

AN ABSTRACT OF THE THESIS OF

David J. Booth for the degree of Doctor of Philosophy in  
Zoology, presented on January 25, 1991

Title: Larval Settlement and Juvenile Group Dynamics in the  
Domino Damselfish (*Dascyllus albisella*)

*Redacted for Privacy*

Abstract approved: \_\_\_\_\_

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Patterns of settlement of larvae and population dynamics of juveniles are poorly known for coral reef fishes. During 1987 to 1989, I studied these phenomena in the domino damselfish (*Dascyllus albisella*), a species endemic to the Hawaiian Islands. Larvae settle onto branching coral heads as new recruits (10-15 mm in length), usually with conspecific groups, and remain on the coral heads through juvenile life until maturity (70 mm total length). By conducting experiments on natural patch reefs and on an artificially distributed grid of coral heads, I found that most larvae settle at night, and that they settle preferentially on corals supporting large conspecific groups compared to small groups or empty corals.

Within a group, juveniles form a linear dominance hierarchy based on fish size; aggressive interactions are mainly directed by larger fish towards smaller fish. Tagging studies demonstrated that growth was retarded in larger groups and for fish of low social status, but that survival,

especially of new recruits, was enhanced in larger groups. Therefore, I identified both a growth cost and a survival benefit to group living. I derived a measure of net benefit of group living by combining size-specific growth and survival data into an estimate of the probability of reaching mature size. This estimate increased with group size in 1988 but not in 1987.

I developed a simulation model which used my field data on settlement rate, settlement preferences, and juvenile growth and survival to predict demography of juvenile groups. The model successfully predicted seasonal fluctuations in mean group size, and estimated the number of fish maturing in 1987 and 1988, as a function of settlement rate and preferences and of juvenile growth and survival. Numbers maturing were directly related to settlement rate in both years, except at high rates in 1987, suggesting that primary recruitment limitation of adult numbers could be occurring. Settlement preferences also influenced numbers maturing. At all settlement rates, numbers maturing differed between years, suggesting that secondary recruitment limitation of adult numbers may also occur.

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Larval Settlement and Juvenile Group  
Dynamics in the Domino Damselfish (*Dascyllus albisella*)

by  
David J. Booth

A THESIS  
submitted to  
Oregon State University

in partial fulfillment of  
the requirements for the  
degree of  
Doctor of Philosophy

Completed January 25, 1990  
Commencement June 1991

APPROVED:

*Redacted for Privacy*

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Date thesis is presented: January 25, 1991

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### Acknowledgements

First and foremost I thank my major professor, Dr. Mark A. Hixon, who acted as my mentor, editor, colleague and friend during my stay at Oregon State. Dr. Hixon's rigorous and enthusiastic approach to science provided an excellent yardstick against which I could assess my progress. The other members of my committee (Drs. A. Blaustein, T. Cowles, B. A. Menge and C. B. Schreck) provided first-rate support and criticism during the development of my research. Manuscript reviews and/or scientific advice were provided by many, including B. Tissot, P. Sikkel, B. Call, D. Meadows, J. Harding, D. Evans, P. Colgan, J. Wass, P. Sale, C. Petersen, V. Taispic and B. Tyler. In Hawaii, my research was made possible and enjoyable by Dr. P. Helfrich (Director, Hawaii Institute of Marine Biology), Dr. G. Losey, Dr. E. Reese, B. Tyler, J. Godwin, F. Stanton, E. Cox, T. von Staden, B. Wagner, D. Baggett, S. Klump, K. Fletcher and B. Call. Funding for my research came from many sources: Zoology Research funds, a Graduate Teaching Assistantship in Zoology, the Center for Field Studies (Earthwatch), the National Geographic Society, the American Museum of Natural History, Sigma Xi Society, and through Dr. M. A. Hixon. Final thanks are due to all my friends in the Zoology Departments at Oregon State University and the University of Hawaii, and to my parents and family, whose spoken and unspoken encouragement over the years have given true meaning to my achievements.

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**Larval settlement and juvenile group dynamics in the domino  
damselfish (*Dascyllus albisella*)**

**General Introduction**

Much recent ecological research conducted with natural populations of animals has concerned the fundamental question posed by Andrewartha and Birch (1954); i.e., what factors control the distribution and abundance of animal populations? The extant distribution of a species reflects its response to both historical events and present-day processes. Biogeographical forces such as climate patterns and plate tectonics have influenced species distributions on the large-scale. Within a habitat, absolute limits to a species' distribution are often physiological in nature (e.g., due to stresses such as desiccation and unfavorable temperatures) and result in individuals occurring only in favorable micro-habitats. The behavioural response of individuals to such stresses and to biological factors, especially at certain critical points in their life cycle, can have a profound influence over the distribution and density of populations. Dispersal of particular life history stages can involve a component of habitat choice interacting with physical factors. Therefore, a study of patterns of local distribution and behavior of an organism may be useful in predicting distribution and abundance over a wider area.

### **Benthic marine animals**

In the ocean environment, animals typically possess larval stages that disperse widely in the plankton (Thorson 1950). Very little is known about this life history stage for most organisms (but see e.g., Stoner 1990), except that mortality is extremely high and variable, and that adult fecundity and larval production are, as a consequence, poor indicators of the number of larvae that will survive to adulthood. Such life cycles have been termed open systems (e.g., Warner and Hughes 1988). In contrast, in closed life cycles (often characteristic of terrestrial animals), adult fecundity is directly related to the number of new individuals appearing in a subsequent generation. It is not surprising that most field studies of the biology of benthic marine organisms only consider the more sedentary juvenile and adult stages, and that community-level hypotheses traditionally concern patterns observed in sedentary adults only. However, it is now apparent that processes occurring during larval and juvenile life may be important in regulating local adult abundances.

### **Coral reef fishes**

When one dives on a coral reef, one is immediately struck by the overwhelming diversity of life. Small (100's m diameter) coral reefs may contain 100's of fish species, an order of magnitude more than the number of similarly-

sized terrestrial vertebrates found in a similarly-sized habitat (e.g., Sale 1980). Hypotheses to explain the maintenance of this diversity have, until recently, focused on processes occurring directly to the adults. For example, an equilibrium hypothesis (Smith and Tyler 1972) contends that high species diversity and stability of adult coral reef fish communities is maintained through competition for space and the existence of a wide variety of niches on reefs. This hypothesis assumes that recruitment into the adult population is not limiting, and that the environment is stable. Recently, interest has been directed at the validity of these assumptions by measuring variation in larval settlement and juvenile demography, and studying their effects on adult population structure.

The lottery hypothesis (Chesson 1974, Sale 1977) asserts that the species diversity of coral reef fishes on any reef is not in a state of equilibrium, because the composition of the larval pool supplying the reef is stochastic, although not limiting. Community diversity and species abundances are considered to be a product of stochastic larval influx and competition for space among adults of different species on the reef. In contrast, the recruitment limitation hypothesis (Doherty 1981) claims that larval abundances are limiting and are the primary regulators of adult abundances. Victor (1986) has termed this primary recruitment limitation, to differentiate it

from regulation of adult abundance through processes occurring to juveniles (e.g., see Jones 1987), which he calls "secondary recruitment limitation" (see Fig. 0.1). To determine the relative importance of primary and secondary recruitment limitation in regulating densities of adult coral reef fish abundance and diversity, field experiments are necessary which can document the patterns of larval settlement and other factors potentially affecting the recruitment of juveniles into the adult population.

### **This study**

This study concerns the population ecology of recruits (newly-settled larvae) and juveniles of the domino damselfish (*Dascyllus albisella* Gill), which live (often in groups) in close association with branching hard corals on reefs in the Hawaiian Islands. In Chapter 1, I examine the diel pattern of settlement of larvae onto coral heads, and describe how sampling methods can affect estimates of settlement rate. Chapter 2 documents results of surveys and experiments designed to measure spatial and temporal patterns of larval settlement and to determine whether larvae exhibit settlement preferences for certain factors (e.g., do larvae prefer to settle with groups of conspecifics?). It also compares larval settlement variation to fluctuations in abundance of larger juveniles

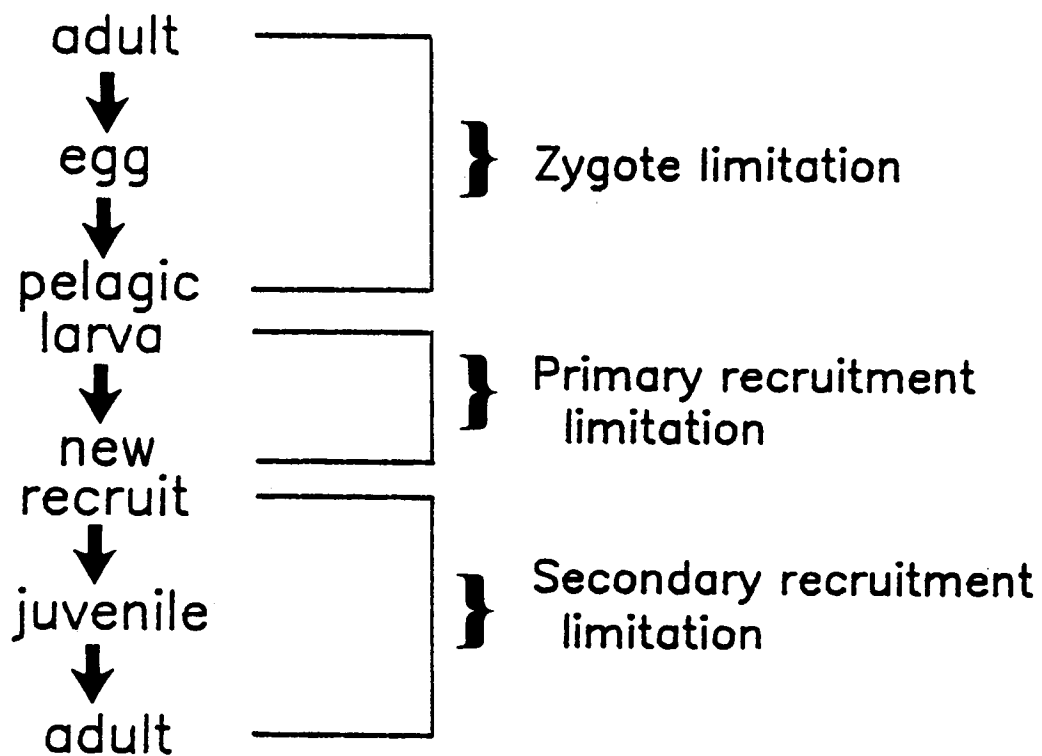
to examine primary recruitment limitation. The costs and benefits (in terms of growth and survival) of group living by juveniles is considered in Chapter 3, and the possible effects of group living on individual fitness are explored. Chapter 4 uses data presented in Chapters 1 to 3 as inputs to a model describing the demography of *D. albisella* groups on a coral patch reef. This model generates predictions on the effects of magnitude and variation in settlement, growth and survival on mean group size and the rate of recruitment of juveniles into the adult population. It considers the relative importance of primary- and secondary recruitment regulation of adult numbers. Finally, I summarize the findings presented in the other chapters. Seven appendices present data which are supplementary to the main thesis chapters.



**Fig. 0.1.** Generalized life cycle of a coral reef fish, illustrating stages at which limitation of adult numbers may occur.

Figure 0.1

## Regulation of adult density



## Chapter 1

### The effects of sampling frequency on estimates of recruitment of the domino damselfish (*Dascyllus albisella* Gill)

#### Abstract

Sampling frequency and methods can potentially affect estimates of demographic rates in population studies. To determine the effects of various sampling protocols on estimating recruitment rate, the rate of larval settlement by the coral reef damselfish *Dascyllus albisella* to an experimental grid of coral heads was monitored over several intervals by either removing newly-settled larvae (recruits) at each census, or not. By sampling every five hours during two 24-hour periods, it was found that most recruits (75% on Day 1 and 81% on Day 2) settled between dusk and dawn. Coral heads that already supported conspecific juvenile groups attracted more recruits than empty coral heads during both 24-hour periods, although this was statistically significant on Day 2 only. Subsequent tagging of recruits from 1 to 19 days after settlement revealed that movement between coral heads was negligible after the first day post-settlement, but apparent mortality was high over the same period. The settlement rate of larvae to the coral grid during a 19-day

period was estimated by employing three protocols of census frequency and recruit removal. This suggested that frequent sampling with recruit removal would most closely estimate true settlement rate for *D. albisella* and probably other species, while less frequent censuses without recruit removal may provide closer estimates of the size of the recruit cohort that will enter the juvenile population. Considerable variation exists in the sampling protocols used by researchers studying settlement rate in damselfishes and I caution against directly comparing results among these studies.

### Introduction

The measurement of demographic rates in benthic marine organisms can be subject to biases associated with sampling methods, including the effects of sampling frequency (Keough and Downes 1982; Roughgarden et. al 1988; Underwood 1989). The development of several hypotheses to explain the diversity of coral reef fish communities (see Doherty and Williams 1988) has given impetus to field studies of coral reef fish population dynamics, including measurement of recruitment rates of fish larvae to the reef. Sampling methods must be carefully developed to estimate recruitment of larvae in the field. Most coral reef fishes have planktonic larval stages which end upon settlement onto coral reefs (Russell 1976; Sale 1980; Leis and Goldman

1987). In recent years, a popular recruitment limitation hypothesis has asserted that patterns of larval settlement have major effects on adult distribution and abundance (Doherty 1981, 1983; Victor 1983, 1986; reviews by Doherty and Williams 1988; Mapstone and Fowler 1988). In order to test for recruitment limitation, a clear measure of variation in settlement rates is necessary. However, relatively little is known about the process of larval settlement in coral reef fishes, probably because larvae are cryptic and may settle at night (Sweatman 1985a; Doherty and Williams 1988). While ichthyoplankton is generally considered to be dispersed primarily by physical factors (review by Kingsford 1988), it is also apparent that larval behavior can influence settlement patterns in reef fishes (Doherty 1983; Sweatman 1985a,b; Kobayashi 1989; Brietburg 1989; Booth in prep.).

Although damselfishes (Pomacentridae) are one of the best studied families of coral reef fishes, little is known of the behaviour of newly-settled larvae (but see Sweatman 1985a). Moreover, there have been a great number of sampling protocols used to measure larval settlement patterns in this family. For instance, four independent studies that estimated settlement rate of larvae in the damselfish genus *Dascyllus* employed census intervals that ranged from daily to monthly, and in some studies, but not others, newly-settled larvae were removed during each

census (Table 1.1). Given the large and often variable rates of mortality among coral reef fishes in the first few weeks after settlement (e.g. Eckert 1987; this study), it would be expected that increased intervals between samples would successively underestimate actual settlement rates.

I undertook a series of field observations to answer the following questions for the domino damselfish (*Dascyllus albisella*): (1) what is the diel pattern of larval settlement, (2) how do sampling frequency and recruit-removal protocols affect estimates of larval settlement rate, 3) what is the extent of post-settlement migration and mortality of new recruits, and how do they affect estimates of settlement among different sampling regimes, and 4) do larvae settle at different rates on coral heads occupied by conspecific juveniles than on empty coral heads? These questions are relevant not only to the ecology of marine organisms, but also to the general process of immigration rates to habitat patches.

## **Materials and Methods**

### *Species and study site*

The domino damselfish is endemic to Hawaii (Randall and Allen 1977). Larvae settle onto branching coral heads at 10-15mm total length (TL). I call these newly settled fish "recruits" until they exceed 15mm in total length,

after which they were classified as "juveniles" to distinguish them from newly-settled fish. Recruits and juveniles inhabit branching coral heads, often in large groups, until they mature at 65 to 70mm TL (Appendix 5) and emigrate to the nearby adult population.

I established a 5 X 12 grid of 60 small (20-35cm diameter) branching coral heads on a uniform sand substrate, at a depth of 3m at the entrance to Kaneohe Bay, Oahu, Hawaii. The coral heads were equally spaced, 10m apart, so that the long axis of the matrix was perpendicular to the major tidal flow into and out of the bay. Using this grid, I designed a factorial experiment to consider the influence of coral species, fish density, coral size and their interactions on larval settlement. The factors were: (1) Coral species: the grid included equal numbers of the two common species of branching coral in Hawaii, *Porites compressa* and *Montipora verrucosa*. (2) Fish density: for each coral species, I randomly assigned juvenile *D. albisella* (35-55 mm TL, collected from patch reefs in Kaneohe Bay) to 20 of the 30 coral heads, so that 10 heads received single juveniles and 10 received groups of 5 to 7 juveniles. The remaining 10 heads were left unoccupied. (3) Coral Size: for each coral species, I assigned 15 corals as small ( $\bar{x} \pm se$ : 24.0 $\pm$ 3.5 cm dia.) and 15 as large ( $\bar{x} \pm se$ : 33.0 $\pm$ 3.5 cm dia.). I analysed results using a 3-way Analysis of Variance, with all factors fixed.

*Diel patterns of settlement*

During two 24-hour periods, September 16-17 (Day 1) and 22-23 (Day 2), 1989, I monitored larval settlement onto the 60 coral heads on the grid as follows. At 1500 hrs, I removed all new recruits using the anaesthetic Quinaldine (Sigma Chemical Co.) and hand nets. At five subsequent times (1900, 2400, 0500, 1000, 1700 hrs), I carefully checked the entire grid for the presence of new recruits. Recruits were counted but not removed at each of these censuses. I had previously verified that recruit counts performed in this way were accurate, by comparing my counts with subsequent complete removals of all recruits from several coral heads, using the anaesthetic Quinaldine (estimates were within 5% of counts after subsequent removals in all cases). At each census, I estimated the number of new recruits on each coral head as the increase in recruits since the previous sample. This method assumes that mortality and migration of recruits are negligible between censuses.

The two sampling dates that I chose had opposite tidal cycles. Bathen (1968) documented that the prevailing currents at my study site essentially followed the tidal direction, and I expected that settlement rates would be higher on an incoming tide.



*The effects of sampling protocols on estimates of larval settlement rate*

To determine the effect of sampling methods on estimates of settlement rate of larvae, I designed a factorial experiment in which I assigned three treatments to 40 coral heads within the previously described grid . The treatments were (1) coral species (2 levels: *Montipora verrucosa* and *Porites compressa*), (2) juvenile conspecific density (2 levels: empty and groups of from 5 to 7 juveniles), and (3) census protocol (2 levels: "removal" and "no removal", see below).

On the mornings of September 27,28,29,30 and October 3,8,10 and 16, 1989, I removed and counted all recruits from the 20 "removal" coral heads and counted the recruits present on the 20 "no removal" coral heads. I estimated the net rate of settlement per coral head for each census after September 27 as: 1) the number of recruits removed from the coral (for "removal" coral heads), or 2) the net increase in recruits on the coral head since the previous census (for "no removal" coral heads).

*Post-settlement migration and mortality of new recruits*

tested the assumption that mortality or migration of new recruits would not affect estimates of settlement rate from repeated censuses, by clipping off the top third of the dorsal fins of 30 new recruits found on "no removal"

coral heads on September 28, and searched the coral grid for these marked recruits in subsequent surveys. I assumed that disappearance of tagged recruits indicated mortality. Observations of 10 fish clipped in this way and held in aquaria for one week suggested that clipping *per se* had no noticeable effect on fish behavior or survival, and that handling mortality was minimal (all 10 fish appeared healthy after one week).

## Results

### *Diel pattern of settlement*

On both 24-hour sample dates, the majority of settling larvae observed (75% of 32 recruits on Day 1; 81% of 91 recruits on Day 2) appeared on the experimental coral grid after dusk (1900 hrs) and before dawn (0500 hrs). These percentages are significantly higher than those expected if larvae settled randomly relative to time of day (G-test, with expected values for each interval proportional to its duration: 8.93,  $p < .05$  for Day 1; 36.2,  $p < .05$  for Day 2), indicating that settlement in *Dascyllus albisella* occurs predominantly at night (Fig. 1.1). Rates of settlement were higher from midnight to dawn than from dusk to midnight on Day 2, but not on Day 1 (Fig. 1.1; G-test: Day 1;  $G=22.67$ ,  $p < .05$ ; Day 2;  $G=.62$ ,  $p > .05$ ). These results do not suggest any consistent relationship between tidal

current direction and the temporal pattern of settlement (Fig. 1.1). Nevertheless, nearly three times as many larvae settled on Day 2 (late night ebb tide) as on Day 1 (late night flood tide; G-test expecting equal proportion of recruits on Days 1 and 2 = 15.21,  $p < .05$ ). Moonrise and lunar phase differed between days: on Day 1, a full moon rose at 8 pm, while on Day 2, a half-moon rose at midnight. However, larval settlement rate did not appear to be affected by the presence or absence of moonlight (Fig. 1.1). Larvae did not appear to settle on individual corals in groups, since the number of corals gaining two or more recruits during any sample interval did not exceed that expected if larvae had settled singly (unpubl. data).

On Day 1, there was no significant effect of coral species, coral size, or conspecific group size on settlement rate (ANOVA, Table 1.2). On Day 2, a significant effect of conspecific group size on settlement was evident over the 24-hour period (ANOVA, Table 1.2, Fig. 1.2b). This effect consisted of significantly higher settlement to both group and single treatments over empty coral treatments (SNK multiple range test,  $\alpha = .05$ ). However, the effect of fish density on settlement was not significant over night on that day (Table 1.2). No other main effects or interactive effects were significant in either day, although coral size X fish density was marginally insignificant (ANOVA,  $p = 0.062$ ) over night on Day

2 (Table 1.2). These patterns are complicated by the fact that on Day 2 the number of recruits after dawn simultaneously dropped on empty coral heads and rose on coral heads occupied by juvenile conspecifics (Fig. 1.2b).

*The effect of sampling protocol on estimates of settlement rate*

Estimated settlement was significantly higher on "removal" coral heads than on "no removal" corals (ANOVA,  $p < .05$ , Table 1.3, see below). Neither coral species nor conspecific group size significantly affected settlement, although their interaction had a significant effect (Table 1.3): on *P. compressa*, settlement was higher to conspecific groups, but on *M. verrucosa*, there was no apparent effect of group size on settlement.

The number of recruits appearing on corals for each sampling protocol was as follows:

(i) **2-6 day sampling, with removals.** The mean number of recruits removed per coral over the 19 days was  $9.1 \pm 1.1$  (se,  $n=20$ ).

(ii) **2-6 day sampling, without removals.** I summed the net gains of recruits over the 19-day period to each coral head in the "no removal" treatment. The mean net gain of recruits on each coral over this time was  $4.9 \pm 0.7$  (se,  $n=20$ ).

(iii) 19-day sample interval without removal. The mean number of recruits on each coral head in the "no removal" treatment on day 19 was  $2.0 \pm 0.4$  (se, n=20).

Therefore, the estimated settlement rate was higher as sampling frequency was increased following the removal of recruits.

#### *Post-settlement migration and mortality*

Only one of 30 recruits marked on the 20 "no removal" corals on September 28 was found away from its original coral head in the six subsequent surveys, and was located on an adjacent coral head. This suggests that migration after the first day, during the first few weeks after settlement, was negligible. However, survivorship of tagged recruits (as estimated using rates of disappearance) was very low over the first week (Fig. 1.3).

### **Discussion**

Censusing method clearly affected the type of information gathered on larval settlement in *Dascyllus albisella*. As expected, more frequent sampling yielded more accurate data concerning patterns of larval settlement by avoiding biases associated with post-settlement migration and mortality of larvae.

