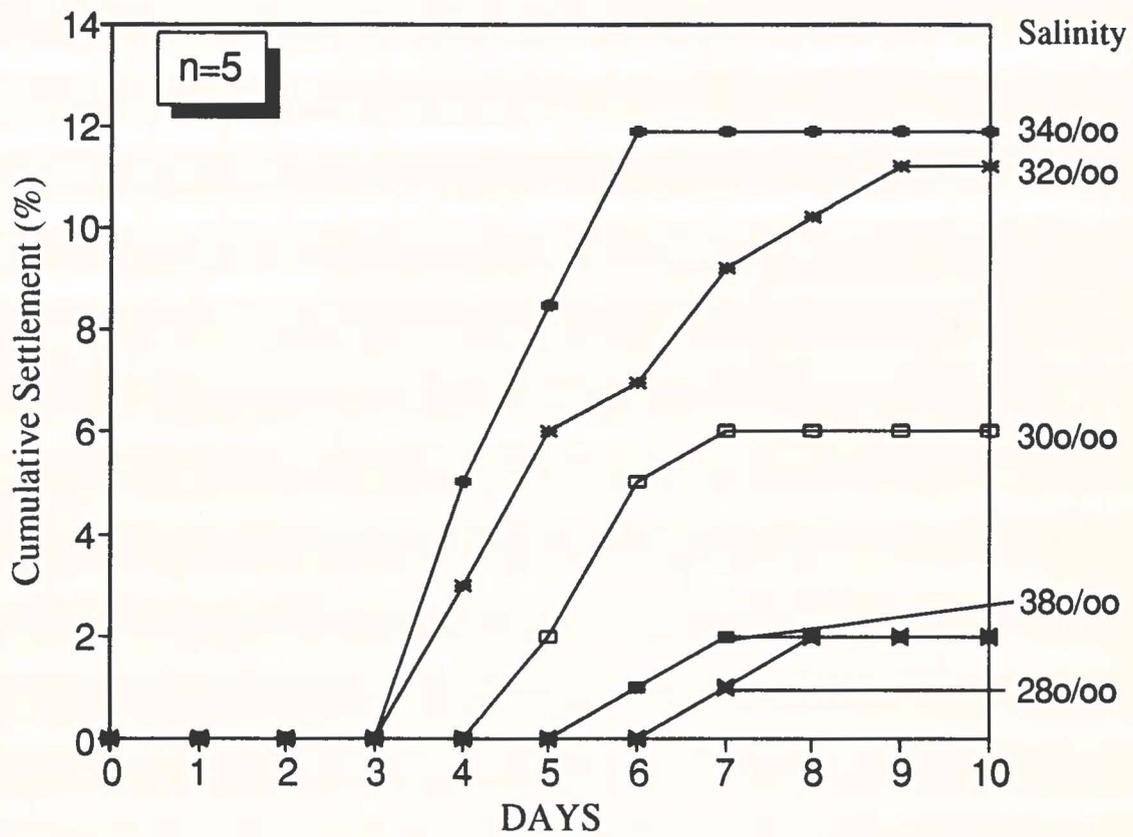


Figure 13. Cumulative settlement of *Leptoria phrygia* larvae during a 10-day period

Larval responses to low salinity

Planulae of the study species exhibited rapid swimming behavior at 34 ‰. When salinity was decreased below 30 ‰ and 28 ‰, planulae entered in to a state of shock, ciliary movement ceased, and larvae immediately stopped swimming and sank to the bottom of the jar. The planulae remained inactive for more than three hours, after which some larvae began swimming very slowly and inconsistently near the bottom of the jar throughout the 10 day study period. Also, larvae of *Pocillopora damicornis* from the salinity treatments of 25 and 27 ‰, which remained in the planktonic stage until the end of the experiment were partially bleached and the epidermis was wrinkled.

DISCUSSION

This study clearly shows that settlement, metamorphosis and survival of coral larvae, and therefore recruitment, are affected by altered salinity. Different tolerances to salinity were observed between a brooding coral and spawning species. Salinity tolerance of larvae appeared to be associated with distribution of adult colonies: reef front corals had more sensitive larvae than those inhabiting the inner reef flat. While previous studies have shown the effects of salinity on adult corals (Coles and Jokiel 1992) and on fertilization (Richmond 1993), this is the first study to show the effects of salinity on larval settlement and metamorphosis.

Salinity tolerance among the five species of coral larvae

The present study showed that settlement and survivorship of coral larvae from the spawning species *Acropora danai*, *A. digitifera*, *Goniastrea retiformis*, and *Leptoria phrygia* and the brooding coral *Pocillopora damicornis*, were significantly affected when exposed to low salinity levels. The fact that *A. digitifera* did not settle at salinities below normal levels to the same extent that the other species did suggests, that this species is especially sensitive to salinity changes. Edmondson (1946) also demonstrated that some species of coral larvae were more sensitive to reduced salinity than others.