Larval settlement rates to the experimental grid of 60

coral heads were higher at night and the diel pattern of settlement seemed independent of the tidal cycle, which is consistent with the hypothesis that larvae do not settle passively. Passive arrival of larvae to the grid would have been indicated by a more even diel pattern of settlement. Although I sampled on two days only, most larvae appeared to settle in the period from midnight to dawn. Kobayashi (1989) found that larvae of two gobiid fishes in Hawaii can remain adjacent to reef areas and resist advection and further dispersal prior to settlement. Such an ability may enable *D. albisella* larvae to settle non-randomly with respect to time of day, as found in my study. Sweatman (1985a) similarly found that larval *Dascyllus aruanus* settle mostly at night at Lizard Island on the Great Barrier Reef, although due to his sampling methods, he could not be sure that all of these larvae settled at night.

My results also suggest the possibility that post-settlement migration of recruits from empty coral heads to previously-occupied corals, during the first 24 hours after settling, could partly account for the higher apparent settlement to occupied corals (Fig. 1.2b; cf. Sweatman 1985a). However, because new recruits were not marked immediately after settlement, the evidence for migration remains circumstantial. Alternatively, differential mortality between occupied and empty coral heads or

stronger settlement preferences for occupied corals after dawn could account for these patterns.

In contrast, recruit tagging studies at this study site showed that migration of marked recruits and juveniles between coral heads was negligible from 1 to 14 days after settlement. Thus, redistribution of recruits, if it occurs, is limited to the first day after settlement. In any case, the influence of immediate post-settlement migration of recruits on apparent patterns of settlement warrants further study. Mortality of recruits in the first week after settlement was very high, which is not unusual for reef fish species (see also Eckert 1987; Sale and Ferrell 1988), and my results indicated a Type-III survivorship curve (Deevey 1947). This result suggests that even shorter (<2 day) intervals between censuses would be necessary to accurately assess absolute settlement rates.

The higher rate of settlement to coral heads already supporting groups of juvenile conspecifics on Day 2 is consistent with the findings of Sweatman (1985b) for *Dascyllus aruanus*, although the weekly sampling regime that he employed likely included components of post-settlement migration and mortality of recruits. In my study, the low rates of settlement of larvae onto the coral grid during late September reduced the likelihood that the effects of treatments on settlement rate of larvae would be

statistically significant. This may account for the lack of an effect of fish density on settlement in most cases (Table 1.2, Day 1; Table 1.3). Monitoring of settlement to the coral grid from March to October 1989 (Chapter 2) indicated that settlement peaks occurred from mid-May to mid-June and from mid-August to early September. Settlement rates during the experiments reported here were well below peak rates (which were up to 270 recruits per day), but I would not expect that diel patterns of settlement to be qualitatively different when settlement was higher.

The data presented here underscore the importance of investigating factors such as migration and mortality of new recruits immediately after settlement, before assuming that patterns based on later and less frequent observations are representative of the actual pattern of larval settlement. In the "no removal" treatment, it was impossible to distinguish new recruits from those present during the previous census, and so the number of new recruits was estimated as the net increase in recruits. This method is probably not justified, considering the low rate of survivorship of recruits. Several recent studies of *Dascyllus* and other damselfishes have utilized weekly and monthly sampling regimes to estimate patterns of settlement (Table 1.1). The results of this study indicate that direct between-study comparisons of rates of



settlement would therefore be difficult.

Each census method provides different insights into recruitment processes. Frequent censuses of isolated sites, with recruit removals, yielded the highest estimate of the rate of larval settlement, and minimized the confounding effects of migration and mortality. Less frequent censuses, without recruit removals, may provide a closer estimate of the number of recruits that survive the mortality gauntlet in the first week after settlement (Fig. 1.3). For instance, the recruitment limitation hypothesis (Doherty 1981) contends that spatial and temporal variability in settlement rate (reflecting patchy distribution of fish larvae in the plankton) can affect adult distribution and abundance in coral reef fishes. Therefore, a field study designed to test this hypothesis should measure actual settlement rates, and involve frequent sampling for recruits to reduce the influence of post-settlement factors on estimated settlement rate.

"Recruitment" generally refers to the entry of individuals of one life stage of an organism into the next (Connell 1985) and therefore has a distinct biological meaning. However, estimates of recruitment are also heavily biased by sampling protocol (see also Keough and Downes 1982; Richards and Lindeman 1987). For reef fishes (e.g. Sale and Ferrell 1988) and marine invertebrates (e.g.

Keough and Downes, 1982) recruitment has been estimated by noting "...the first occasion on which metamorphosed larvae become visible at a site." (p. 74, Mapstone and Fowler 1988). Because the relationship between recruitment in this purely operational sense and recruitment as a biological concept (defined by Connell 1985) depends on the frequency and thoroughness of sampling, methods to assess recruitment onto the reef should either include frequent sampling, or account for the intensity and effects of migration and mortality of larvae between censuses (see also Keough and Downes, 1982).

**Table 1.1:** Sampling protocols used in estimations of settlement rates in damselfishes (Pomacentridae).

Species	Sample Unit	Days between samples	Recruits Removed?	Reference
<i>Dascyllus albisella</i>	Wire coils	1	Yes	Schroeder (1987)
	Reefs	3	No	
<i>Dascyllus albisella</i>	Coral heads	1-2	Yes	this study
	Patch reefs	5	No	
<i>D. aruanus</i> , <i>D. reticulatus</i>	Coral heads	7	Yes	Sweatman (1985b)
<i>D. aruanus</i> ,	Coral heads	30	Yes	Jones (1987)
<i>Pomacentrus amboinensis</i>	Coral heads	7	Yes	"
<i>P. wardi</i>	Patch reefs	28-42	No	Doherty (1983)
Caribbean damselfishes	Patch reefs	3-7	No	Shulman et al. (1983)
	"	1-11	No	Shulman (1984)
	"	3-10	No	" (1985a)
	"	1	Yes	" (1985b)

**Table 1.2:** 3-way ANOVA's on effects of coral species, coral size and fish density on settlement of *D. albisella* during two 24-hour periods. Day 1: September 16-17; Day 2: September 22-23, 1989. "Night" refers to the period between dusk and dawn; \*:  $p < .05$ . Assumptions of data normality and homoscedasticity (Bartlett's Test) were met.

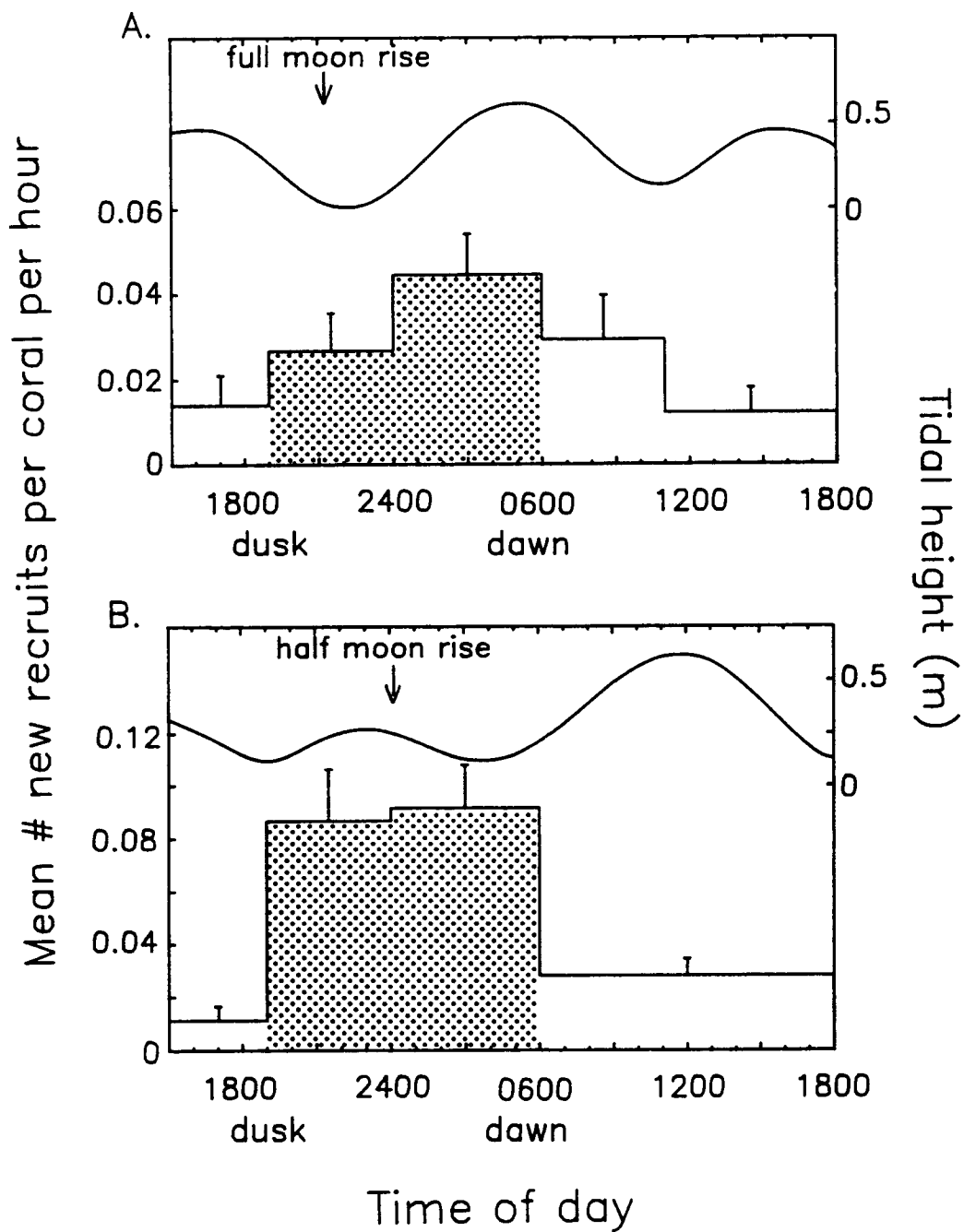
Source	df	F- ratio			
		Day 1		Day 2	
		24 hr	Night	24 hr	Night
Coral Species	1	0.766	0.658	4.080	3.245
Coral Size	1	2.197	1.286	1.067	2.097
Fish Density	2	0.060	0.720	4.551*	0.917
Species*Size	1	0.001	0.272	0.004	0.225
Species*Density	2	0.630	0.604	0.478	0.101
Size*Density	2	0.536	0.948	2.329	2.593
Size*Density* Species	2	0.424	0.973	0.410	0.662
Error	48				

**Table 1.3:** 3-way ANOVA on effects of coral species, fish density and sampling protocol ("removal": recruits removed each census, vs. "no removal") on settlement of *D. albisella* from September 27 to October 10, 1989. \*:  $p < .05$ . Assumptions of data normality and homoscedasticity (Bartlett's Test) were met,  $n=40$ .

Source	ss	df	ms	F-ratio	p
Coral Species	15.83	1	15.83	0.753	0.392
Fish Density	33.32	1	33.32	1.585	0.217
Protocol	89.40	1	89.40	4.252	0.048*
Species*Density	114.6	1	114.6	5.450	0.026*
Species*Protocol	15.83	1	15.83	0.753	0.392
Density*Protocol	5.280	1	5.280	0.251	0.620
Species*Density *Protocol	79.40	1	79.40	3.777	0.061
Error	672.7	32	21.023		

**Fig. 1.1.** Diel patterns of settlement of *Dascyllus albisella* (histograms, mean number of new recruits per hour in each time interval,  $\pm$  se, n=60) compared with tidal cycles during two 24-hour sampling periods: A: September 16-17 (Day 1); B: September 22-23, 1989 (Day 2). The stippled area indicates night-time, and arrows indicate moonrise. Note the different scales of the ordinates.

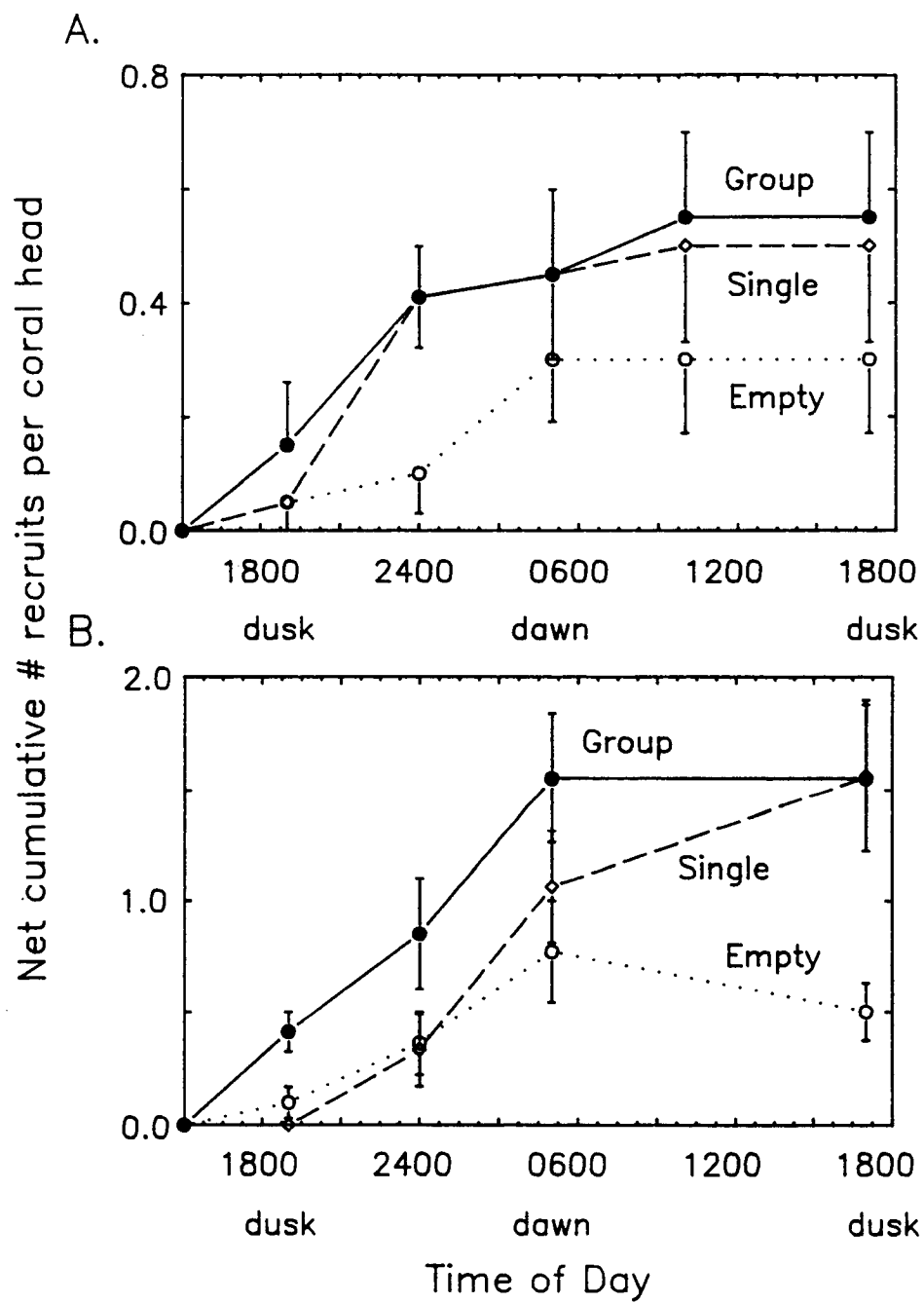
Figure 1.1



**Fig. 1.2.** Accumulation of recruit *Dascyllus albisella* on three conspecific juvenile density treatments ("group" (5-7 fish), "single" and "empty",  $\bar{X} \pm se$ , n=20 for each) during two 24-hour sampling periods: A: September 16-17 (Day 1); B: September 22-23, 1989 (Day 2). Note the different scales of the ordinates. Daytime drop in number of recruits on empty coral heads occurred simultaneously with complementary increases in the number of recruits on occupied heads on Day 1 (between dawn and 1000 hrs) and Day 2 (between dawn and 1700 hrs).

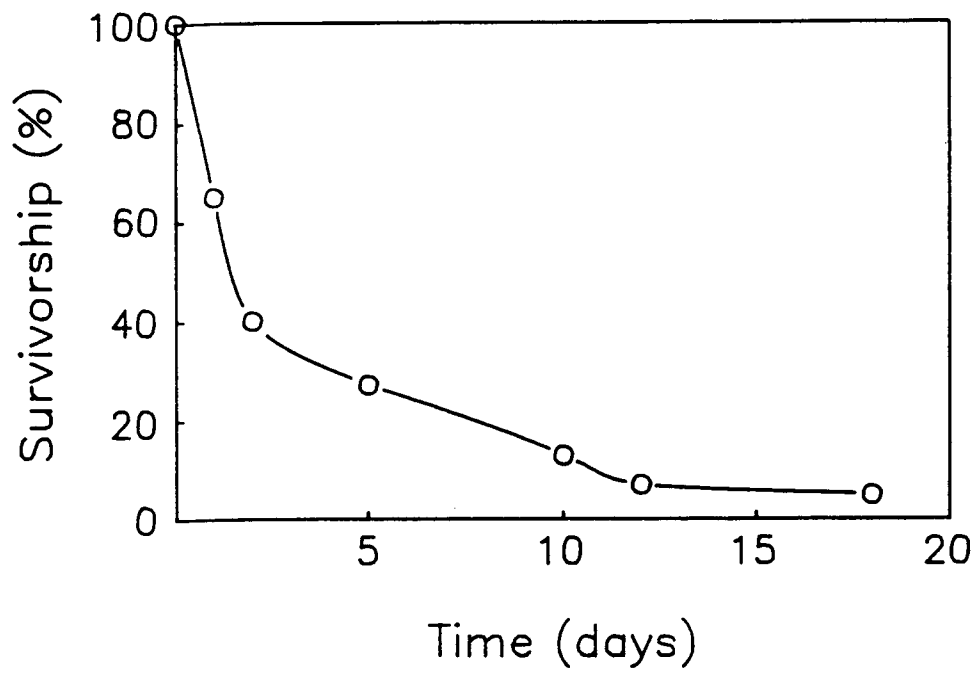


Figure 1.2



**Fig. 1.3.** Apparent survival of 30 tagged recruits occupying 20 coral heads over an 18 day period in September, 1989.

Figure 1.3



## Chapter 2

### Larval settlement patterns and preferences by domino damsel fish (*Dascyllus albisella*)

#### Abstract

In open populations, larval settlement dynamics may be an important determinant of subsequent distribution and abundance of juveniles and adults. I conducted a correlative and experimental study of larval settlement in the domino damselfish (*Dascyllus albisella*) onto coral reefs off Oahu, Hawaii, by considering settlement patterns, larval habitat choice and the effects of a pulse of settlement on juvenile abundance. Conspecific juveniles live in transient groups on small, branching coral heads and do not interact with adults. By repeatedly censusing a natural patch reef over two summers, and employing a multifactorial experiment on a grid of isolated coral heads, I identified conspecific juvenile density as the major factor influencing settlement. Using a series of field and laboratory binary choice experiments, I confirmed that larvae preferred to settle with larger groups of conspecific juveniles than with single conspecifics, empty coral heads or heterospecific groups. The laboratory experiment also indicated that preferences were established through visual cues, suggesting that vision may supplement chemical cues in facilitating larval settlement

preferences. A distinct pulse of settlement on a natural patch reef was not later evident as a strong cohort of larger juveniles. This suggested that temporal variation in settlement was not a primary determinant of the abundance of larger juvenile size classes, and that post-settlement mortality largely determined the abundance of juveniles. On a larger spatial scale, patterns of settlement at five sites covering 25km of Oahu's coastline suggested that two distinct peaks of larval settlement occurred in the summer of 1989 and that settlement was synchronous among these sites. Although settlement pulses appeared to occur simultaneously over a broad area, the lack of evidence for recruitment limitation suggests that settlement peaks would not cause subsequent increases in recruitment to adult populations.

### **Introduction**

Much recent research has centered on the dynamics of open populations, i.e., populations in which entry of new individuals into the population (recruitment) is not directly related to reproductive output of adults in that population (e.g., Roughgarden et al. 1985, Warner and Hughes 1988, Hughes 1990). In contrast to closed populations, in which population structure can be predicted from life tables which incorporate values for fecundity of adults and age- or size-specific growth or survival (e.g.,

Kirkpatrick 1984), the structure of open populations does not directly depend on adult fecundity patterns. A typical open life cycle involves a dispersive stage (spore, larva, or zygote contained in a seed or other propagule) and more sedentary, site-attached juvenile and adult stages. Examples include terrestrial plants in which seeds are widely dispersed (see Harper 1977) and benthic marine invertebrates and fishes (see Crisp 1984, Sale 1980).

Larval recruitment patterns in marine organisms can be important in structuring open populations and communities of adults. The population and community structure of intertidal invertebrates, for instance, has been described by incorporating highly variable larval recruitment into various mathematical and conceptual models (e.g., Roughgarden et al. 1985, Menge and Sutherland 1987, Scheltema 1985, Bence and Nisbet 1988). The mechanisms involved in the regulation of open populations are currently being evaluated for coral reef fishes (e.g., reviews in Sale 1991). Coral reef fishes typically have a pelagic larval stage followed by sedentary, site-attached juvenile and adult stages (Sale 1980). Because reproductive output on any reef appears to be unrelated to subsequent larval settlement rate, most coral reef fishes are considered to possess open life cycles (Warner and Hughes 1988). Several hypotheses that advocate a role for variable larval recruitment in regulating adult abundances

have been developed for coral reef fishes and are applicable for open populations in general. They predict that adult community or population structures are largely the result of the unpredictable patterns of larval settlement characteristic of coral reef fishes. The lottery hypothesis (Sale 1978) predicts that adult fish species compositions on coral reefs are determined by patterns of larval settlement onto reefs and strong prior residency effects, despite competition for living sites. This hypothesis has also been successfully used to describe the stochastic nature of species assemblages in English grassland communities (Grubb 1977). The recruitment limitation hypothesis (Doherty 1981) asserts that variability in generally low larval settlement rates, and not processes occurring during juvenile or adult stages, is the primary determinant of adult abundances. Alternative hypotheses include the more traditional ideas that interactions during juvenile (e.g., Jones 1987) or adult stages (e.g., Smith and Tyler 1972) determine adult distribution and abundance. A knowledge of the process of larval settlement onto reefs is therefore critical to evaluate the relative importance of these hypotheses for coral reef fishes and other open populations. In this study, I consider patterns of larval settlement in a coral reef fish, the domino damselfish (*Dascyllus albisella* Gill), and the role of larval habitat choice on these

patterns.

*Habitat choice at settlement*

Habitat selection is widespread in both terrestrial and aquatic species (e.g., Grant 1972, Werner and Hall 1974). Such habitat choice may have an adaptive basis, increasing an animal's fitness through, for example, enhanced shelter from predators or access to higher densities of food (e.g., Pulliam and Caraco 1984). Much recent research has focussed on the role of habitat choice by larvae of marine organisms in structuring adult communities (e.g., reviews by Hadfield 1986, Doherty and Williams 1988). Many benthic or sedentary marine animals have a pelagic larval stage, but the relative importance of larval choice and extrinsic physical factors to subsequent settlement and persistence in the benthic environment is unclear (e.g., Hadfield 1986, Richards and Lindeman 1987). In some marine invertebrates with sessile juvenile and adult stages, larval habitat selection can strongly affect the distribution and abundance of adults (Hoagland 1978, McGee and Targett 1989, Stoner 1990).

Little is known about the behaviour of larvae of marine reef fish, either before or during the settlement process (Richards and Lindeman 1987, Sale 1990). This is partly due to the general difficulty of observing larvae in the field and the inadequacy of laboratory experiments



to simulate natural conditions. Since coral reefs are often areas of high water visibility and warm water, they are ideal for examining larval fish settlement *in situ*. Coral reef fish larvae may show settlement preferences for certain habitat types (e.g., Shulman 1984, 1985, Shapiro 1987) or for conspecifics (e.g., Sweatman 1985a,b). Larval aggregating behaviour immediately prior to arriving at a reef habitat may also influence settlement patterns (Leis 1986, Pitcher 1988a, Kobayashi 1989, Brietburg 1989). Within-habitat larval distribution patterns are usually interpreted to indicate larval preferences, although the patterns may be artifacts of other processes. For example, larvae may settle more often on large than small coral heads (e.g., Sale 1972, Fricke 1980) because large corals are simply easier to detect than smaller corals, and not necessarily as a result of larval preferences. Actual settlement preferences can only be established by offering larvae simultaneous choices of alternative settlement sites (e.g., Crisp 1974). It is critical to determine whether differential settlement is due to larval settlement preferences if conclusions are to be drawn regarding the adaptive significance of larval settlement behavior.

In many species of coral reef fishes, juveniles and/or adults exist in groups which are highly site-attached (Sale 1980). For example, juveniles of the damselfish *Dascyllus aruanus* live in such groups on small, branching coral

heads. Sweatman (1985a) demonstrated that larvae of this species settle more often with conspecifics than to empty coral heads or to coral heads with heterospecifics. This differential settlement was interpreted by Sweatman (1985b) as having an adaptive basis, because the larvae should have reduced risk of predation and greater opportunities to find mates in larger groups of conspecifics (e.g., Jones 1987). However, growth of *D. aruanus* in large groups was retarded as a result of density-dependent competition for food (Coates 1980, Jones 1987), so the adaptive significance of this pattern of settlement is not yet clear.

Juvenile domino damselfish often occur in transient groups on branching coral heads. Based on the concepts and findings presented above, and extending previous research on this topic, I tested the following predictions concerning larval settlement preferences:

**Prediction 1.** Effects of conspecific groups on larval settlement:

(a) Larval settlement rate is positively related to conspecific group size.

(b) Higher larval settlement with conspecific groups is due to larval settlement preferences for groups, and is not a by-product of other processes.

**Prediction 2.** Effects of other habitat variables on larval settlement:

(a) More rugose (branching) corals will attract more

larvae by providing more shelter.

(b) Coral species will affect settlement rate (e.g., Jones 1988).

(c) Settlement rate will be higher on larger corals (see Sale 1972, Shapiro 1987).

(d) Settlement rate will increase with water depth (e.g., Shapiro 1987).

(e) Settlement rate will be highest on the north-east edge of reefs, facing prevailing currents (Bathen 1968).

**Prediction 3.** The presence of conspecifics will influence settlement rate more than heterospecifics or all other variables (#2 above). Although most experimental studies that have demonstrated settlement preferences for conspecifics have used standardized coral habitat units (e.g., Sweatman 1983) and so did not report the role of other habitat variables in settlement, the primary role of conspecifics has been implicit and needs experimental confirmation.

#### *Recruitment synchronicity among sites*

Seasonal settlement patterns may be similar for some species over large areas (e.g., Victor 1984, Doherty 1988), or may exhibit extreme spatial patchiness (e.g., Williams 1983, Sale et al. 1984, Doherty 1987). Patches of fish larvae may be large (>65km diameter) and result in settlement synchronicity over a large area (e.g., Victor 1984). Large-scale variation in larval settlement of coral

reef fishes is generally considered to represent the effects of a combination of physical and biological factors (Kingsford 1988). These factors can include currents, tides, lunar phase and adult reproductive cycles (e.g., Richards and Lindeman 1987, Kingsford 1988, Pitcher 1988a). For instance, large-scale current patterns partly explained the different rates of settlement of coral reef fish in separate regions of the Great Barrier Reef (Williams et al. 1984).

Synchronous peaks of settlement over a wide area would allow results of settlement monitoring at one site to be of greater generality. If such a peak coincided with a major disturbance event (e.g., a tropical storm), then an entire year class of new juveniles could be wiped out (M.A. Hixon, *personal communication*). I made the following prediction for *D. albisella*:

**Prediction 4.** Seasonal patterns of larval settlement will be similar among reef sites separated by 10s of kilometers.

*Effects of settlement pulses on juvenile abundance*

Larval settlement patterns in coral reef fishes are characterized by high seasonal variation (e.g., Williams 1983, Sale et al. 1984, Doherty 1987). Especially for coral reef fishes at higher latitudes, settlement is negligible during winter months. In many species, most annual settlement occurs in the few days around some new or

full moons in summer (e.g., Williams 1983, Figure 15 in Doherty and Williams 1988). Such episodic settlement may serve to reduce predation risk by swamping predators (e.g., Johannes 1978). The recruitment limitation hypothesis (Doherty 1981) predicts that such pulses of settlement will be reflected in subsequent pulses in the abundance of larger juveniles and ultimately adults. If so, then settlement pulses could have a significant role in regulating adult densities. If recruitment limitation is important for *D. albisella*, I predicted the following:

**Prediction 5.** A strong pulse of larval settlement will be reflected in subsequent peaks in the abundance of larger juveniles.

## Methods

### *Study system*

The domino damselfish is an endemic Hawaiian reef fish (Randall and Allen 1977). Females lay demersal eggs which are fertilized and guarded by the male for several days (Stevenson 1963, pers. obs.), after which larvae are dispersed pelagically (Leis and Rennis 1984). Settlement generally occurs after a 25-29 day pelagic phase (Wellington and Victor 1989, Appendix 7), and larvae settle primarily on branching coral heads (Stevenson 1963, Groll 1984, Schroeder 1985a,b, pers. obs.). Newly settled fish

("recruits") are between 10 and 15mm total length, while juveniles are between 15 and 70mm TL. Recruits and juveniles remain closely associated with branching coral heads until they attain a total length of 65-70mm, when they become sexually mature (D. Booth, unpubl. manuscript) and join the nearby but spatially distinct adult population as schooling planktivores. This spatial segregation of juvenile and adult stages contrasts with other species of *Dascyllus*, in which social groups of adults and juveniles cohabit the same coral heads (Sale 1972, Fricke 1980, Sweatman 1983, 1985a,b, Shpigel and Fishelson 1986, Jones 1987). Therefore, unlike studies involving other species, this system allowed me to examine larval settlement without the confounding effects of adult-juvenile interactions and complex mating systems.

My study was run from March 1988 to October 1989 on patch reefs and adjacent sand flats within Kaneohe Bay, Oahu, Hawaii (near the Hawaii Institute of Marine Biology, Coconut Island), and at sites several kilometres to the north and south of the bay, on Oahu's windward side (Fig. 2.1). The study reefs were between 0.6 and 2.7 hectares in area, roughly circular in shape (Roy 1970), and supported a 30-40% cover of live hard corals, mainly *Porites compressa* and *Montipora verrucosa*.

*Settlement on natural patch reefs*

*Predictions 1 - 3: factors affecting larval settlement:* I

used a correlative approach to consider the effects of several physical and biological features of a coral patch reef on larval settlement. From March to October in both 1988 and 1989, I conducted regular SCUBA censuses of a natural patch reef (reef No. 23: Fig. 2.1) to monitor larval settlement to 39 numbered coral heads already supporting groups of juvenile *D. albisella*. I surveyed these coral heads at 5-day intervals, and on most surveys also searched for fish on the remaining 159 coral heads on the same reef. For each of the numbered coral heads, I counted the number of fish per coral head ("group size"), and estimated the lengths of each fish (assigned to 5mm length classes). I had previously verified the accuracy of these counts and length estimations, by censusing and subsequently removing and measuring all fish from several coral heads, using an anaesthetic (Quinaldine, Sigma Chemical Co.).

I also measured six characteristics of each tagged coral head that I predicted would affect larval settlement:

- (1) coral species: *P. compressa* or *M. verrucosa*;
- (2) coral size: maximum width of the coral head X perpendicular width;
- (3) water depth: at low tide;
- (4) coral isolation: mean distance to the three nearest

coral heads;

(5) location: compass bearing along the reef's circular perimeter; and

(6) coral rugosity: measured using a scale of 0 (no fine branching) to 5 (surface of coral covered in fine branches).

I used linear multiple regression models to interpret the relationship between settlement (total number of recruits per coral head) and the above variables. I also used partial correlation analysis to investigate the effects of each variable on settlement in both years (Sokal and Rohlf, 1981).

*Prediction 3: relative importance of conspecifics and habitat variables to settlement:* The habitat correlations may have been confounded by the fact that conspecifics occupied some coral heads and not others. That is, larvae could be attracted to sites occupied by conspecifics and not conspecific presence *per se*. Therefore, I conducted a manipulative study to determine the effects of settlement site on larval settlement rate independent of the presence of previous settlers. On each of two natural patch reefs (Reefs 21 and 22; Fig. 2.1), I established four 10m X 10m quadrats (one each on the north, south, east and west sides of each reef). Each quadrat extended from about 2 meters below the reef crest, down the reef slope to a depth of



around 10 metres. Within each quadrat, I mapped the locations of all coral heads, and noted the locations of all groups of juveniles. Subsequently, I removed these groups (42 groups from reef 21; 23 groups from reef 22), and monitored the colonization by recruits and juveniles to coral heads within the eight quadrats over the next month. If a higher proportion of previously-occupied than previously-empty coral heads received recruits, then the hypothesis that larvae exhibited preferences based on locational cues or on aspects of certain coral heads, independent of conspecific presence, would be supported.

Concurrently, I monitored larval settlement to 44 occupied and 154 empty coral heads on patch reef 23, but did not remove groups of juveniles at this site. If a higher proportion of occupied coral heads on reef 23 received recruits than previously-occupied coral heads on the other two patch reefs, this would suggest that conspecific presence positively affected settlement rates.

*Predictions 1 - 3: settlement on an experimental coral grid*

To investigate the effects of juvenile group size, coral species and coral head size on larval settlement, I conducted a factorial experiment using an isolated grid of coral heads adjacent to Sampan Channel (Fig. 2.1). The grid consisted of 60 coral heads on a uniform sandy bottom in 3-4 meters of water. I arranged coral heads in 5 rows of 12, so that each coral was separated by 10 metres from

adjacent corals. The 10 metre distance exceeded the maximum water visibility during the study and was greater than the mean distance between occupied coral heads on patch reefs ( $\bar{X} \pm \text{sem}$ :  $4.6 \pm 0.3$  m,  $n=39$ ), reducing the possibility of migration of fish between coral heads. The grid was oriented so that its long axis was parallel to the shoreline (NW to SE, see Fig. 2.1). Each coral head rested on coral rubble and was supported by wooden stakes.

The factorial treatments were: two levels of coral species (*Porites compressa* and *Montipora verrucosa*), two levels of coral size (small:  $\bar{X} \pm \text{se}$ :  $24.0 \pm 3.5$  cm dia.; large:  $33.0 \pm 3.5$  cm dia., covering the range of coral head sizes on the study reefs), and three levels of juvenile group size (empty corals, single fish and groups of from 3 to 10 juveniles: mean = 4.5 fish/ group). I employed a randomized-block design by randomly assigning each of the 12 treatment combinations to one of the 12 coral heads in each of the five rows. Every one to three days during March to June and August to October, 1989, and less frequently during July, 1989, I counted all recruits on each coral head and removed them using Quinaldine and handnets. I released all removed recruits on Coconut Island reef and nearby reefs (see Fig. 2.1). This protocol allowed more accurate estimates of settlement rates to be made than censusing less often without removing recruits

(Booth 1990: Chapter 1). I examined my results using a 3-way Analysis of Covariance (ANCOVA) with coral rugosity as the covariate (Sokal and Rohlf 1981). This enabled me to consider interactions between factors, and evaluate the possible effects of coral rugosity on larval settlement.

*Predictions 1 and 3: larval settlement preferences- binary choice experiments: Field experiment:* To investigate larval settlement preferences, I established isolated pairs of coral heads adjacent to the coral grid in Sampan Channel (Fig. 2.1). Coral heads within pairs were 2 metres apart, to increase the likelihood that incoming larvae would be offered a simultaneous choice of two settlement sites. Adjacent pairs were separated by 10 metres of sandy substrate, and no coral head was closer than 100 metres to a natural reef. I monitored larval settlement rates to pairs of coral heads supporting the following three treatment comparisons: (1) coral size: small (19 to 25 cm dia.) vs. large (28 to 36 cm dia.) *P. compressa* corals; (2) coral species: *M. verrucosa* vs. *P. compressa* coral species; (3) conspecific presence: empty *P. compressa* v. *P. compressa* supporting 4 to 6 conspecific juveniles. I counted and removed recruits from these corals on a daily basis for 1-3 weeks. Within a coral pair, higher settlement on one treatment than the other would support the hypothesis that larvae settle preferentially on the former treatment. Preliminary trials determined that

recruit migration between corals was minimal, and that settlement rates to these corals were similar to those on the adjacent Sampan grid coral heads. Because I expected average settlement to coral pairs in the binary choice experiment to differ greatly between days, I scored settlement to one coral relative to the other in a pair each day as "greater than, less than, or equal to", and did not consider absolute differences in numbers of recruits. I used these scores as replicates in a Wilcoxon's Signed Ranks Test (Sokal and Rohlf 1981) for each of the three treatment comparisons.

*Laboratory experiment:* To test the hypothesis that larvae use visual cues in settlement, I performed an experiment using a outdoor fiberglass aquarium (1.5m length x 1.0m width x 0.8m depth). The tank contained two treatment compartments and a transparent cylinder of plexiglass 8cm in diameter which extended for the length of the aquarium (Fig. 2.2). Each treatment compartment was 40cm diameter and 20cm high, and was surrounded by clear plexiglass. I sealed and submerged the plexiglass cylinder which contained a newly settled *D. albisella* (the "test fish") so that the cylinder was suspended immediately above both treatment compartments, thus isolating the test fish from chemical cues outside the cylinder. The test fish could therefore swim the length of the large aquarium and pass above both treatments.

I divided the tank into five sections: two "treatment" sections" a "middle" section and two "end" sections (Fig. 2.2). If the test fish was within the middle section or in either end section, I decided that it was exhibiting no preference for either treatment. At the beginning of each trial, the test fish was in the center of the cylinder, and I observed its location every 2 minutes for 20 minutes. After 20 minutes, I switched the two treatments and observed the test fish for an additional 20 minutes, to control for possible preferences by the test fish for either of the aquarium ends. If the test fish was not exhibiting preferences for any of the tank sections, the proportion of the 40 observation times that the fish occurred in that section would be equal to the length of that section, expressed as a proportion of the total tank length. If the test fish spent significantly more of the 40 observation times in any section (G-test,  $p < .05$ ), I concluded that the fish was exhibiting a preference for that section.

I conducted five trials, each using a new test fish, for each of five treatment pairs. Four of the treatment pairs compared a group of 4 conspecific juveniles on a small coral head with (1) an empty coral head of similar size, (2) a single conspecific on a coral head, (3) a group of 4 conspecific recruits on a coral head, or (4) a group

of 4 confamilial fish (*Plectroglyphidodon johnstonianus*) on a coral head. I expected the conspecific juvenile group to be preferred in each comparison. The fifth comparison paired an empty treatment compartment with one containing an empty coral head. I expected that the compartment containing the coral head to be preferred. All coral heads used were *P. compressa* of 20cm diameter.

*Prediction 4: comparison of patterns of settlement among sites:* I monitored the rates of larval settlement at five sites in and around Kaneohe Bay between April 1 and October 15, 1989, to determine patterns of settlement among reef sites in time and space. Two sites were natural patch reefs within Kaneohe Bay (Reefs 11 and 23: Fig. 2.1), two were open reef flat sites outside the Bay (Kaaawa, 5km to the north west, and Waimanalo, 10km to the south east), and the fifth site was the coral grid near Sampan Channel (Fig. 2.1). Within Kaneohe Bay at reef 23, I conducted 25 searches for new recruits on the 39 numbered and 159 other coral heads mentioned previously at roughly 5-day intervals, with no sampling from late June through July. For each of the 39 numbered coral heads, I summed the number of new recruits found at each census time to calculate total summer settlement to each coral head. Patch reef 11 was located directly inshore and 300 metres from the Sampan coral grid. I surveyed 30 numbered coral heads around its perimeter for the presence of recruits on

7 occasions over the summer. At each of the two sites outside Kaneohe Bay (Fig. 2.1), I surveyed 10 numbered coral heads for the presence of recruits on seven occasions during the summer. I monitored larval settlement to the Sampan coral grid (Fig. 2.1) by removing recruits from the 60 coral heads on each of 60 census days at intervals of from 1 to 3 days, using the methods described previously.

*Prediction 5: fate of a settlement pulse:* My regular censusing of patch reef 23 during 1989 included length estimates for all juvenile *D. albisella*, which I grouped into 5 length classes (10-15mm, 15-20mm, 20-30mm, 30-40mm, and 40-60mm). I was then able to develop frequency curves for each size class over the season, and to compare settlement rate over the same period (as described previously). My aim was to identify whether a pulse of settlement had occurred, and to estimate the expected time of appearance of this discrete cohort in larger size classes. To do this, I used data that I had collected previously on size-specific growth rates of juveniles (*D. Booth*, unpubl. manuscript). If no abundant cohort appeared when expected on the basis of estimated growth rates for recruits, then post-settlement mortality was most likely dampening the settlement pulse.

## Results

*Predictions 1 - 3: factors affecting larval settlement:* I

found very few recruits or juveniles in the top 2-3 meters of patch reefs in Kaneohe Bay, an area of dense, continuous cover of *P. compressa*. Over 90% of recruits in both years on reef 23 settled on 39 of a total of 198 coral heads at depths of between 4 and 12 metres. Summer settlement per coral head was significantly related to the number of conspecifics already occupying the head in 1988 and 1989, supporting Prediction 1 (Tab. 2.1a, Fig. 2.3). In contrast, Prediction 2 was not supported, because there was no significant relationship between settlement and the other habitat variables (Table 2.1a). There were significant simple correlations in 1989 between larval settlement and coral rugosity and between the number of resident conspecifics and coral rugosity (Table 2.1b), although the lack of such a correlation in 1988 suggests that these patterns may not have been causal. However, such collinearity between habitat variables complicates the interpretation of multiple regression results for 1989 (Sokal and Rohlf 1981).

There was no evidence from these analyses that certain of the 39 numbered coral heads both attracted more settling larvae and supported large juvenile groups, because there was no significant correlation between settlement in 1988 and 1989 to individual coral heads ( $r=-.007$ ,  $p>.05$ ,  $n=39$ ), although there was a significant correlation between juvenile group size on corals in the successive years



( $r=.326$ ,  $p=.046$ ,  $n=39$ ).

These results are consistent with the hypothesis that conspecific juvenile presence is the main factor influencing larval settlement patterns at the scale of a small patch reef.

*Prediction 3: relative importance of conspecifics and habitat variables to settlement:* The experiment was designed to determine whether coral heads that harboured resident fish were attractive to settling larvae, independent of the presence of the residents. If so, larvae should continue to settle in higher numbers on these corals compared to empty corals, when the residents were removed. Only 14% of the 482 coral heads within the eight 100 m<sup>2</sup> quadrats established on two natural patch reefs initially supported resident fish (Table 2.2). After I removed juveniles, immigration of other juveniles from surrounding areas into quadrats over the following month was negligible (6 juveniles total), and colonization was almost entirely by new recruits (74 recruits total). Because the number of colonized coral heads was low in some quadrats, I pooled data for all four quadrats on each of the two patch reefs before analysis. Previously-occupied coral heads received significantly more recruits than expected by chance in quadrats on both reefs (Table 2.2; G-test,  $p<.05$ ). Therefore, aspects of certain coral heads

appear to have attracted larvae, independent of conspecific juvenile presence.

However, while 34% of previously-occupied corals were recolonized in quadrats on the two patch reefs where I removed juveniles, a significantly higher proportion (84%) of occupied coral heads on patch reef 23 received recruits during the same period (G-test,  $p < .05$ ). This may have been partly due to higher overall settlement rates on reef 23 (52 recruits to 198 corals) compared to Reefs 21 and 22 (74 recruits to 482 corals, G-test,  $p < .05$ ). However, the presence of conspecifics appears to have enhanced larval settlement more than other habitat factors, supporting Prediction 3.

*Predictions 1 - 3: settlement on the experimental coral grid:* I calculated larval settlement (as the total number of recruits removed) on each of the 60 coral heads over two periods (May 15 to June 4 and September 15 to 22, 1989). Outside those two periods, movements of the larger conspecific juveniles used in the fish density treatments precluded multifactorial analysis. Three-way analyses of covariance of data from the two sampling periods showed that conspecific group size significantly affected larval settlement, again supporting Prediction 1 (Table 2.3). Group and single conspecific density treatments attracted more recruits than empty coral heads at both times (Fig. 4, SNK multiple range test,  $p < .05$ ). For the two sampling

periods, no interactions between the main factors were significant, and in the September period only, coral head size significantly affected larval settlement rate, with large corals receiving more recruits than small corals (Table 2.3). Only group size significantly affected settlement rate in both periods, supporting Prediction 3.

Although coral rugosity was higher for *P. compressa* (mean $\pm$ se,n: 3.3  $\pm$ .13, 30) than for *M. verrucosa* (mean $\pm$ se,n: 2.6 $\pm$ .13, 30), t-test,  $p < .05$ ), rugosity did not appear to affect larval settlement (Table 2.3).

*Predictions 1 - 3: binary settlement choice experiments:*

*Field experiment:* Settlement to coral heads with conspecifics was higher than to empty coral heads (Table 2.4), supporting Predictions 1 and 3. Settlement was also higher on *P. compressa* than on *M. verrucosa* corals (supporting Prediction 2b), and no difference in settlement between small and large corals was evident (Wilcoxon Sign Ranks Tests, Table 2.4). Therefore, it appears that larvae exhibited preferences for coral heads which supported conspecifics compared to empty coral heads, and apparently distinguished between coral species.

*Laboratory experiment:* Test fish exhibited preferences for large groups of conspecifics over single fish, juveniles over recruits, conspecifics over heterospecifics, and occupied over empty coral heads (G-tests,  $p < .05$ , Fig. 2.5a-

d), supporting Predictions 1 and 3. However, test fish showed no preferences between empty coral heads and empty treatments (G-test,  $p > .05$ , Fig. 2.5e). Preference for particular ends of the aquarium were not exhibited by test fish, although there was some variation in the way test fish partitioned time between treatments (Fig. 2.5a-e).

*Prediction 4: seasonal settlement patterns between sites:*

On the Sampan Channel coral grid, I counted and removed 11,120 recruits during the summer of 1989. Two major settlement periods occurred during this period: one from mid-May until early June, and a second from mid-August until mid-September (Fig. 2.6a). Settlement was negligible during the previous winter. After the second pulse, settlement dropped dramatically and was negligible when monitoring ceased in mid-October. The two settlement pulses were not correlated with lunar phase (Fig. 2.6a; c.f., Groll 1984).