Salinity tolerance versus distribution

The tolerance of coral larvae to low salinity levels appears related to the range of salinities encountered by parent colonies. Colonies of *P. damicornis* occur in waters as shallow as 10 cm at the inner reef flat of Agana Bay (pers. obs.). In such locations, colonies and larvae may be exposed to greatly decreased salinity during heavy rains. The presence of these colonies at this location indicates that there are capable of tolerating salinity changes. Coles (1993) described that *P. damicornis* colonies from Hawaii can tolerate salinity levels as low as 25 ‰. Randall and Birkeland (1978) reported that colonies of *Pocillopora damicornis* were present at the head of the mouth of two river enbayments in Fouha and Ylig Bays, Guam.

The lack of settlement and the higher mortality of *A. digitifera* and *A. danai* at low levels of salinity may be associated with their distribution, since they are restricted to the reef margin and hence less exposed to salinity variations.

Larval responses to low salinity

Planulae in this study stopped swimming and sank to the bottom when exposed to decreased salinity. Similar responses to low salinities have also been previously observed for *P. damicornis* larvae (Edmondson 1946) and cirripede larvae (Cawthorne and Davenport 1980). There may be a synergistic effect in which low salinity will affect larval physiology and substratum recognition. In order to metamorphose and settle, larvae must encounter specific chemicals in the substratum (Hadfield 1978, Morse and Morse 1991). Damage or loss of the epidermis may decrease the ability of

larvae to detect these settling cues. Furthermore, benthic organisms that provide the settling cues, may themselves be damaged by low salinity or may be absent in hyposaline environments. Such responses to changes in salinity decrease settlement success, and may extend the time required for recruitment to take place.

Larvae of *Pocillopora damicornis* have several characteristics that tend to make them more successful than the other species studied in unpredictable environments. Planulae of *P. damicornis* that settled at 25 ‰ and metamorphosed into primary polyps, reverted to the planktonic stage forty-eight hours later (pers. obs.). Also a planktonic polyp form developed during the experiments. These phenomena have already been described by Richmond (1985, 1987), and are interpreted as behaviors that may enhance survivorship.

Tolerance to elevated salinity

Corals can tolerate salinity levels up to 42 ‰ (Coles 1993). Coles and Jokiel (1992) have shown that corals can survive at salinities of 42 ‰ under natural conditions. Corals such as *Stylophora pistillata* and *Porites compressa* have survived 20 days of exposure to 49 ‰ in the Arabian Gulf (Coles 1993). *Porites lutea*, *P. australiensis*, *Galaxea fascicularis* and *Goniastrea pectinata* survive at salinities of 43 ‰ under laboratory conditions (Nakano et al. 1993). Since many corals inhabit hypersaline areas, their planulae should also be able to tolerate and settle at similar salinities. In this study, larvae of the spawning species *Goniastrea retiformis* settled as successfully at 38 ‰ as at normal salinity levels. This species is commonly found

on shallow reef flats and on reef fronts, and can survive several hours of aerial exposure during low tide (Randall 1974, Veron 1986). In contrast, larvae of *Leptoria phrygia* exhibited low settlement rates when tested at salinities above control levels. *L. phrygia* is commonly found in deeper, calmer waters of upper reef slopes (Veron 1986). The depth range of this species according to Randall (1974) is 1-15 m, between the outer reef front and the submarine terrace. Therefore, individuals that lived at these depths would be exposed to less salinity variation, and may be less tolerant to such variations.

Salinity in the environment

Several studies have documented that fresh-water runoff from land strongly influences coral reef ecosystems. Freshwater recently caused a catastrophic mortality of reef organisms, including corals, in Hawaii (Holthus et al. 1989). Low salinity was the cause of the coral kill after a runoff episode in Okinawa (Sakai and Nishihira 1991). Reduced salinity killed coral reef organisms after a storm flood in Hawaii (Jokiel et al. 1993). Edmondson (1946) described that fresh water was detrimental to coral larvae. If planulae of the studied species react in nature as in the experimental treatments, larvae carried from healthy reefs to areas of such low salinity would have less probability of settlement and survivorship.

This study demonstrates that salinity below normal levels strongly influences settlement and survival of coral larvae. The spawning period of many corals coincides with the rainy season on Guam, and the competency period of coral larvae is limited.

Nearshore salinity levels below normal, caused by runoff from land, may be a major obstacle to settlement and survivorship for coral larvae. Studies on the combined effects of reduced salinity and sedimentation and their impact on coral larvae are needed, since these two events often occur on coastal reefs in developing islands. It is important to realize that increased freshwater runoff affects not only the reproduction of corals, but also their recruitment.

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