Elsewhere in Kaneohe Bay, larval settlement rates to reef 23 (Fig. 2.6b) and reef 11 (Fig. 2.6c) showed patterns similar to that at the Sampan coral grid (Spearman Rank Correlation with Sampan grid:  $r = .75$ ,  $p < .01$ , for reef 23;  $r = .96$ ,  $p < .01$ , for reef 11). At Kaaawa, 5km north of Kaneohe Bay, settlement showed the same temporal pattern as in the Sampan grid (Fig. 2.6c, Spearman Rank Correlation:  $r = .97$ ,  $p < .01$ ), but at Waimanalo, 15km south of Kaneohe Bay,

settlement periodicity was only weakly correlated with that at Sampan grid (Fig. 2.6c; Spearman Rank Correlation:  $r=.51$ ,  $p>.05$ ). Overall, these data indicate that settlement was synchronous among the five sites, supporting Prediction 4.

*Prediction 5: fate of a settlement pulse:* I recorded two strong pulses of larval settlement on natural patch reef 23 in 1989 (Fig. 2.6b). For the mid-May settlement peak, using data on growth rates of tagged fish (Chapter 3), I estimated that peaks of abundance for larger size classes should be evident around June 1 (15-20mm size class), June 29 (20-30mm size class), August 7 (30-40mm class), and October 10 (40-60mm class). While the 15-20mm size class peaked in abundance near to the expected time (Fig. 2.7a), no increases in the abundance of larger size classes occurred at the expected times (Fig. 2.7b). That is, there was no evidence that the strong recruit pulse in May survived through the summer. Therefore, Prediction 5 was not supported.

However, the large pulse of recruits in late August was reflected in peaks in the 15-20mm size class (early September), and the 20-30mm size class (late September, Fig. 2.7a), so may have persisted as a pulse of larger juveniles. Unfortunately, sampling ceased in mid-October, so the movement of this cohort through larger size classes

was not recorded.

### Discussion

#### *Larval settlement patterns: adaptive habitat selection?*

The presence of conspecifics appears to be the major cue for settlement in *D. albisella*, accounting for 37% of the variation in settlement to a natural patch reef in 1988 and 57% in 1989. This pattern is consistent with results of experiments on *D. aruanus* on the Great Barrier Reef (Sweatman 1983, 1985a,b). However, in contrast to other species in the genus, *D. albisella* juveniles and recruits are spatially isolated from and thus not directly influenced by the presence of adults or confamilials (c.f., Sweatman 1983, 1985a, Jones 1987). The enhancement of settlement by previously seeded conspecifics in the multifactorial coral-grid experiment corroborated results from the natural population on a patch reef, although experimental groups of conspecifics did not, on average, receive higher settlement than corals seeded with single fish.

Larger coral heads received higher settlement than smaller heads in one factorial experiment, but not in the other. This may be due to increased shelter for recruits in larger corals, and consequent lower predation risk (e.g., Hixon 1991), or to higher likelihood of detection of

larger corals by larvae.

The juvenile-removal experiment on two natural patch reefs indicated that certain coral heads were more likely than others to receive recruits, regardless of the presence of juveniles. This result may be due to intrinsic characteristics of those coral heads or to their location on the reef. For example, four of the coral heads that originally supported juvenile groups and later attracted larvae after being denuded, protruded out of the reef matrix to a greater extent than most other coral heads.

Although these and previous field data (e.g., Sweatman 1983, 1985a,b, Jones 1987) are consistent with the hypothesis that larvae exhibit settlement preferences towards conspecific groups, such results could also be explained by various alternative hypotheses:

- 1) Local water current regimes direct larvae to particular coral heads. Larger groups of juvenile group are found on these corals as a consequence.

- 2) Certain coral heads are simply more conspicuous to larvae, perhaps because they support conspicuous fish. A combination of larval sensory constraints and a tendency of larvae to settle on the first coral detected would result in higher larval settlement to corals with fish if such coral heads were therefore more conspicuous.

- 3) Settlement may be equal on all coral heads, but mortality of larvae soon after they settle may selectively

remove larvae from previously-empty coral heads.

4) Soon after settlement, new recruits may migrate from empty coral heads to those supporting juvenile groups. However, monitoring of diel settlement and recruit tagging studies (Booth 1990: Chapter 1) suggest that this is unlikely.

5) Certain coral heads *per se* may be actively preferred by incoming larvae on natural reef for other reasons (e.g., as a superior shelter site or due to a high local density of planktonic food). Juvenile groups may be a consequence of this preference.

The first four alternative hypotheses do not invoke larval preferences, while the fifth involves larval preferences for certain coral heads, and is partly consistent with the results of my patch reef recolonization experiment. Therefore, on the basis of multifactorial coral-grid experiments and censuses of natural patch reefs alone, it was not possible to conclude that larvae settle preferentially with larger groups of conspecifics. Such a conclusion required verification by binary choice experiments.

To demonstrate actual settlement preferences by larvae, it is necessary to offer larvae a direct choice of settlement sites. The binary choice experiments that I conducted represent the simplest habitat choice design



possible, and are somewhat analogous to "Y-maze" laboratory experiments. My field binary choice trials confirmed that larvae preferred coral heads supporting conspecific groups over empty corals, and also indicated a preference for *P. compressa* over *M. verrucosa* corals. The latter result is puzzling, given no evidence of higher settlement to *P. compressa* coral heads on a natural patch reef, and the scarcity of recruits on *P. compressa* in shallow water on this reef. The higher rugosity of isolated *P. compressa* coral heads used in binary choice experiments may, by providing increased shelter, partly explain higher settlement to this species of coral (see e.g., Hixon 1991), although rugosity did not influence larval settlement on the natural patch reef (Table 2.1a) or the coral grid (Table 2.3).

Larval preferences mediated through visual cues, as documented in my aquarium experiment, complement the experiments of Katzir (1981), who demonstrated that larger juvenile *D. aruanus* were visually attracted to conspecifics in preference to congeners. He argued that these visual cues functioned in species recognition, and my findings that recruits preferred to associate with conspecific over confamilial juveniles are consistent with this conclusion. The utility of visual cues for settlement by larval *D. albisella* is unclear, because most larvae settle at night (Booth 1990: Chapter 1). Chemical cues are therefore

likely to represent an important proximate mechanism of settlement in this species. Sweatman (1988) reported results of a preliminary field experiment which suggested that *Dascyllus* larvae are attracted to groups of conspecifics through olfactory cues. It is possible, however, that ambient light levels at night, especially in moonlight, may be high enough for vision to be used by larvae as at least a supplementary mechanism with which to detect settlement sites (e.g., McFarland and Munz 1976). Visual cues may also help recruits remain in groups after settlement, as suggested for group cohesion in other fishes (e.g., Shaw 1978) and toad tadpoles (O'Hara and Blaustein 1982). Some larvae of marine invertebrates evaluate available substrates prior to settlement (e.g., barnacles: Crisp 1984; gastropods: McGee and Targett 1989). The mechanisms for such habitat selection are typically complex and may involve a combination of visual, tactile and chemical cues (Crisp 1974, 1984, Hadfield 1986). Settlement cues for fish larvae may therefore not be restricted to visual or chemical stimuli.

Habitat selection in animals is often assumed to have an adaptive basis. *Dascyllus* larvae may join large groups to enhance survivorship or the probability of obtaining mates (Sweatman 1985b, Jones 1987, D. Booth, unpubl. manuscript). For *D. albisella*, the potential for increased survivorship in large groups may account for such larval

settlement preferences, but any direct mating advantage is unlikely because the groups are composed strictly of immature conspecifics.

It is also possible that the presence of juveniles is an accurate predictor of a suitable habitat for settlement in terms of adequate food, shelter or a lack of predators. In this scenario, larger groups of juveniles may either indicate a superior settlement site or act as a "supernormal sign stimulus" to larvae (sensu Tinbergen 1951). However, it is important to consider costs to larvae that settle with large groups. A significant cost that has been identified for *Dascyllus* is that of reduced growth of fish in large groups (Jones 1987, Booth, Chapter 3). This reduction in growth is probably the result of interference or exploitation competition for planktonic food (e.g., Coates 1980, Forrester pers. comm). Larvae join groups as the lowest members of the social dominance hierarchy, and so suffer the greatest costs in terms of reduced growth in larger groups (Booth, Chapter 3). Elsewhere, I examine the demographic consequences of the trade-off between the increased-survivorship benefit and the decreased-growth cost of group living in this species (Chapter 4).

#### *Seasonal patterns of settlement among sites*

The onset, termination, and timing of pulses of

settlement of *D. albisella* larvae during 1989 were synchronous among five sites along 25km of the west coast of Oahu, Hawaii. The mechanism for this synchronization may have been a combination of the occurrence of peak spawning periods for this species in March-April and in July (Stevenson 1963), and the 4 week duration of the planktonic larval stage (Wellington and Victor 1989). Watson and Leis (1974) recorded peaks of larval pomacentrid abundance in Sampan Channel in May and early August, corresponding with peaks found in my study. The daily settlement estimates for the Sampan coral grid suggest a lack of any clear lunar periodicity in larval settlement during 1989. This contrasts with the results of Groll (1984), who reported strong pulses of settlement of *D. albisella* larvae in Kaneohe Bay around the time of full moon. Larval settlement occurs predominantly at night (Booth 1990: Chapter 1), and larvae may therefore avoid diurnal peaks in predator activity (e.g., Johannes 1978).

#### *Recruitment limitation in D. albisella?*

A pulse of larval settlement on a natural patch reef did not increase the subsequent abundance of larger size classes, and so does not offer support to the recruitment limitation hypothesis (Doherty 1981). Because the abundance of new settlers in the pulse was high relative to the abundance of juveniles on the natural patch reef, the settlement pulse should have been clearly visible as a

strong cohort of larger juveniles. Its absence indicates that mortality occurring subsequent to settlement, probably due to predation, may regulate juvenile densities (e.g., Holm 1990, Hixon 1991). Indeed, predation on new recruits on my study reefs by piscivorous fish and invertebrates is common (personal observation, Groll 1984).

Alternatively, variation in growth rate between members of a recruit cohort may serve to dampen a strong pulse of settlement as the cohort moves into larger size classes. Such "growth depensation", a temporal increase in the variance of a size frequency distribution due to differences in individual growth rates (Koebele 1985), may result in size overlap between members of adjacent cohorts which originally were part of discrete settlement pulses. However, it seems unlikely that the strength of the May 1989 settlement pulse on the natural patch reef would have been dampened significantly by growth depensation alone.

For *D. albisella*, then, fluctuations in the abundance of larger juveniles in 1989 were poor indicators of the May 1989 settlement pulse. If this is generally the case, then methods of otolith reconstruction of settlement patterns using samples of larger juveniles (e.g., Victor 1982, 1983, 1986, Pitcher 1988b) would be untenable for this species, and indeed any species in which recruitment was not limiting (but see Holm 1990). The most appropriate species

for this post-hoc method of settlement monitoring would be characterized by both discrete bouts of settlement and recruitment limitation of the juveniles collected for otolith analysis.

The results of my study concur with those of Jones (1987), who showed that juvenile population dynamics in the damselfish *Pomacentrus amboinensis* probably had more effect on the numbers of juveniles maturing than did settlement variation.

For *D. albisella* juvenile populations, the sizes of conspecific groups on natural patch reefs may potentially affect recruitment into the adult population through effects on larval settlement (this chapter) and on growth and survival of juveniles (Chapter 3). Larval settlement preferences for conspecific groups, by increasing the average size of juvenile groups, could therefore influence the number of juveniles maturing on a reef (Chapter 4) and potentially adult density as well.

**Table 2.1a:** Multiple regression of factors affecting summer settlement of larval *Dascyllus albisella* on patch reef 23 in Kaneohe Bay, Hawaii, in 1988 and 1989. "Coeff." is the coefficient of the variable, and "R<sup>2</sup> partial" is the partial regression coefficient. All data were Z-transformed prior to analysis to facilitate comparison of coefficients. \* indicates significance at p<.05 by F-test, n=39.

Independent variable	Relationship to settlement			
	1988		1989	
	Coeff.	R <sup>2</sup> partial	Coeff.	R <sup>2</sup> partial
Group size	.624	.198*	.741	.227*
Coral rugosity	-.113	.009	.078	.003
Coral species	.094	.005	.039	.001
Coral size	.052	.003	.047	.002
Depth	.217	.033	-.102	.007
Distance to nearest neighbour	.074	.005	.084	.005
Location on reef	-.194	.029	-.052	.002
Overall		.522*		.674*

**Table 2.1b:** Simple correlation coefficients between pairs of variables used in a multiple regression model for larval settlement on a natural patch reef. Upper right side: 1988; lower left side: 1989; \* indicates correlation significant at  $p < .05$  for  $n=39$ . Correlations between physical variables are only reported once (for 1988), since they did not change between years.

	# of recs	# of juvs	coral rug.	coral spp.	coral size	water depth	nbr dist.	loca tion
# of recs	-.01	.61*	.02	.41*	.003	.29	-.003	-.16
# of juvs	.76*	.33*	.41	.38*	.04	-.07	-.16	-.08
coral rug	.54*	.58*	-	.14	.012	-.25	-.17	-.15
coral spec	-.04	-.16	-	-	.21	.41*	.18	-.20
coral size	.08	-.02	-	-	-	.07	-.11	-.03
water depth	-.11	-.14	-	-	-	-	.36*	-.32
neighbour dist	.12	.06	-	-	-	-	-	-.02
loca- tion	-.04	-.04	-	-	-	-	-	-



**Table 2.2:** Numbers of previously occupied and previously empty coral heads colonized by recruits in eight quadrats on Reefs 21 and 22, where all fish were removed, and Reef 23, where no fish were removed. \* indicates significance at  $p < .05$  (G-test: superscripts show comparisons tested, with expected values generated using numbers of corals available).

-----						
<b>Treatment:</b>						
<b>Quadrat location</b>	<b># corals</b>		<b># recolonized</b>		<b>G-test</b>	
	-----		-----			
	<b>previously empty occupied</b>		<b>previously empty occupied</b>			
-----						
All fish removed: Reef 21	North	27	6	3	3	
	East	37	9	3	3	
	South	33	10	4	4	
	West	40	16	2	6	
	Combined	137	42	12 <sup>a</sup>	16 <sup>b</sup>	18.1 <sup>ab*</sup>
-----						
All fish removed: Reef 22	North	70	8	1	0	
	East	63	6	3	2	
	South	69	2	0	2	
	West	78	7	3	2	
	Combined	280	23	7 <sup>c</sup>	6 <sup>d</sup>	15.4 <sup>cd*</sup>
-----						
Overall	417	65	19 <sup>f</sup>	22 <sup>g</sup>	42.8 <sup>fg*</sup>	
-----						
No removals: Reef 23		154	44	9 <sup>h</sup>	37 <sup>j</sup>	28.6 <sup>hj*</sup>
-----						
Reefs 21 and 22 vs. Reef 23:						107.5 <sup>gj*</sup>
-----						

**Table 2.3:** Analysis of covariance for coral grid colonization experiment during two periods in 1989. Larval settlement is the dependent variable, and coral rugosity is the covariate. \* indicates effects which are significant at  $\alpha=.05$ ,  $n=5$  per replicate. Data conform to assumptions of normality and homoscedasticity (Bartlett's Test).

(a) **May 15- June 4, 1989:**

Source	Sum Squares	df	Mean Square	F-ratio	
Block	5471	4	1368	3.46	0.015*
Rugosity	333.3	1	333.3	0.84	0.363
Fish Density	2795	2	1397	3.54	0.039*
Coral Species	596.0	1	596.0	1.51	0.226
Coral Size	57.59	1	57.59	0.15	0.704
Species*Size	11.90	1	11.90	0.03	0.863
Species*Density	194.4	2	97.19	0.25	0.783
Size*Density	556.9	2	278.4	0.71	0.500
Species*Size *Density	391.5	2	195.7	0.50	0.613

**Table 2.3 (cont)****(b) September 15-22, 1989:**

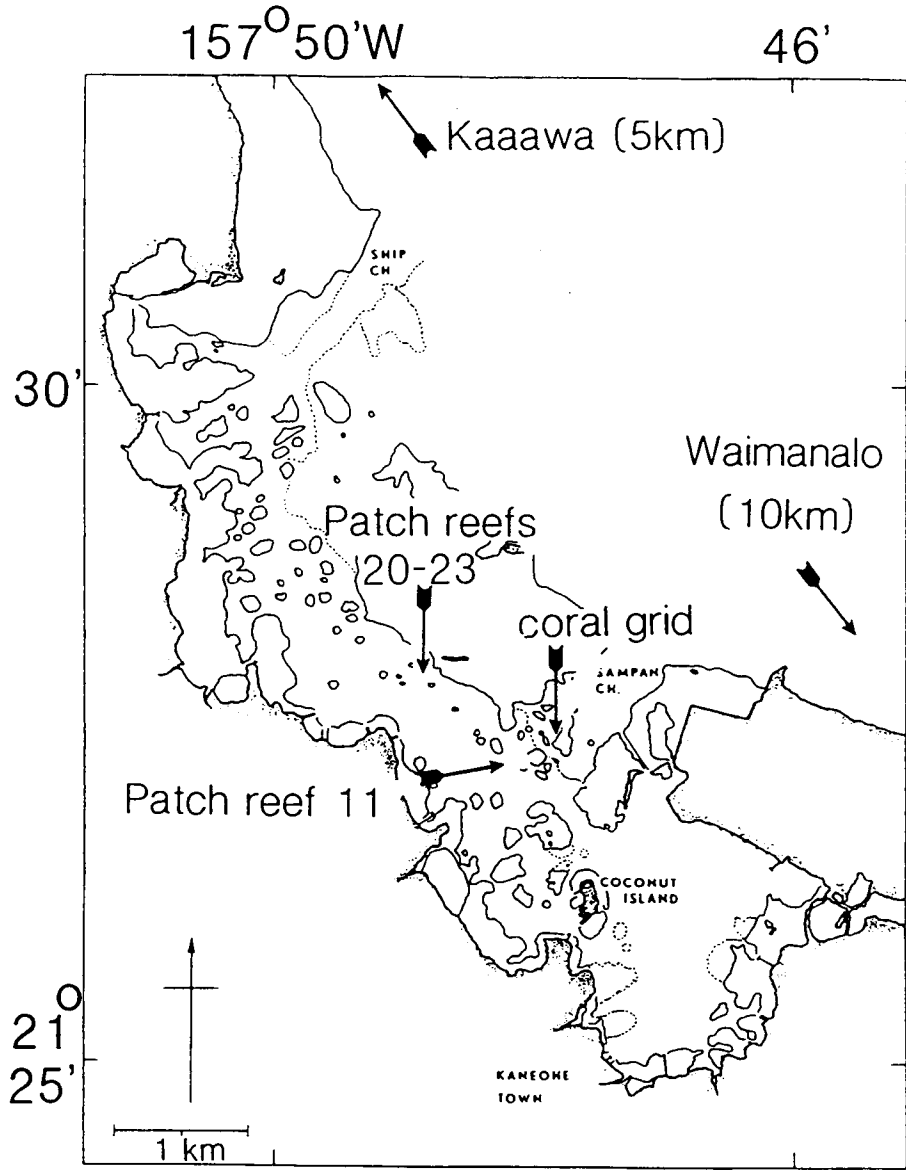
Source	Sum Squares	df	Mean Square	F-ratio	P
Block	898.1	4	224.5	2.42	0.063
Rugosity	75.90	1	75.90	0.82	0.371
Fish Density	1967	2	983.8	10.5	0.0004*
Coral Species	8.270	1	8.270	0.09	0.767
Coral Size	1350	1	1350	14.5	0.0002*
Species*Size	6.299	1	6.299	0.07	0.796
Species*Density	88.92	2	44.46	0.48	0.623
Size*Density	45.68	2	22.84	0.25	0.783
Species*Size *Density	504.6	2	252.3	2.72	0.077

**Table 2.4:** Settlement patterns of larvae during *in situ* binary choice experiments. "A > B", "B > A" and "A = B" denote the frequency of outcomes in which settlement was greater to Treatment A or B, or equal to both, respectively. Treatments indicated by "\*" received significantly more recruits than the treatment with which it was paired (Wilcoxon Sign-ranked test at  $\alpha=.05$ ).

Comparison	Tmt A	Tmt B	Outcome (number of trials)		
			A > B	B > A	A = B
Fish density	Group*	Empty	13	5	4
Coral species	<i>Porites</i> *	<i>Montipora</i>	47	18	8
Coral size	Large	Small	12	10	13

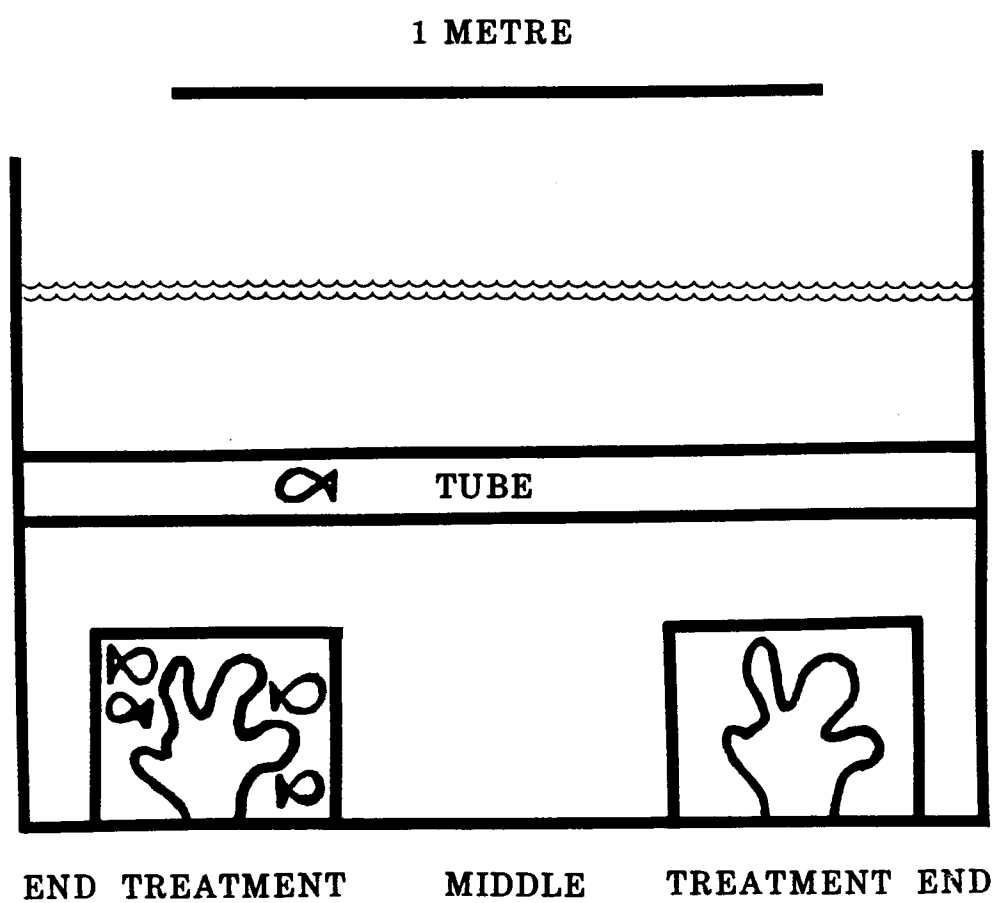
**Figure 2.1:** Study sites in and around Kaneohe Bay, Oahu, Hawaii.

Figure 2.1



**Figure 2.2:** Side view of aquarium used in larval visual choice trials. "Tube" is a transparent plexiglass cylinder, holding the test fish, and "Treatment" indicates the positions of the two transparent plexiglass containers that held treatment fish and corals (see text). "Middle" is the center 45 cm of the tank length, and "end" represents a 7.5cm length at either end of the tank. Fish not drawn to scale.

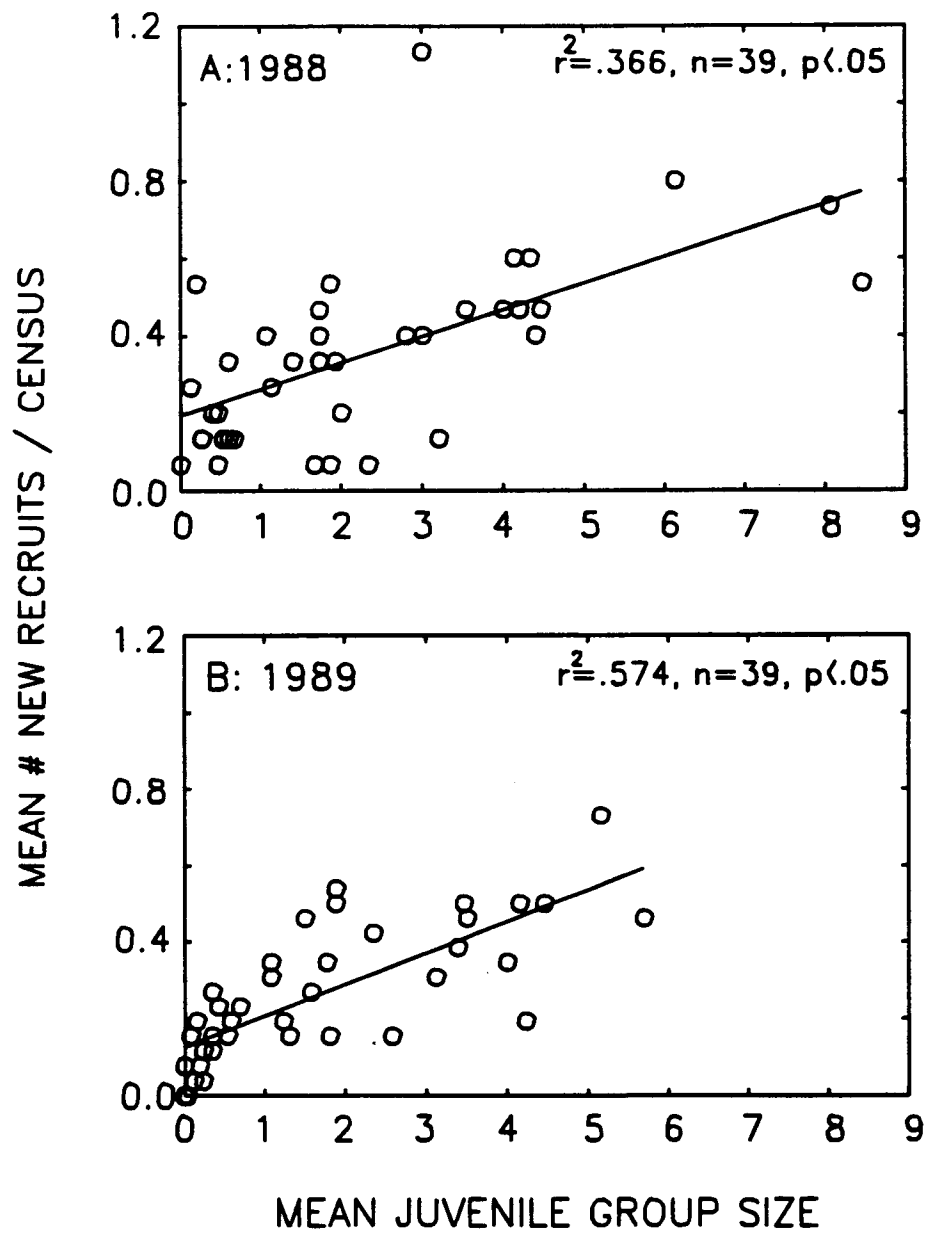
Figure 2.2





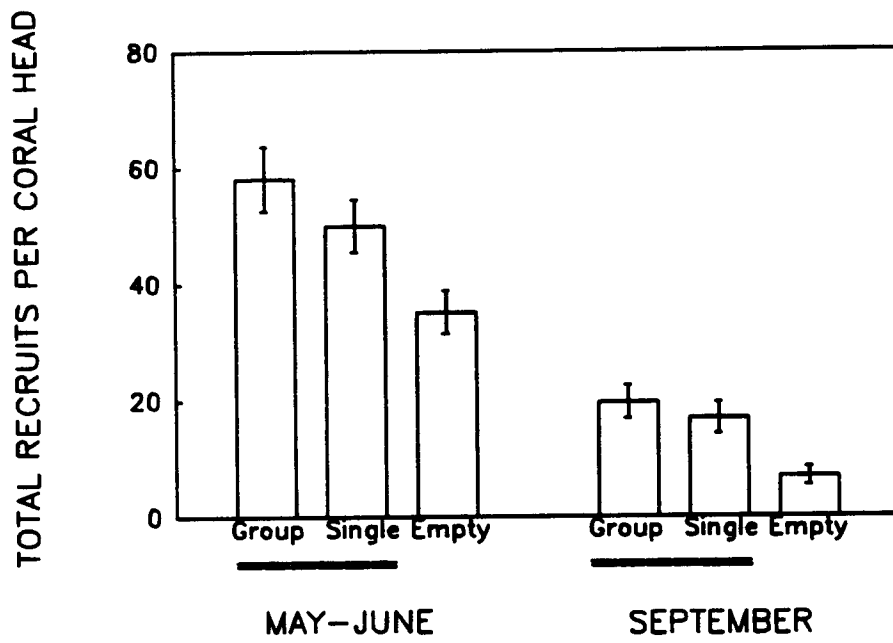
**Figure 2.3:** Relationship between mean settlement of larval *D. albisella* and mean juvenile group size on 39 coral heads on patch reef 23 during the summers of a) 1988, and b) 1989.

Figure 2.3



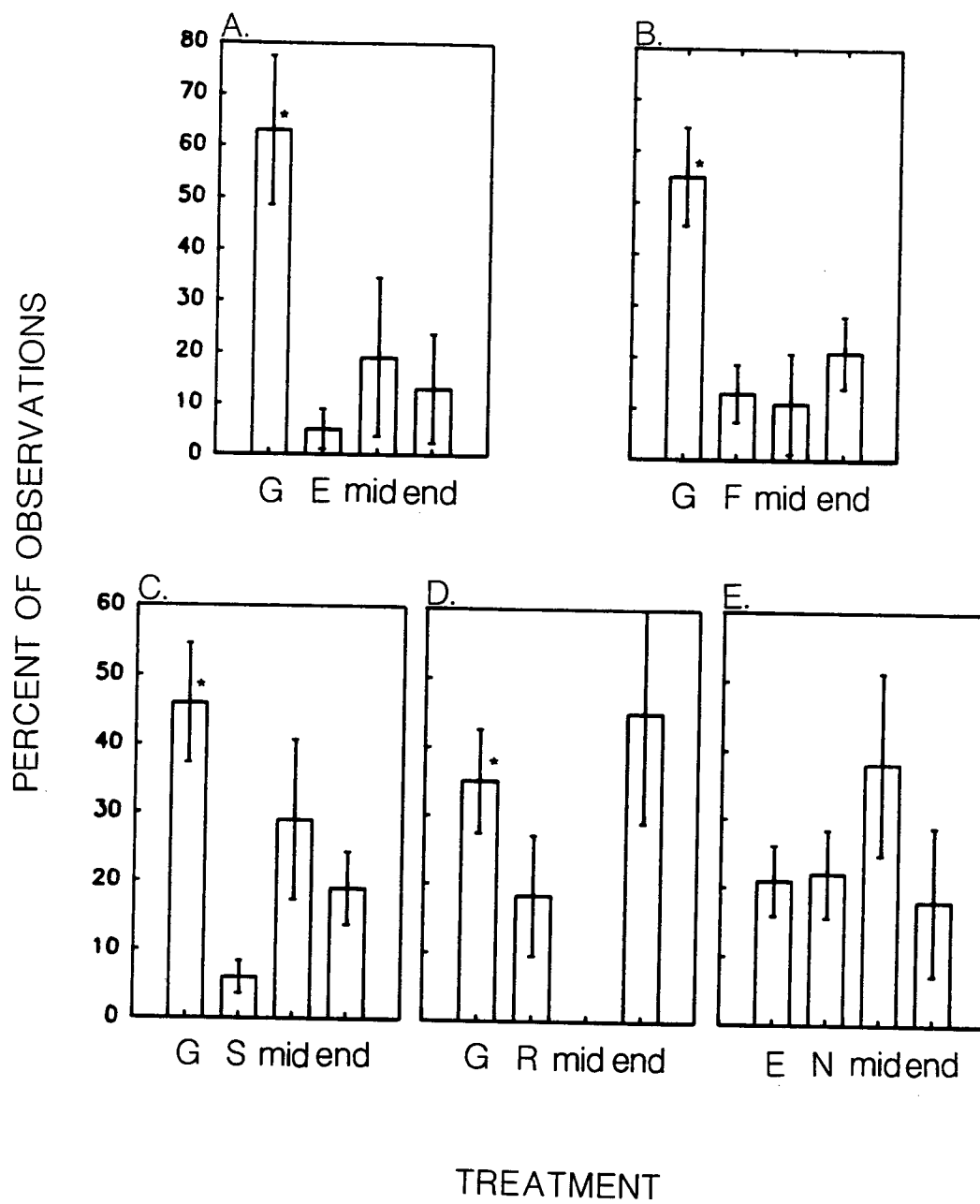
**Figure 2.4:** Relationships between conspecific density and settlement of larval *D. albisella* (measured as total number of recruits in each of 3 fish density treatments) on 60 coral heads in Sampan Channel, Oahu, Hawaii, during May-June, 1989, and September, 1989. Conspecific density treatments for which settlement was not significantly different are linked by horizontal lines (ANCOVA,  $p < .05$  for both 1988 and 1989, see Table 2.3; SNK multiple-range test,  $p < .05$  for both 1988 and 1989). Each bar shows the mean and standard error for that treatment ( $n=5$  for each treatment).

Figure 2.4



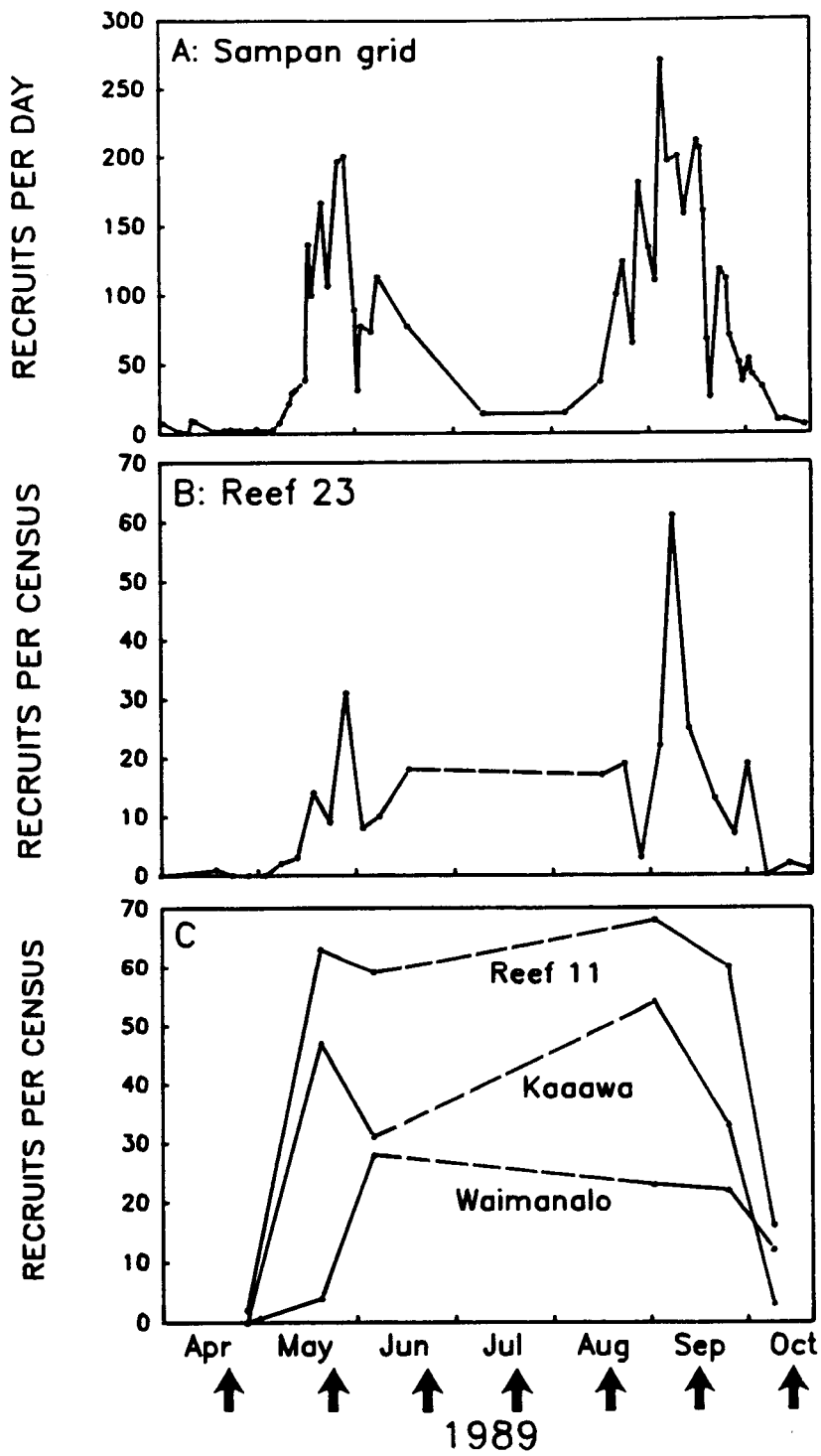
**Figure 2.5:** Mean percent ( $\pm$  s.e.) of 40 observations of 5 test fish near each of two treatments, in the middle section ("mid") and at the ends of a plexiglass tube ("end") during aquarium binary choice experiment (see Fig. 2.2). Treatment codes: G: conspecific juvenile group; E: empty coral head; F: confamilial juvenile group; S: single conspecific juvenile; R: conspecific recruit group; N: empty compartment. Asterisks indicate treatments with a significantly greater percent of observations than expected (see text, G-test,  $p < .05$ ).

Figure 2.5



**Figure 2.6:** Settlement of *D. albisella* larvae to five sites on the windward side of Oahu during 1989: a) Sampan channel, b) Patch reef 23, c) Patch reef 11, Kaaawa, and Waimanalo. Dashed curve represents a sampling hiatus. Full moons indicated by arrows.

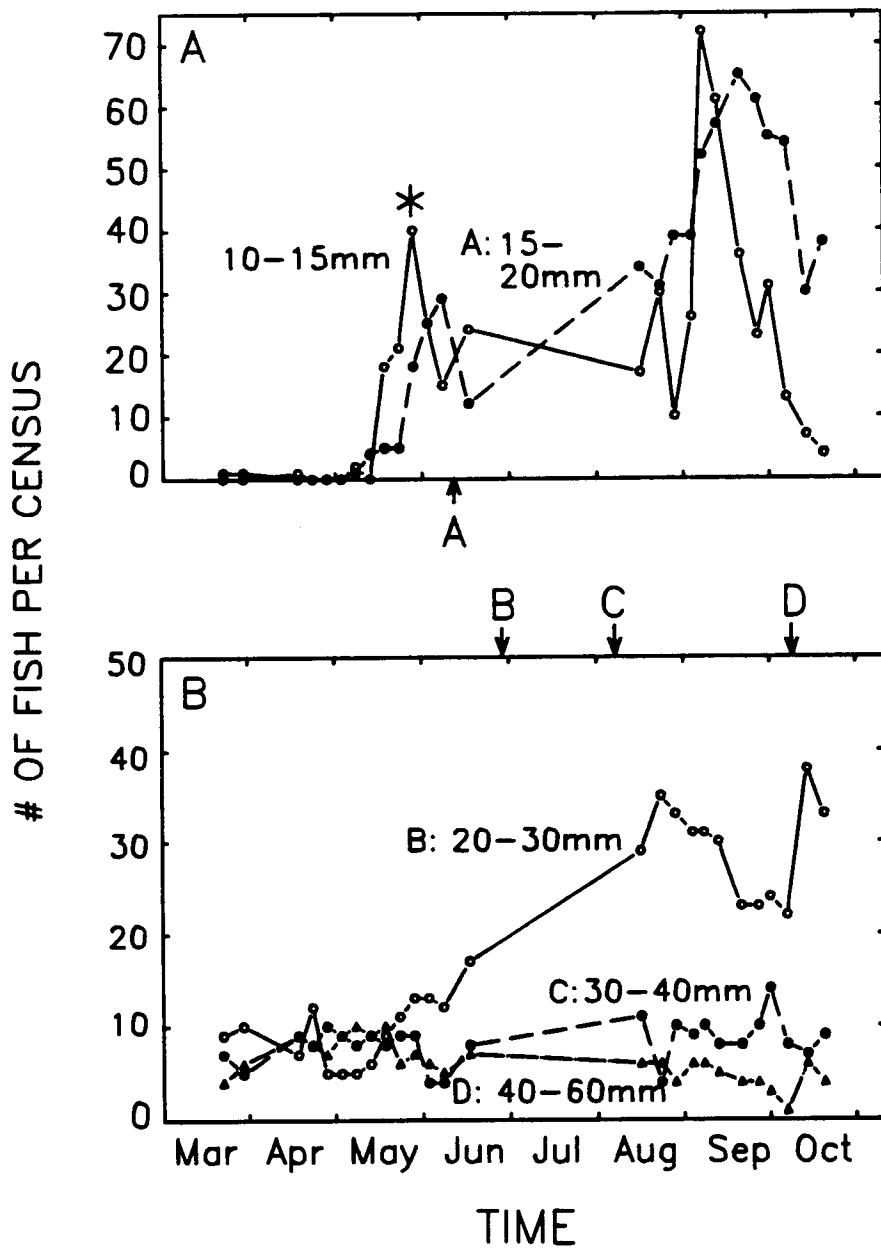
Figure 2.6





**Figure 2.7:** Abundance of juvenile *D. albisella* in each of five size classes censused during summer 1988 on patch reef 23, Kaneohe Bay, Hawaii: (a) 10-15mm (recruit) and 15-20mm size classes; and (b) 20-30mm, 30-40mm and 40-60mm size classes. Data points indicate census times. Arrows indicate the estimated time of entrance of the May recruit pulse (\*) into each subsequent size class, as follows: A: 15-20mm; B: 20-30mm; C: 30-40mm; D: 40-60mm.

Figure 2.7



### Chapter 3

#### **Growth and survivorship of juvenile domino damselfish (*Dascyllus albisella*): costs and benefits of group living**

##### **Abstract**

Costs and benefits to group living in animals may offer insights into the functions of grouping behavior. In 1987 and 1988, I examined the effects of group living on the growth and survival of juveniles of an Hawaiian coral-reef damselfish (*Dascyllus albisella*). In this species, pelagic larvae settle on individual coral heads, joining temporary groups of up to 15 juveniles, in which fish form a dominance hierarchy based on size. Upon reaching maturity, fish leave these groups and enter the nearby adult population. Tagging studies of fish on small coral heads, both on natural patch reefs and in an experimental grid, suggested that growth of individuals was retarded in larger groups and for fish of low social status. However, survival, especially of smaller recruits, was enhanced in larger groups. The frequency of aggressive chases per individual was not related to group size, so probably did not contribute to the lower growth of fish in larger groups. Lower-ranked (smaller) fish within groups were chased more often, which may have contributed to the positive relationship between social status and growth. I

used growth and survival data to estimate the relationship between group size and two parameters that may affect lifetime reproductive success: the time to maturity (a function of growth rate) and the probability of reaching maturity (a function of size-specific growth and survival). The time to maturity increased with group size in both years, suggesting that fish living alone or in small groups would enter the adult population earlier than those in larger groups. However, the probability of reaching maturity increased with group size in 1988 but not in 1987. In other studies conducted in both years, I found that larvae exhibit strong settlement preferences for larger groups of conspecifics. While these preferences would not have enhanced attainment of maturity in both years, they may represent the best strategy in general.

### Introduction

A group of animals can be defined as "any set of organisms... that remain together for a period of time, interacting with one another to a distinctly greater degree than other [individuals]" (Wilson 1975, page 6). Groups may occur through independent attraction of individuals to patchily-distributed resources (e.g. to food or shelter, see Brown and Orians 1970), as a consequence of differential predation, or as a result of a well developed social system (Alexander 1974; Wilson 1975; Brown 1975).

Numerous costs and benefits to group living have been identified. Costs have included competition for food (e.g., Caraco and Wolf 1975) and mates (e.g., Cohen 1975), higher rates of disease transmission (e.g., Hoagland 1979) and increased predation (e.g., Ward and Zahavi 1975). Benefits include increased likelihood of finding food (e.g., Pulliam 1973), or a mate (e.g., Kynard 1978, Gross 1980), decreased risk of predation through enhanced vigilance (e.g., Pulliam 1973) or group protection (e.g., Hamilton 1971), and improved thermoregulation (e.g., Stamp and Bowers 1990).

Recently, a theoretical framework has developed to evaluate the significance of group living on individual fitness. Optimality models have been constructed which consider both the costs and benefits that accrue to an individual as the result of belonging to a particular group (e.g. Pulliam and Caraco 1984; Clark and Mangel 1986). The optimal group size is defined as that at which the net benefit to an individual (benefits minus costs) is maximal. It is predicted that animals will preferentially seek membership in groups that are close to the optimal size (Pulliam and Caraco 1984; but see Clark and Mangel 1986).

The evaluation of costs and benefits becomes complicated when the effects of social dominance hierarchies or kin groups need to be considered (Rodman

1981; Baker et al. 1981; Clifton 1990). For instance, many of the advantages to living in groups may accrue disproportionately to older or larger individuals, leading to an asymmetry of net benefit among individuals within groups (see Clifton 1990, models by Clark and Mangel 1986). An individual joining a group may be initially subordinate to all group members. While such an individual would enjoy higher short-term benefits by living alone, its long-term net benefit may be maximized by joining a large group. If individuals can move freely between groups, and incur no costs (such as greater risk of predation) in doing so, the best decision may be to switch between groups as the individual grows (e.g., primates: Cohen 1969, elephants: Holgate 1967). Therefore, the optimal group size may change temporally for an individual. If costs of switching between groups are high, animals should instead join a group that would maximize long-term net benefit.

Groups found in nature will not necessarily be of "optimal" size. Groups smaller than the predicted optimal size may occur due to low rates of recruitment or immigration into the habitat, or through high rates of mortality or emigration of group members (Cohen 1975). Groups larger than expected may result from high immigration, low mortality, limited availability of habitat, or high costs associated with leaving a "sub-optimal" larger group. Such "overflocking" may, in fact,

represent an evolutionarily stable strategy (Sibley 1983). Optimal group size may also change seasonally and with the life stage of the animal (e.g., Werner and Gilliam 1984). Therefore, group sizes in a population do not always provide reliable information on the costs and benefits of group living.

Many costs and benefits of group living have been identified for fishes. Shaw (1978) estimated that up to 50% of larval and juvenile fishes travel in shoals (*sensu* Pitcher 1986) or live in sedentary groups, and adults of over 25% of teleost species school. Shoals may confer a hydrodynamic advantage to individuals (Abrahams and Colgan 1985), while groups in general may reduce the risk of predation (e.g., Motta 1983; Seghers 1974; Godin and Morgan 1985), enhance prey capture (Barlow 1975; Major 1978), reduce parasite load (Sikkel 1986; Poulin and FitzGerald 1989), or confer a competitive advantage (e.g., Barlow 1974; Robertson et al. 1976; Foster 1985). However, group living may increase competition for food (e.g., Coates 1980) and lead to reduced growth rates (e.g., Jones 1987, 1988). Relatively few studies have evaluated the effects of both costs and benefits for fish to determine the net benefit to group living (but see Barlow 1974; Seghers 1981; Clifton 1990).

My objective in this paper is to evaluate the costs and benefits of group living in the domino damselfish

(*Dascyllus albisella* Gill). Like many species of damselfishes (Pomacentridae), domino damselfish live in groups on branching coral heads (e.g., Stevenson 1963; Sweatman 1985; Allen 1990). Coral heads presumably provide shelter from predators (e.g., Shpigel and Fishelson 1986). Groups of coral reef fishes may be composed of unrelated individuals (e.g., Avise and Shapiro 1986; Booth 1990), so complications due to relatedness in determining individual benefits can be avoided. Since domino damselfish groups are composed strictly of juveniles, the effects of complex mating systems and adult-juvenile interactions can be ignored (c.f., Jones 1987, 1988).

I hypothesized that predation risk would be lower and competition for food would be greater in relatively large groups (fish were found singly or in groups of up to 15). Therefore, I expected that increased survivorship would be a benefit, and decreased growth rate a cost, to group membership. Juveniles in groups form linear, size-based dominance hierarchies (see Results and Coates 1980), so I also hypothesized that fish of higher social rank within a group would enjoy higher growth and survival. Since maturity is size-based in this species (Booth, unpubl. data), growth and survival could directly influence attainment of maturity. I tested the following predictions concerning these costs and benefits of group living:



1. **Migration** between coral heads should be negligible.

2. **Survival:**

(a) Survival of juveniles should increase with conspecific group size.

(b) Survival of juveniles should increase with body size and social rank.

3. **Growth rate:**

(a) Growth of juveniles should be a negative function of group size.

(b) Growth should be a positive function of social status (independent of body size) within a group.

(c) Growth should be affected by physical characteristics of the habitat. In particular, growth will be higher on the upcurrent side of a reef, where planktonic food would be more abundant (e.g., Bray and Geesey 1981; Hamner et al. 1988).

(d) Fish should be involved in more chases (aggressive interactions) in larger groups, and this should contribute to lower growth in larger groups.

(e) Within groups, most chases should be directed by socially-dominant fish towards subordinates, contributing to lower growth for lower-ranked fish within groups.

4. **Maturity:**

(a) A net benefit to living alone would be decreased time to attain mature size, due to faster growth than fish in larger groups.

(b) A net benefit to group living would be an enhanced

probability of reaching maturity in larger groups, due to higher size-specific survivorship.

### Methods

Domino damselfish are endemic to Hawaiian coral reefs (Randall and Allen 1977). I conducted observations and experiments on several natural patch reefs in Kaneohe Bay, Hawaii, (Reefs 20, 21 and 23 of Roy 1970) and on an artificially-constructed coral grid in Sampan Channel (Fig. 3.1). The Sampan coral grid consisted of 60 small (20-38 cm dia.) *Porites compressa* and *Montipora verrucosa* coral heads (the two common coral species on patch reefs, 30 each), arranged in a 5 x 12 array, so that corals were spaced 10 metres apart. This distance is greater than the average distance between occupied coral heads on the natural patch reef ( $\bar{X} \pm se$ :  $4.6 \pm 0.3m$ ,  $n=39$ ) to reduce the likelihood that fish would migrate.

1. *Fish tagging and migration.* I numbered all coral heads on patch reef 23 that supported juvenile *D. albisella*. Fish were captured and anesthetized with Quinaldine (2-methoquinone: Sigma Chem. Co.) and marked with tattoo ink (following Thresher and Gronell 1978), then returned directly to the coral heads. Laboratory trials confirmed that tagging had no noticeable effect on survival or behaviour of fish after at least 24 hours, although some

mortality of recruits (about 5% of tagged fish under 20mm TL) occurred immediately after tagging (Booth, unpubl. data). I monitored migration of fish by noting the coral heads on which each fish was tagged and recaptured.

2. *Survivorship*. I measured survival of individuals up to 70 mm TL (sexual maturity) as their persistence on a coral head, that is, the time elapsing between first tagging of a juvenile and its eventual disappearance. Disappearance was apparently due to mortality, since migration was uncommon for juveniles (see Results) except those approaching 70 mm TL, which eventually left groups to join nearby schooling adults.

*Survival of juveniles on a natural patch reef*: I censused tagged juveniles on patch reef 23 at roughly 5-day intervals during March to October in 1987 and 1988, and at irregular intervals at other times of year. For each tagged fish, I recorded its group size, social rank and body length. The largest fish in a group was assigned a rank of 1, with ranks assigned to other fish based on body size. By using a multiple regression model (SYSTAT multiple regression and diagnostics package) I was able to examine the effects of these variables on persistence.

*Survival of recruits on natural patch reefs*: I conducted two experiments in 1989 to determine the effects of group size on survival of recruits. In Experiment 1, I

transplanted *D. albisella* recruits (10-15mm TL) that had settled the previous evening to the Sampan coral grid, onto coral heads on patch reef 23. I placed one recruit on each of 60 coral heads with 0 to 12 juvenile conspecifics. After 3 hours, 5 recruits were missing and were omitted from further analysis. I located the surviving transplanted recruits by means of a thorough search of these and nearby coral heads, at five-day intervals for 35 days thereafter. During this 35-day period, I recorded no natural settlement on the reef, allowing transplanted recruits to be positively identified. From day 35 onward, natural settlement occurred, so the censuses of transplanted recruits were terminated at that time. I described the relationship between group size and recruit persistence using linear regression analyses (Sokal and Rohlf 1981).

In Experiment 2, conducted on Reefs 20 and 21, I tagged transplanted recruits by clipping the dorsal fin, to distinguish them from naturally-settling recruits, and recorded their body lengths. I manipulated juvenile group sizes and randomly assigned three conspecific density treatments to 60 coral heads. Twenty corals were empty, twenty supported small groups (1-2 fish), and twenty supported large groups (4-6 fish). This manipulation randomized (with respect to the conspecific density treatment) any effects on recruit survival due to coral

head location on the patch reefs. I analysed persistence of transplanted recruits relative to group size and body length in a one-way Analysis of Covariance, with group size (3 levels) included as a fixed factor, and fish length as the covariate (Sokal and Rohlf 1981).

3. *Growth rate.* I measured growth rate as change in total length of tagged fish over a two-week period. It was possible to determine total length more accurately in the field than standard length, and the two measures were highly correlated ( $r=.996$ ,  $n=40$ ,  $p<.05$ , Appendix 4).

*Growth rates on a natural patch reef:* During March to October in 1987 and 1988, and December 1988 to January 1989, I measured growth rates (mm per day) of tagged juveniles on coral heads on patch reef 23. When I recaptured each fish I recorded its group size, social rank and body length. In 1988, I measured the following seven habitat variables that I expected may affect growth rate:

- (1) Location: The location of each tagged coral head on the reef by its compass bearing along the reef's circular perimeter. I assigned a value of "1" to coral heads within the upcurrent quadrant of the reef (north to east, Bathen 1968), a value of "3" to those in the downcurrent quadrant (south to west) and a value of "2" to corals in the remaining two quadrants.
- (2) Coral isolation: The mean distance to the three nearest coral heads.

(3) Day of tagging: The day on which the fish was tagged, measured as the number of days since March 1 in that year.

(4) Coral head size: The maximum width of the coral head multiplied by the width perpendicular to this, to obtain an estimate of coral size.

(5) Coral Species: *P. compressa* or *M. verrucosa* coral heads.

(6) Coral Rugosity: Estimated by a linear visual scale from 0 (no fine branching) to 5 (surface of coral covered in fine branches).

(7) Water Depth: Measured at low tide.

I incorporated these variables into a multiple regression model for both years, with growth rate as the dependent variable.

*Relative effects of group size and social rank on growth rate:* I chose pairs of tagged individuals of similar length ( $\pm 1\text{mm}$ ) from separate groups that I had established on coral heads within the Sampan coral grid, to conduct a series of reciprocal exchanges. The exchanges were to either measure (1) the effects of social rank on growth rate by exchanging fish of different social ranks, keeping group size constant, or (2) the effects of group size on growth rate by exchanging fish of the same social rank between groups of different sizes. Disappearance and migration of individual fish in exchanged pairs precluded these comparisons, so I partitioned growth results into

four treatments:

- (1) fish exchanged to a larger group and occupying a lower rank than before;
- (2) fish exchanged to a smaller group and occupying a higher rank than before;
- (3) fish exchanged to a smaller group, but occupying the same rank as before; and
- (4) controls, where fish were removed and replaced with the same group or a similarly-sized group.

Treatments 1 and 2 tested the simultaneous effects of group size and social rank on growth rate, while Treatment 3 measured the effect of group size on growth rate, independent of social rank.

*Behavioral interactions:* Preliminary observations indicated that aggression within groups was expressed through chases, i.e., one individual accelerated for a short distance toward another, which fled immediately. Chases were easily distinguished from all other observed activities. Over the course of the study, I observed 50 groups of *D. albisella* juveniles, both naturally-occurring and assigned to coral heads on the Sampan coral grid. For 11 of these groups, I also assigned a size-rank to all fish either through recorded lengths of tagged individuals or by visually estimating lengths just prior to the observation period. For each group, I approached to within about 5 metres (depending on water visibility) and waited

motionless on the bottom for 5 minutes. If during this time, group members either approached me or reacted to my presence in any other observable way, I abandoned observation of that group. Otherwise, I observed the group for a further 10 minutes, recording all chases and the size ranks of fish involved. In this way, I was able to determine the relationship between group size, social status, and frequency of aggressive chases.

4. *Attainment of maturity.* I incorporated field data into computer simulation models (BASIC language) that predicted the time to reach maturity and the probability of reaching maturity as a function of group size, as follows. I used the relationship between growth rate, group size and body length (this study) to determine the time to maturity for new recruits in groups of various sizes in 1987 and 1988. The model estimated daily length increments for fish in group sizes of 1 to 10, and calculated the number of days to grow from 14mm (mean length of new recruit) to 70mm TL (size at maturity). I incorporated natural variation in growth rate into the simulation model by randomly assigning new values to regression coefficients for group size and body length in the regression equation that predicted growth rate, on each daily iteration of the model. These assigned values ranged from one standard error below to one standard error above the mean value for each coefficient in the regression equations. In this way, I was able to



follow the estimated growth trajectories for 100 recruits in group sizes from 1 to 10.

I used data on size-specific growth rate and survivorship in another simulation model that estimated the probability that a new recruit would reach mature size, when living alone or in groups of 2 to 10 individuals. I ran 100 simulations for each group size, and incorporated natural variation in growth and survivorship into the model, as described above.

## Results

### 1. Migration:

Of 361 juvenile fish tagged on reef 23 during 1987 and 1988, 216 were recaptured on at least one subsequent occasion, and 199 of these were found on their original coral head (Table 3.1). 16 of the 17 fish that were recaptured on other coral heads (4.8% of all tagged fish), were larger than 30mm (Table 3.1). Therefore, migration between coral heads was minimal, particularly for smaller fish, supporting Prediction 1. There was no tendency for larger groups to either attract or lose an unusually large proportion of migrant fish (Booth, unpubl. data). Also, there was no migration of recruits that were transplanted to coral heads for survivorship experiments.

## 2. Survival:

Persistence of tagged fish on reef 23 varied from 1 to 80 days. I considered the relationship between persistence and group size, fish social rank and body length for 5 length classes: 10-15mm (recruits), 16-20mm, 21-30mm, 31-40mm and 41-70mm, in both 1987 and 1988. For smaller fish, group size and rank of an individual were highly correlated (Table 3.2). Following regression diagnostics (SYSTAT), I excluded social rank from regression analysis for fish of 30mm TL or less. In 1987, persistence could be significantly predicted by multiple regression models for fish of total length 30mm or less (Table 3.3), and persistence increased with group size and body size. However, in 1988, there was no significant relationship between persistence and group size, social rank or body length for fish of 40mm TL or less, although the effect of group size on persistence of recruits was marginally non-significant ( $t=1.93$ ,  $n=33$ ,  $p=.071$ ). For larger juveniles (41-70mm TL) in 1988, fish of higher social rank persisted for less time. Therefore, the prediction that survival was higher for fish in large groups (#2a) was supported only for recruits in 1987, but not for 1988.

*Recruit survival:* Transplant Experiment 1 confirmed that persistence of recruits increased with group size, supporting Prediction 2a, although variation was high ( $r^2=.075$ ,  $p<.05$ ,  $n=58$ ). Survivorship curves for each of

three density treatments (Fig. 3.2a) illustrate that survival was low in general, but levelled out after about one week, perhaps due to growth or increased experience of recruits. The curves for "large" and "small" treatments were typical of a Type-II survivorship regime (Deevey 1947), while that for the "empty" treatment was Type-III. The only recruits remaining at 35 days were in the "large" group treatment.

Both group size and recruit length affected persistence of transplanted recruits in Experiment 2 (Table 3.4), supporting Predictions 2a and b. Persistence in large groups was higher than either small groups or empty coral heads (SNK multiple range test,  $\alpha = .05$ ). As in Experiment 1, survivorship was of Type-III in the "empty" treatment (Fig. 3.2b).

### 3. Growth:

*Natural patch reefs:* In both years, there was a significant negative relationship between growth and group size (supporting Prediction 3a, see Table 3.5). In 1988 only, growth rate was negatively related to social rank (i.e., fish of higher social status grew faster, supporting Prediction 3b). Fish on more isolated corals and those tagged later in the season grew faster in both years, but unexpectedly, growth was higher in the downcurrent quadrant of the reef in both years, so Prediction 3c was only partly

supported. A stepwise multiple regression model for both years included the above variables, and significantly predicted growth of tagged fish (1987:  $r^2=.560$ ,  $p=.0004$ ; 1988:  $r^2=.398$ ,  $p=.0005$ , Table 3.5). Although correlations between some predictor variables were significant (Table 3.6), regression diagnostics (SYSTAT) did not indicate strong multicollinearity.

*Reciprocal exchanges:* I expected growth rates to decrease after exchanging for fish in Treatment 1 (larger group, lower rank), to increase in Treatment 2 (smaller group, higher rank), to increase in Treatment 3 (smaller group, rank unchanged) and to remain unchanged in Treatment 4 (control). I found that fish in the control treatment grew faster after the manipulation, so I considered this relative change (+4.5%) to represent the change in growth rate in a treatment that had no significant effect on growth rate (Table 3.7). Compared to this, fish in Treatment 1 changed growth rate less after exchanging (mean= -4.9%), and fish in Treatments 2 and 3 grew faster after exchanging (+9.7% and +6.9%, respectively). Both group size and social rank appeared to affect growth rate independently, since the positive effect of simultaneously reducing group size and increasing social rank (Treatment 2) exceeded that of reducing group size only (Treatment 3). However, there was no significant difference between mean growth of fish before and after manipulation among the four

treatments (paired t-tests,  $p > .05$ ), so these results provide only weak experimental support for the prediction (#2a).

*Behavioral interactions:* Although there was a significant positive relationship between group size and the total number of chases in a group ( $r^2 = .25$ ,  $n = 50$ ,  $p < .05$ ), the number of chases per fish was unrelated to group size (Fig. 3.3a). Therefore, the prediction that slower growth in larger groups results from more frequent aggressive interactions per individual on average (#3d) is not supported.

Fish within groups exhibited a strong linear dominance hierarchy based on body length, with only 6 of 432 recorded chases directed at larger individuals. This result supports the prediction that reduced growth of lower-ranked fish may be due to lower-ranked fish being subjected to a higher frequency of aggressive chases (#3e). However, while the number of chases by an individual decreased monotonically with decreasing social status (i.e., higher-ranked fish chased more often), the number of times that a fish was chased increased until rank 3, then dropped slightly (Fig. 3.3b). The net effect was that fish of intermediate rank were involved (as chaser or recipient) in the most aggressive chases.

#### 4. Group size and attainment of maturity:

The mean time to reach mature size (70mm TL) for a new recruit increased with group size in both years, from 150 days for single fish to 220 days for fish in a group of 10 in 1987, and from 210 to 235 days over the same group size range in 1988 (Fig. 3.4a). The prediction that decreased time to maturity in smaller groups represents a benefit to living alone (#4a) was therefore supported in both years.

The probability of surviving to mature size was unrelated to group size in 1987, but increased with group size in 1988 from .037 ( $\pm$  .018s.d.) when recruits were alone to .079 ( $\pm$  .025 s.d.)% when in a group of 10 conspecifics (t-test,  $p < .05$ , Fig. 3.4b). The prediction that a benefit to living in large groups is a higher probability of attaining maturity (# 4b) was therefore supported for 1988, but not for 1987.

#### Discussion

Conspecific group size affected the growth and survival of recruits and juveniles, and as a consequence, their attainment of sexual maturity, although these results were highly variable within and between years. Part of this variation was attributable to the social status (social rank) of individual fish within groups.

*Effects of group living on survival*

Group living benefitted recruits by enhancing survivorship, probably through decreased risk of predation. Living in large groups may reduce risk of predation on prey fishes through increased vigilance (e.g., Eibl-Eibesfeldt 1962; Pitcher et al. 1983), predator confusion (e.g., Neill and Cullen 1974), or by a probabilistic dilution effect (see review by Pitcher 1986). All of these mechanisms may be operating to enhance survivorship of recruits in large groups in my study. Larger fish exhibited higher persistence, probably because they were less vulnerable to predators than smaller recruits. Groll (1984) documented in laboratory experiments that the smallest *D. albisella* recruits (<12mm TL) were more likely to be captured by cornetfish (*Fistularis* sp.) and stomatopods (Crustacea), and that *D. albisella* found in stomachs of cornetfish and lizardfish (*Synodus* sp.) caught on one of the patch reefs used in my study were mainly recruits of 10-13mm TL. Therefore, smaller recruits apparently are at greater risk from predation.

Results from other studies contrast with these findings. Robertson (1988), Jones (1987 1988) and Forrester (1990) found that conspecific juvenile density had a negative effect on damselfish recruit survival. The low overall recruit survivorship documented in this study (less than 20% of recruits survived 35 days: Fig. 3.2)

contrasts with findings of Sale and Ferrell (1988) who calculated that 80% of *D. aruanus* settling onto small patch reefs survived at least 50 days (although fish were not tagged in their study).

Since stomachs of recruit *D. albisella* were usually full (Stevenson 1963; Booth, Ph. D. thesis, Appendix 3), starvation is an unlikely alternative explanation to predation in accounting for the low persistence of recruits in my study. Although handling of recruits was minimized during tagging, it may have contributed to lower overall survival through increased stress (see Schreck 1981). However, handling effects were apparently small compared to treatment effects.

Because social rank and group size were statistically confounded for fish under 30mm TL in my study, it was not possible to consider the effects of these two factors on survival, separately. Neither group size nor body length affected persistence of larger juveniles (>30mm TL) on patch reef 23, perhaps because these fish were above predator-vulnerable sizes. Therefore, the survival benefit to group living only accrued to smaller fish.

The influence of group size on survival was stronger in 1987 than in 1988. This difference may be partly due to inter-year variability in predator abundance on patch reefs (e.g., Wass 1967; Stimson et al. 1982), such that predation



intensity may have been higher in 1987 than in 1988. In other studies, variability in mortality rates of reef fishes of up to an order of magnitude have been documented both between years (Aldenhoven 1986; Eckert 1987) and between reefs (Aldenhoven 1986; Victor 1986; Robertson 1988).

#### *Effects of group living on growth rate*

Growth was clearly retarded for individuals in larger groups in 1987 and 1988, and for fish of lower social rank in 1988. Several studies have detected effects of conspecific density on growth of coral reef fish. Doherty (1983) documented a negative effect of juvenile density on growth of *Pomacentrus wardi*, and Jones (1987, 1988) showed that growth of recruits was negatively related to conspecific density in *P. amboinensis*, but was unaffected by adult presence. Forrester (1990) found that mean growth of *Dascyllus aruanus* recruits was suppressed at high recruit densities. The influence of social status on growth rate has been recognized in salmonids (e.g., Davis and Olla 1987) and has been implied in food competition studies for coral reef fishes by Coates (1980) and Forrester (pers. comm.).

Ideally, the reciprocal-exchange experiment on the Sampan coral grid would have evaluated the separate effects of group size and social rank on growth rate. Although the

results were consistent with the hypothesis that both influenced growth rate, high variability precluded statistically significant results. Migration of exchanged fish in this experiment was higher than anticipated, and was possibly an artifact of disturbance during exchanging of fish.

Koebele (1985) listed two possible mechanisms that would result in the depression of growth rate of fish at higher densities: (1) differential food acquisition through dominance relationships or absolute food limitation, and (2) loss of potential growth energy due to enhanced stress or the energetic cost of aggression in larger groups. Interference competition for food within *D. albisella* groups (mechanism (1)) may explain lower growth rates for fish of lower social status. Coates (1980) experimentally determined that small individuals in groups of *Dascyllus aruanus* took smaller prey in the presence of large, socially-dominant conspecifics. He proposed that larger fish were interfering with the feeding patterns of smaller fish by denying them access to large, energetically profitable prey items. I have previously found that maximum prey size is positively related to social status (independent of body size) in *D. albisella* (D. Booth, Ph.D. thesis, Appendix 3), so Coates' mechanism may occur. Absolute food limitation may not have been a normal occurrence on patch reefs, since stomachs of fish were

usually full, regardless of group size (D. Booth, Ph.D. thesis, Appendix 3).

The number of chases per individual was unrelated to group size, which is not consistent with mechanism (2), although stress levels, especially for fish of lower social status (which were chased more often), may have been related to group size. Observations of chases in *D. aruanus* groups by Sale (1972) also demonstrated no relationship between chases per fish and group size, although Allen (1972) found that stunting in juvenile anemonefish (*Amphiprion* sp.) resulted from chasing by adults. Intraspecific aggression (e.g., chasing) may also serve to maintain or establish dominance hierarchies (Magnuson 1962, Yamagishi et al. 1974). However, it appears that interference competition for food may be is the main cause of reduced growth rates in larger groups.

In a study on patch reef 23 in 1987, I found that lipid content of individual fish increased with body length and social status (D. Booth, Ph.D. thesis, Appendix 2), so these results support the findings of the present study. Of the growth variation unexplained by the multiple regression models above (45% in 1987, 63% in 1988, Table 3.5), only 39% in 1987 and 1.5% in 1988 could be attributed to intrinsic differences in growth rate between individuals (D. Booth, Ph.D. thesis, Appendix 7). The remainder may be

partly due to variations in zooplankton supply among coral heads supporting fish (e.g., Hamner et al. 1988).

Regardless of this density-independent variation, my study has identified strong density-dependence of growth rate.

*Effects of group living on individual fitness- is there an optimal group size?*

Due to slower growth of fish in larger groups, there was a clear increase in the time required to reach maturity with increasing group size. If the age at first reproduction is related to the age at maturity, as seems likely, then the generation time of fish in small groups may be lower, and their lifetime reproductive success may be higher than fish settling to larger groups. Settlement occurs during March to October (D. Booth, unpubl. manuscript), and most breeding occurs during March-April (Stevenson 1963). Winter growth was negligible for fish between 20 and 45 mm TL on patch reef 23 ( $0.018 \pm .012$  [ $\bar{X} \pm se$ ,  $n=10$ ])mm per day. If the winter growth hiatus extends from December through February, then larvae settling on empty coral heads before late July would be of mature size at the start of the following year's breeding season. Of larvae settling with groups of ten conspecifics, only those settling before late March would be of mature size before the next breeding season. Therefore, between late March and late July, typically a period of high settlement (D. Booth, Ph.D thesis Chapter 2), only larvae joining small

groups would reach mature size by the next breeding season. Similarly, Ochi (1986) demonstrated that timing of settlement within a season for anemonefish (*Amphiprion* sp.) can affect growth rates and attainment of maturity. It would be most beneficial then, in terms of minimizing time to reach mature size, for larvae to settle on empty coral heads and live alone.

The relationship between probability of survival to maturity and group size varied between years. The strong positive relationship in 1988 suggests that membership in a larger group would be advantageous. The "optimal group size" to maximize probability of reaching maturity would be large in 1988 only. Therefore, predicted optimal group size to minimize time to maturity and maximize probability of reaching maturity differ. Determination of an optimal group size for attainment of maturity would require knowledge of the relative merits of maturing quickly and maturing surely.

In previous experiments conducted in 1987 to 1989 (Booth 1990 and Ph. D. thesis, Chapter 2), I demonstrated that larvae exhibit strong settlement preferences for corals supporting larger groups of conspecifics (see also Sweatman 1985). Settlement choices by larvae may therefore affect individual fitness through effects on growth and survival, as documented in the present study. If such

habitat choice has an adaptive basis, then some component of fitness of fish should be enhanced by joining larger groups compared to joining smaller groups or living alone. Results from the present study indicate that net benefits to group membership would vary between years, perhaps as a result of unpredictable inter-annual variation in planktonic food supply and predator density. Larval preference for large groups, however, may represent the best decision on average, if the probability of reaching maturity is positively related to group size (as in 1988) in most years. Alternatively, larvae may prefer to settle with large groups because:

- (1) they do not behave adaptively, or
- (2) they make optimal habitat choices, but use criteria that enhance fitness other than maximization of juvenile growth and survival. For example, high predation pressure on arriving larvae immediately adjacent to patch reefs (e.g., Hamner et al. 1988) may select for larvae that simply settle on the first coral head detected. Settlement with larger groups may therefore be an artifact of the greater conspicuousness of corals supporting larger groups.

In this species, then, I found no consistent net benefit for fish joining a larger group, since net benefits differed between years. Conclusions regarding the adaptive value of group membership for attainment of maturity were therefore different between the two years of my study,

highlighting the significance of temporal variation in costs and benefits of group living.

**Table 3.1.** Number of tagged juvenile *Dascyllus albisella* on a natural patch reef in 1987 and 1988 that either were recaptured on their original coral head ("# recap.") or had emigrated to another coral head ("# emig.").

Length	1987			1988		
	# tag	# recap.	# emig.	# tag	# recap.	# emig.
10-20mm	29	17	0	88	29	1
21-30mm	17	13	0	71	50	0
31-40mm	46	42	2	40	26	5
41-50mm	36	26	5	18	10	2
51-70mm	13	2	1	7	4	1
Total	137	96 (70%)	8 (6%)	224	120 (54%)	9 (4%)



**Table 3.2.** Correlations between pairs of variables used in multiple regression models of persistence of juvenile *Dascyllus albisella* on a natural patch reef. p: persistence (days, see text); gs: group size; r: social rank; l: total length (mm). \* p<.05.

	Corr. 1987 (length class,mm)				1988 (length class,mm)				
	10-15	15-30	30-40	40-60	10-15	15-20	20-30	30-40	40-60
p vs gs	.27	.46*	.04	.01	.23	.11	.09	-.13	-.41*
p vs r	.29	.40*	-.06	.11	.25	-.07	.07	-.10	-.49*
p vs l	.50*	.63*	.17	-.44*	.11	.05	.06	-.26	-.35
gs vs r	.99*	.94*	.80*	.33*	.98*	.92*	.79*	.83*	.76*
gs vs l	-.19	.38*	.04	.03	.04	.08	.14	.13	-.05
r vs l	-.23	.25	-.38*	-.44*	-.02	.03	-.06	.14	-.30
N	18	16	36	32	33	44	65	38	22

**Table 3.3:** Multiple regression model for persistence (days) of tagged *Dascyllus albisella* on a natural patch reef in 1987 and 1989. \*:  $p < .05$ .

Year	Length	Independent variables, t-values			N	R <sup>2</sup>	overall p value
		Group size	Rank	Length			
1987	10-15mm	2.33*	-	2.39*	18	.38	.026*
	16-30mm	1.54	-	2.20*	16	.44	.022*
	31-40mm	-0.19	-0.15	0.64	36	.04	.686
	41-70mm	-0.72	-0.48	-1.72	32	.14	.219
1988	10-15mm	1.93	-	0.38	33	.11	.160
	16-20mm	0.82	-	-0.42	44	.02	.548
	21-30mm	0.39	-0.13	-0.07	65	.01	.999
	31-40mm	0.02	-0.66	-1.54	38	.09	.343
	41-70mm	-0.59	-2.61*	-1.66	22	.49	.006*

**Table 3.4:** Analysis of covariance of effects of group size and body length on persistence of recruit *Dascyllus albisella* on natural patch reefs. There was no significant interaction between the main factor (group size) and the covariate (body length). \*:  $p < .05$ .

Source	df	Mean square	F ratio	p value
Group Size	2	3.053	3.443	0.038*
Body length	1	17.749	19.710	0.000*
Error	63	0.887		

**Table 3.5.** Multiple regression model for growth of tagged juvenile *Dascyllus albisella* on a natural patch reef in 1987 and 1988. \*:  $p < .05$ . "In model" means that the variable was identified to include in the multiple regression model, using stepwise procedures.

Variable	1987			1988		
	In model	t-value	p	In model	t-value	p
Group size	yes	-4.32	.000*	yes	-2.86	.011*
Social rank	no	-	-	yes	-4.36	.000*
Body length	yes	3.31	.004*	yes	1.96	.053
Location	yes	2.34	.030*	yes	2.17	.032*
Isolation	yes	2.67	.015*	yes	3.25	.002*
Day	yes	2.49	.022*	yes	4.57	.000*
Coral Size	no	-	-	no	-	-
Coral Species	no	-	-	no	-	-
Coral Rugosity	no	-	-	no	-	-
Water Depth	no	-	-	no	-	-
overall $R^2$ :	.548 (1987)			.372 (1988)		
N :	26			112		
p :	.0004			.0001		

**Table 3.6.** Simple correlation between pairs of variables used in multiple regression model of growth of tagged juvenile *Dascyllus albisella* on a natural patch reef in 1987 and 1988. \*:  $p < .05$ . Lower left diagonal of matrix gives 1987 data (n=26); upper right diagonal of matrix gives 1988 data (n=112); correlations between physical characteristics of coral heads only reported in 1988, because they were identical in both years.

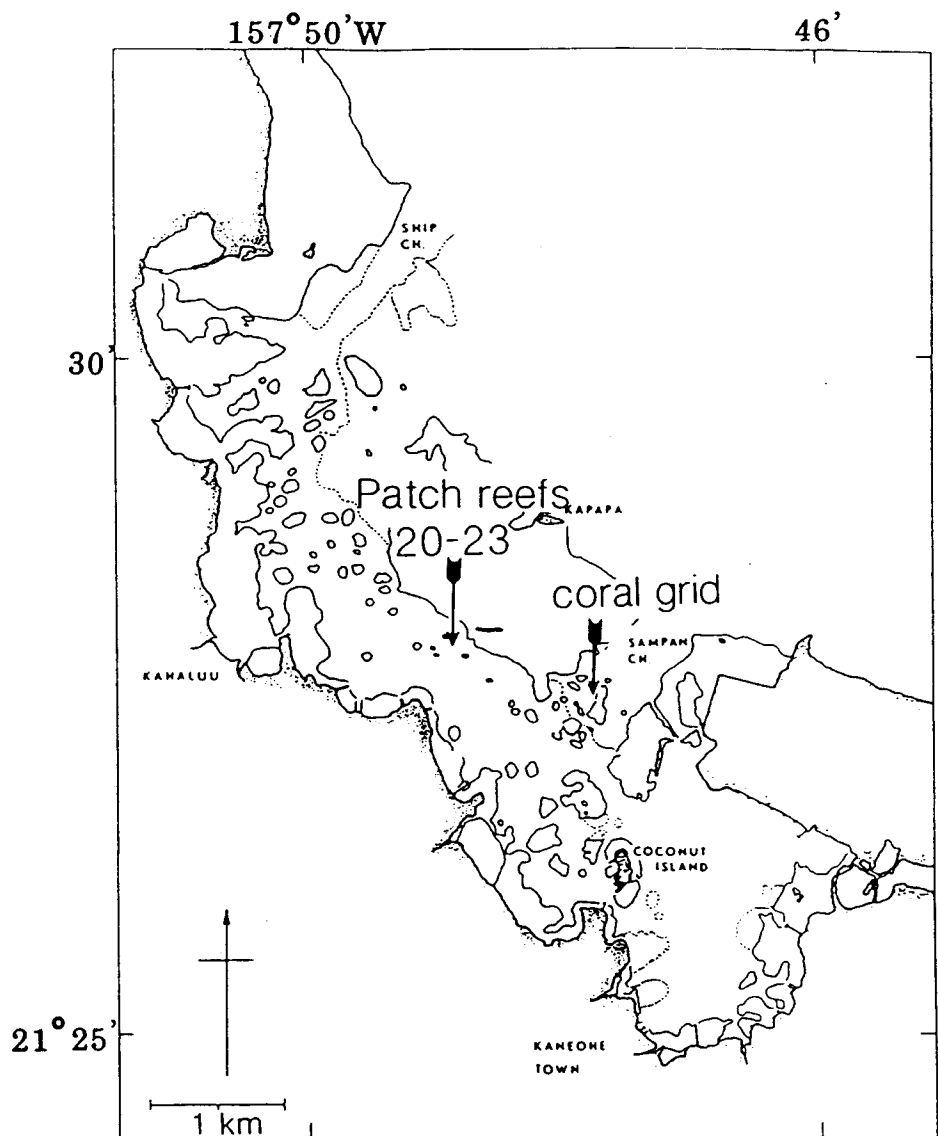
	Fish				Coral					
	growth	gs	rank	len	size	rug	dep	loc	species	day
growth	-	-.06	-.21*	.11	-.20*	-.13	.17	-.30*	-.10	.39*
group size(gs)	-.33	-	.64*	.15	.05	.11	-.24*	-.38*	-.41*	.23*
rank	-.26	.17	-	-.39*	.09	.07	-.11	-.25*	-.30*	.27*
length (len)	.07	.29	-.62*	-	.12	.09	-.20*	-.06	.05	.17
coral size	-.17	.28	.32	.11	-	.16	-.10	-.17	.15	.14
coral rugosity	-.08	.01	-.05	.09	-	-	.04	-.28*	.11	.01
depth	-.28	.41	.10	.06	-	-	-	-.13	.44*	.15
location	.25	.20	.26	-.20	-	-	-	-	-.22*	-
coral species	-.23	.06	.15	-.08	-	-	-	-	-	-
day	.21	-.01	.52*	-.59*	-	-	-	-	-	-

**Table 3.7.** Growth of tagged juvenile *Dascyllus albisella* on coral grid before and after exchanging fish (see text). Growth is expressed in mm/day (mean  $\pm$  se).

Treatment	Growth			n
	before	after	% change	
(1) Increase gs, decrease rank	0.347 (0.068)	0.332 (0.038)	- 4.9	8
(2) Decrease gs, increase rank	0.310 (0.022)	0.340 (0.027)	+ 9.7	20
(3) Decrease gs, same rank	0.288 (0.086)	0.308 (0.028)	+ 6.9	8
(4) Control	0.332 (0.063)	0.347 (0.043)	+ 4.5	8

**Figure 3.1.** Map of Kaneohe Bay, Hawaii, showing locations of patch reefs and the Sampan coral grid used in this study.

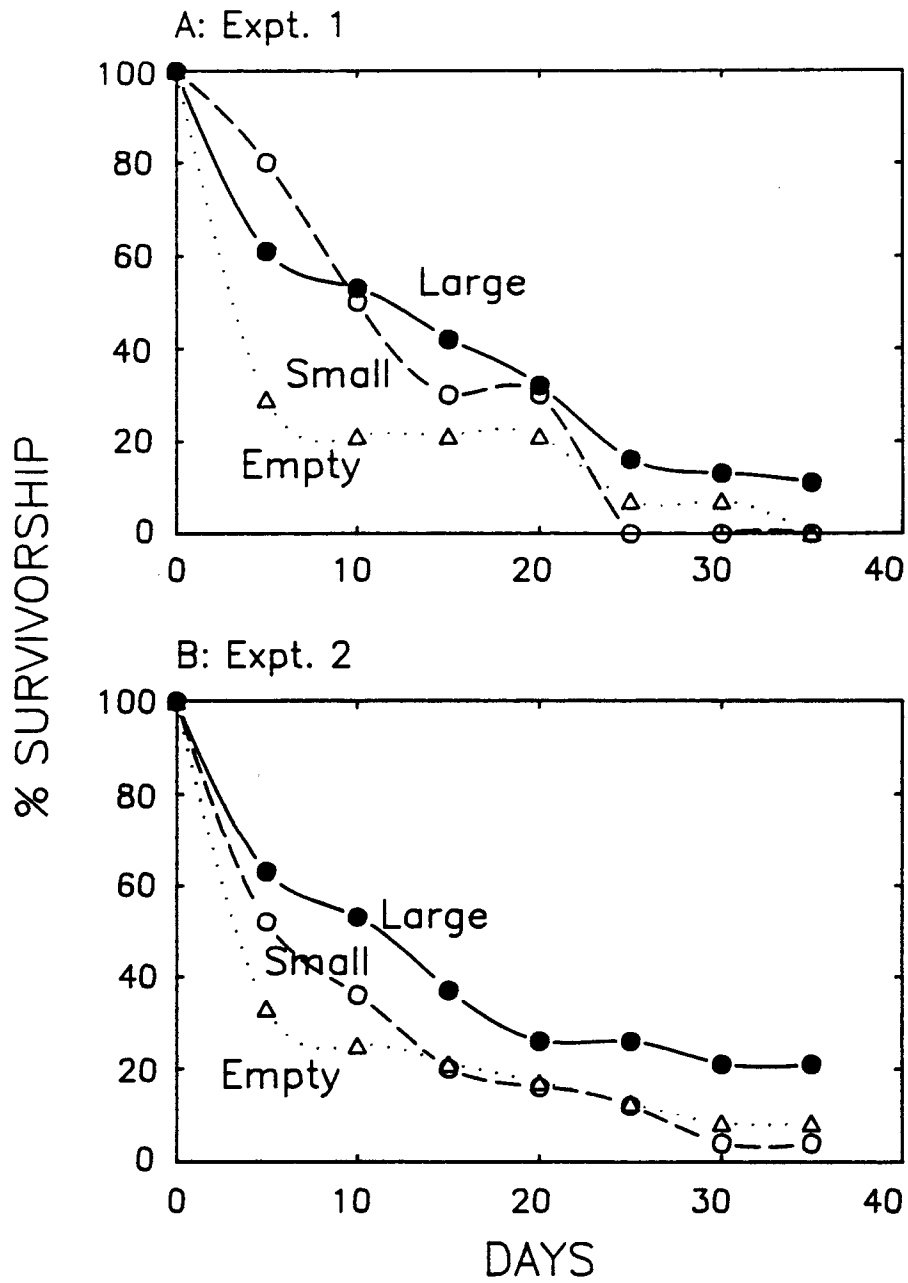
Figure 3.1





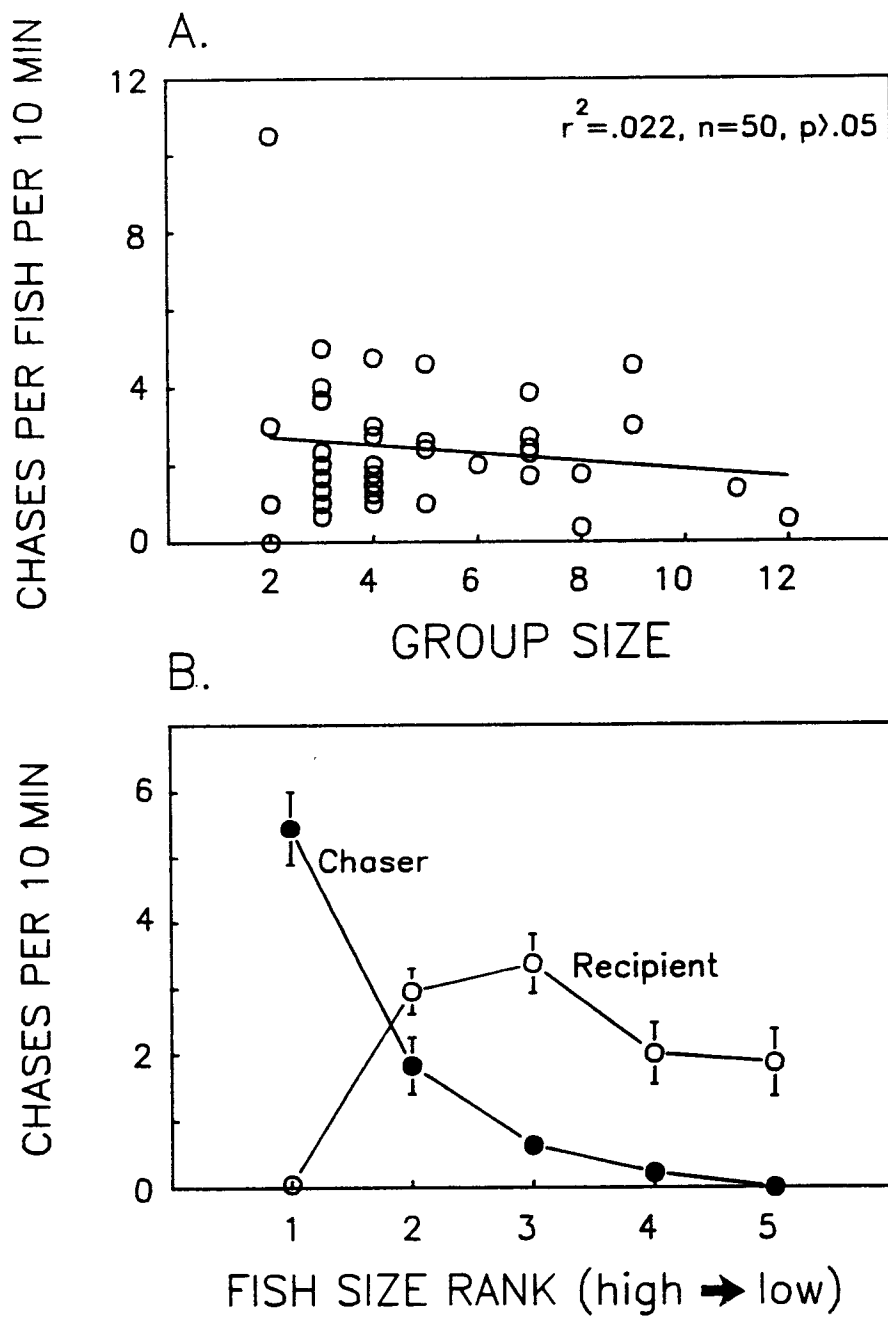
**Figure 3.2.** Survivorship curves for recruit *D. albisella* transplanted to coral heads and subject to one of three conspecific group size treatments: large (5-8 conspecifics), small (1-2 conspecifics), and empty (no fish). A: Reef 23, no group size manipulation; B: Reefs 20 and 21, group sizes manipulated. n=20 for each treatment.

Figure 3.2



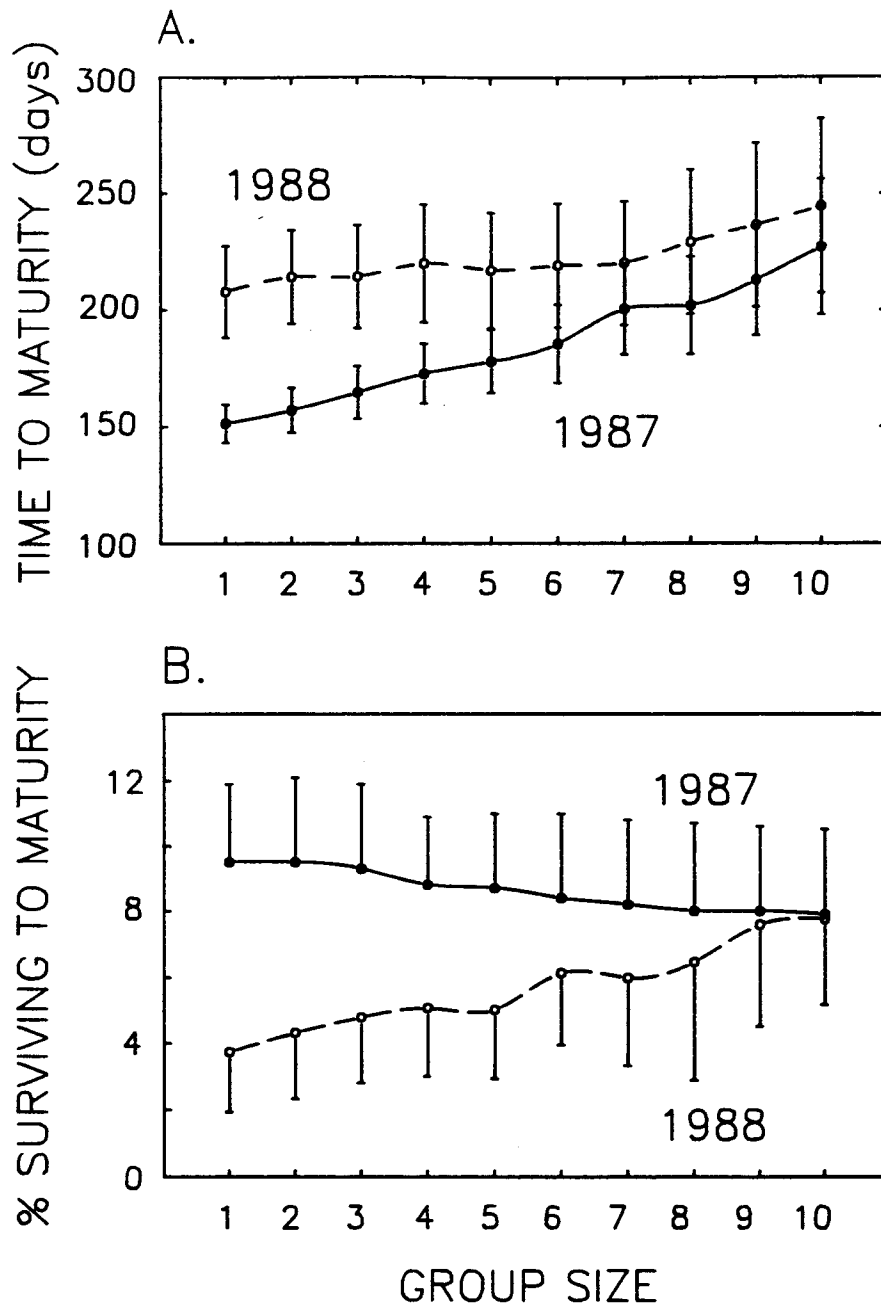
**Figure 3.3.** Aggressive chases for juvenile *D. albisella* as a function of a) group size (n=50), and b) social rank (n=11).

Figure 3.3



**Figure 3.4.** Results of simulation models considering the effect of conspecific group size on (a) the estimated time to maturity, and (b) the estimated probability of reaching maturity, for juvenile *D. albisella* on natural patch reefs ( $\bar{X} \pm$  standard deviation, n=100 simulations each).

Figure 3.4



## Chapter 4

### Effects of larval settlement patterns on the demography of juvenile groups in a coral reef fish: a simulation based on field data

#### Abstract

The relationship between larval settlement and adult density in open populations, such as coral reef fishes, is currently unclear. Hypotheses to account for variation in adult density range from those arguing that larval settlement rates exclusively determine adult densities (primary recruitment limitation) to those that argue that processes acting directly on juveniles, such as predation, regulate population density (secondary recruitment limitation). Larvae of the Hawaiian domino damselfish settle onto isolated coral heads, where they live in small groups for about one year. Larvae settle preferentially on corals supporting juvenile conspecific groups. They then mature and emigrate to nearby but distinct adult populations. I used field-based measurements of larval settlement and juvenile growth and survival for the domino damselfish to develop a simulation model that predicts the rate of maturity and emigration to the adult population, juvenile group size and other aspects of juvenile

demography. Using parameters measured over two years in the field, I was able to accurately predict seasonal variations in group sizes. I found that, at different settlement rates observed over the two years, the number of juveniles attaining maturity was proportional to the settlement rate. Thus, primary recruitment limitation of adult density could have operated in this system. However, at higher settlement rates in one year, there would have been no relationship between settlement rate and number maturing, indicating that primary recruitment limitation would not operate at these higher settlement rates. In one year but not another, preferential settlement for larger groups affected numbers maturing, relative to random settlement. Differences in the growth and survival of juveniles between years affected numbers maturing, suggesting that secondary recruitment limitation may also have operated. Since growth and survival of juveniles was related to group size, the size-distribution of groups on a reef could affect the rate of maturity of juveniles into the adult population.

### **Introduction**

A controversial issue in marine ecology is the relative importance of processes affecting larvae, juveniles and adults in structuring adult populations (Roughgarden et al. 1985; Davis 1987; Doherty and Williams



1988). For coral reef fishes, it has variously been argued that adult populations and communities are structured exclusively by pre-settlement processes (recruitment limitation: Doherty 1981), combinations of pre- and post-settlement processes (competitive lottery: Sale 1978), factors affecting juvenile populations, such as predation (secondary recruitment limitation: Victor 1986, Jones 1987, 1988), adult populations (e.g., competition for space: Smith and Tyler 1972), or both (e.g., predation: Hixon 1991).

Due to extensive pelagic dispersal of larvae, patterns of larval settlement are generally considered to be unrelated to adult reproductive output on any given reef. It has been proposed, therefore, that most coral reef fishes have open life cycles (e.g. Warner and Hughes 1988), and that the supply of larvae onto a reef will limit the distribution and abundance of the adult population there (e.g., Mapstone and Fowler 1988). If primary recruitment limitation is operating, then recruitment rates of juveniles into the adult population should be directly related to settlement rates of larvae. If secondary recruitment limitation is operating, variations in juvenile demography should affect numbers maturing. To test these predictions, it is necessary to closely monitor the arrival of settling larvae onto reefs and to follow the fate of individuals through adulthood. Such observations are

extremely difficult to accomplish in the field, especially for long-lived species (e.g., Underwood and Denley 1984; Connell 1985; Warner and Hughes 1988; but see Jones 1990). However, by monitoring larval settlement and subsequent growth and survival of fish over a period of months and incorporating the empirical results into a population model, it may be possible to test predictions regarding the relationship between larval settlement, juvenile demography and subsequent recruitment of juveniles into the adult population.

The distribution and abundance of organisms within a habitat is a function of the patterns of arrival (settlement, immigration) to and departure (mortality, emigration) from that habitat. Demographic models have been developed which attempt to predict population dynamics by considering the effects of birth, immigration, death and emigration of individuals (e.g., the BIDE models of Boswell et al. 1974 and Pulliam 1988). Several models have used field data on the rates of such processes to simulate aspects of the population dynamics of coral reef fishes (e.g., Doherty et al. 1985; Warner and Hughes 1988; Holm 1990). However, despite the high levels of variation measured in the field for biological processes in general, surprisingly little attention has been paid to the effects of larval habitat selection on the distribution and abundance of reef fish populations, or to the sensitivity

of population models to variation in input parameters. In particular, habitat preferences by coral reef fish larvae at settlement may affect the demography of fish on reefs (e.g., Sweatman 1985; Stimson 1990; Booth 1990).

In this study, I use field data collected over two summers on larval settlement patterns and juvenile growth and survival of domino damselfish (*Dascyllus albisella* Gill) on a patch reef, to predict various aspects of juvenile demography and the rate of recruitment of fish from isolated juvenile groups to the nearby but distinct adult population. I previously demonstrated that larvae settle preferentially with larger groups of conspecifics (Booth, 1991, and submitted), and here I consider how such habitat choice affects juvenile demography. Specifically, I ask:

- (1) Can larval settlement rate and presence or absence of settlement preferences for conspecific groups directly affect the rate of recruitment of juveniles into the adult population?
- (2) How do larval settlement rates and settlement preferences affect juvenile group sizes?
- (3) Can field data on settlement, growth, and survival of fish be used to predict actual seasonal variations in juvenile group sizes on the reef?

### **Study species**

The domino damselfish is endemic to the Hawaiian archipelago. Juveniles are typically found in groups on small branching coral heads. Migration between coral heads of juveniles less than mature size is negligible (Booth, submitted). Larvae settle onto the coral heads in the summer months (March to October) at a length of 10-15mm TL ( $\bar{X} \pm \text{sem}$ :  $13.9 \pm 0.3$ ,  $n=55$ ) and juveniles remain closely associated with corals until they mature at about 70mm TL. For individual fish, attainment of maturity will depend on size-specific growth and survival.

### **The simulation model**

I developed a BASIC model that simulates larval settlement to 40 coral heads and tracks the growth of juveniles until the fish either suffer mortality or reach mature size and emigrate to the adult population. On each weekly iteration, a new pulse of larval settlement occurs, and both new larvae and juveniles already present grow and pass through a mortality gauntlet. This method is analogous to those employing Leslie transition matrices (e.g., Warner and Hughes 1988). I derived the functions in the model empirically from my observations of actual fish growth and survival in various group sizes on 40 coral heads at a patch reef in Kaneohe Bay, Hawaii (reef #23 in Roy 1970).

Roy 1970).

I ran the model for 100 weeks (2 years), with settlement occurring for the first 25 weeks of each 50 week period, and growth occurring for the first 40 weeks of the 50 week period. Based on my field data, I assumed that growth did not occur over 10 weeks of winter each year. I also assumed that survivorship did not vary seasonally (see Discussion). Model outputs were the number of fish maturing each week and the size of groups on each of the 40 coral heads. Figure 4.1 summarizes the following details of the model:

**Larval settlement:** (a) Settlement preferences: I simulated two patterns of larval settlement to coral heads: "random" and "preferential". The former involved assigning recruits to coral heads using a random number generator. The latter involved a linear increase in the probability of a coral head receiving recruits with increasing group size (Table 4.1), as demonstrated in previous field experiments (Booth, submitted).

(b) Settlement rates: I used rates which covered most of the range of settlement rates measured from 1987 to 1989. The mean settlement rate of larvae onto 40 tagged coral heads on the study reef was 2 per week (range 0-4) in 1987, 10 (1-31) in 1988, and 14 (0-66) in 1989. I ran the simulation model for the following rates of settlement: 3, 6, 9, 12, 15, 18, 21, 24, 27 30,

33, 36, 39 and 42 recruits per week.

To consider the effects of natural weekly variation in settlement onto the reef on group sizes, I ran separate simulations using actual settlement measured during weekly censuses at the patch reef in 1988 and 1989.

**Juvenile growth and survival:** I developed multiple regression models for growth and survival as a function of group size, social rank and body length from data collected during tagging studies on the study reef during 1987 and 1988 (Booth submitted). I monitored growth of fish by successive measurements of tagged individuals at bi-weekly intervals. Growth was negligible over the winter months, and otherwise was negatively density-dependent, varying inversely with group size (Table 1 and Booth, in prep.). Fish within groups formed a linear size-based dominance hierarchy, with the largest fish having a rank of one. I monitored survival of fish by noting disappearances of tagged individuals and verifying that fish rarely migrated from their resident coral head. Survival was positively density-dependent, varying directly with group size (Table 1 and Booth, in prep). I considered variation in growth and survival rates by including the measured variation in the coefficients of group size and body length in the regression equations for growth and survival. For each fish at each weekly iteration of the model, I assigned new

coefficients, assigned randomly and falling within one standard error of the mean value for each coefficient to equations describing growth and survival (Table 1).

## Results

### Survival and maturity

The percentage of recruits reaching maturity declined with increasing settlement rate for both random and preferential settlement regimes for 1987 data, with the decline being greater for the preferential settlement regime (Fig. 4.2, ANCOVA comparing slopes,  $F=7.5$ ,  $p<.05$ ). In contrast, in 1988 about 3% of recruits reached maturity for both random and preferential settlement regimes at all settlement rates examined (Fig. 4.2). This meant that, for 1987 data, the rate of increase in number of juveniles maturing was lower at higher settlement rates (Fig. 3). In fact, at settlement rates above 30 recruits per week for preferential settlement in 1987, the number of juveniles maturing was independent of settlement rate. In contrast, the number of juveniles maturing was directly proportional to settlement rate in 1988, and was similar for both random and preferential settlement regimes (Fig. 4.3). Since the strengths of settlement preferences were similar between years, between-year differences in the relationship between settlement rate and number maturing were due to differences in density-dependent growth and survival between years.

## Group size

At all settlement rates, mean group size exhibited a characteristically cyclical increase and decrease every 50 weeks (Fig. 4.4). As expected, settlement preferences for conspecific groups generally increased mean group size at each settlement rate (Fig. 4.4). While a ten-fold increase in settlement rate (3 to 30 recruits per week) did increase mean group sizes in both years, this increase was only up to about four-fold.

Censuses on the study reef from 1988 to 1989 showed that actual larval settlement occurred during roughly 25-week periods each year (Fig. 4.5a). Mean group size fluctuated on a seasonal basis, and peaked each year in mid-late summer (Fig. 4.5b). Simulations employing actual weekly settlement rates for 1988 and 1989 and growth data for 1988 yielded seasonal fluctuations in group size (Fig. 4.6a) that were similar to those observed in nature (Fig. 4.5b). However, the mean group sizes observed in nature over the winter of 1988/1989 (mean  $\pm$  SE:  $1.75 \pm 0.27$ ,  $n=15$ ) were larger than expected from results of the simulation model during the same period (mean  $\pm$  SE:  $0.33 \pm 0.33$ ,  $n=6$ ). The number of groups on the reef fluctuated seasonally, as predicted by the simulation model, although the number of groups in winter (15 groups) was higher than expected (6 groups, Fig. 4.6b).



## Discussion

The results of the simulations indicated that:

- (a) preferences of larvae for larger groups can affect group sizes and the number of juveniles reaching mature size, but the magnitude and direction of this relationship was variable between years;
- (b) the number of juveniles maturing was directly related to settlement rate for 1988 and partly for 1987, but not so at the highest settlement rates in 1987; and
- (c) field data on settlement rate, growth and survival can be used to approximately predict seasonal fluctuations in juvenile group sizes.

The occurrence of larger group sizes than predicted for winter 1988/89 (Fig. 4.5b) may have resulted from simplifying assumptions concerning growth and survival in the model. For instance, although I assumed that growth rate did not vary seasonally during the 40 week growth period, the actual growth rate increased slightly in the latter part of the summer (Booth submitted). Also, I assumed that survivorship did not vary seasonally. I did not measure actual survivorship in the winter months. Given that the predominant source of mortality for juvenile reef fish is probably predation (Hixon 1991), survival may have been higher in winter than summer due to lower predator densities or lower food requirements of individual

predators. If higher survivorship in winter were included in the simulation model, the occurrence of larger group sizes than predicted may have been accounted for.

**Primary or secondary recruitment limitation?** Both primary and secondary recruitment limitation may have operated in this system because both settlement rate and juvenile growth and survival affected the number of fish maturing. The evidence that primary recruitment limitation was occurring is that the number maturing was generally positively related to settlement rate. However, for 1987 data, at settlement rates above about 30 recruits per week, primary recruitment limitation could not have occurred, although the settlement rates that I did record in 1987 were much lower. Secondary recruitment limitation (regulation of adult densities by processes occurring during juvenile stages) may have operated because, since there were differences between numbers maturing in 1987 and 1988 due to differences in the strengths of density-dependent juvenile growth and survival between years. In 1988, growth rates were not strongly affected by group size or social rank, and growth rate was lower on average than in 1987. As a consequence, fewer fish matured in 1988 than 1987 at all settlement rates.

The simulations demonstrated that settlement preferences as well as density-dependent growth and survival patterns can affect attainment of maturity, and

that these effects can vary on a yearly basis. Jones (1987, 1990) showed experimentally that density-dependent growth can affect the number of a damselfish, *Pomacentrus amboinensis*, reaching maturity. My field results also showed large amounts of variation in growth and survival between and within years that were not density-dependent in nature (Table 1), and may have been due to variations in predator or food abundances. This density-independent component could reduce the significance of density-dependent growth and survival on population structure, despite of Hughes' (1990) assertion that populations cannot be regulated by density independent growth or survival.

**Settlement patterns, juvenile growth and survival, and adult population size:** The influence of settlement patterns on adult population size is mediated through the influence of settlement rate on juvenile attainment of maturity. If the number of juveniles reaching maturity is not related to settlement rate (e.g., at rates of above 30 recruits per week using the 1987 growth and survival data; Fig. 3), then settlement rate would not have a significant influence on adult densities. However, even when there is a direct relationship between the number of fish settling and the number of fish maturing, settlement may still not have a significant role in regulation of adult population sizes. The role of settlement also depends on at least two other factors. First, sexual maturity alone does not

guarantee successful entry into the adult population. For example, recently-mature adults of several damselfish species must locate suitable space to establish a territory (Sale 1978). Adult fish without territories disappear. Second, the effects of settlement rate on adult population density are reduced with increasing longevity of adults. Warner and Chesson (1984) and Warner and Hughes (1988) have called this phenomenon the "storage effect". While this effect is not significant for short-lived organisms (e.g., Hughes 1990), damselfishes are relatively long-lived. *D. albisella*, for instance, has a reported maximum lifespan of 11 years (Hill and Radtke 1988), and other coral reef fishes may also live in excess of 5 years (e.g., MacDonald 1981; Aldenhoven 1986; Eckert 1987; Mapstone 1988). Storage effects may effectively maintain adult numbers despite a poor settlement year.

If the adult population size is large relative to the number of juveniles maturing, recruitment limitation may be obscured. At my study reef, surveys from December 1988 to October 1989 showed that the number of adults on the reef averaged 169 individuals (range: 130-220). Over that time, I recorded 280 recruits settling on the reef. If 3% of those fish attained maturity (Fig. 4.2), their addition to the adult population would increase the adult population by 8 to 9%. This increase may be difficult to detect, given the range of adult densities reported above.

Therefore, the significance of settlement patterns and juvenile growth and survival to population regulation in adults depends on not only number of juveniles maturing, but also the significance of storage effects and factors limiting the survival of new adults.

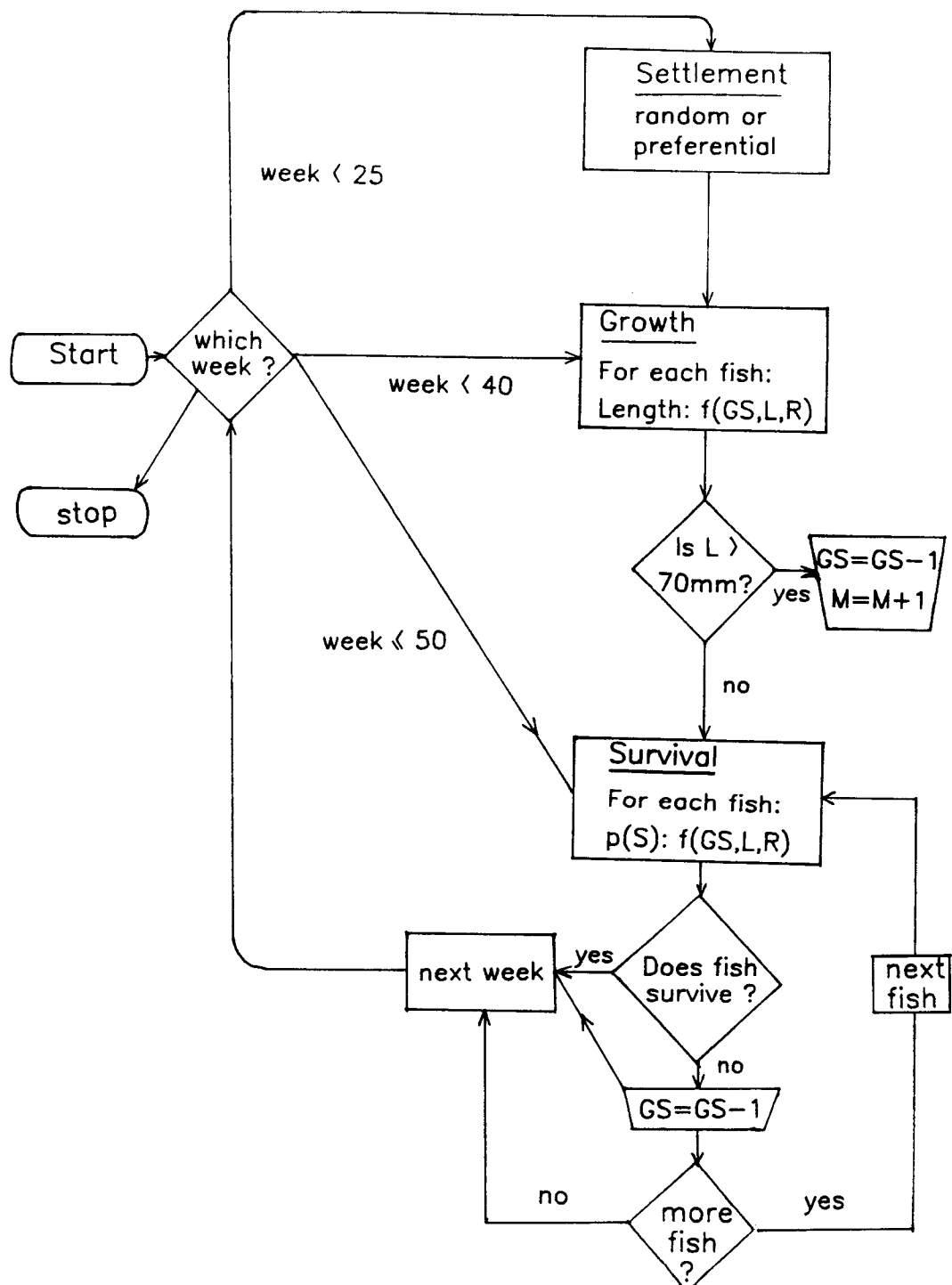
The alternative and more direct approach to testing for primary recruitment limitation involves monitoring larval settlement and adult population size in the field over an "appropriate" length of time, and was attempted by Jones (1990). He found that adult densities of the damselfish *Pomacentrus amboinensis* on small patch reefs increased with experimentally-controlled recruitment rates, but at lower recruitment rates only. At higher densities, adult population sizes were unrelated to recruitment rate, as found in my study. However, recruitment rate in Jones' study was measured as the density of recruits at the end of the settlement season, and as such probably represents settlement patterns ameliorated by the combination of density-dependent growth and survival (see Jones 1988, Booth 1991). Therefore, it would be difficult to separate primary and secondary recruitment limitation in this case. To test for primary recruitment limitation, it would be necessary to manipulate or monitor actual settlement rates of incoming larvae. In any case, it would have to be demonstrated that the number of settlers limited the population below levels where resources were limiting.



**Figure 4.1:** Flow diagram of simulation model.

Abbreviations: GS=group size; L=total length; R=social rank; M=number maturing;  $p(S)$ =probability of survival during the week; week=number of weeks since settlement;  $f(GS,L,R)$ =function of GS, L and R.

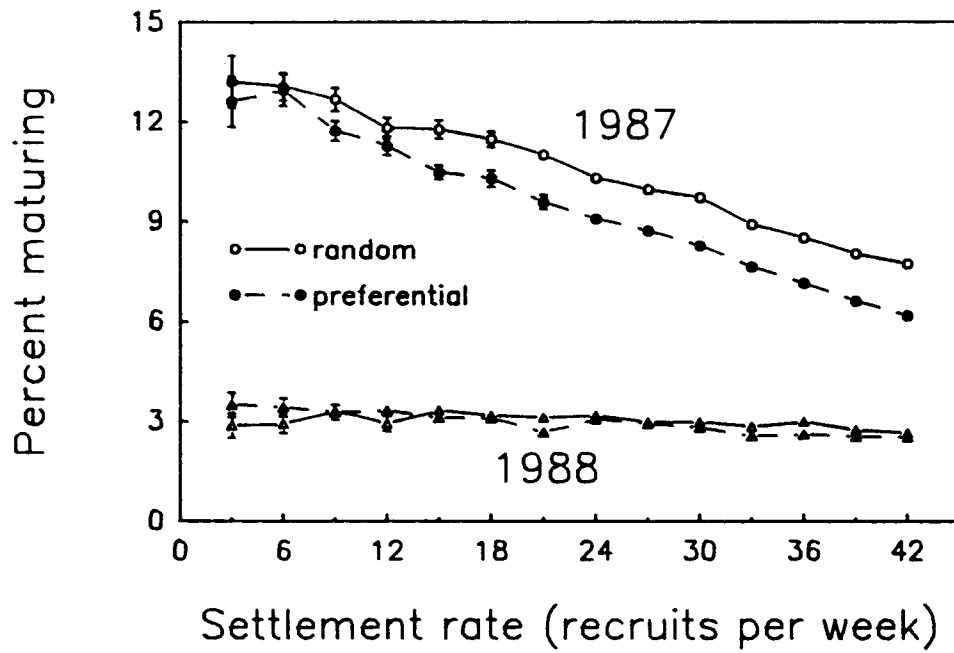
Figure 4.1





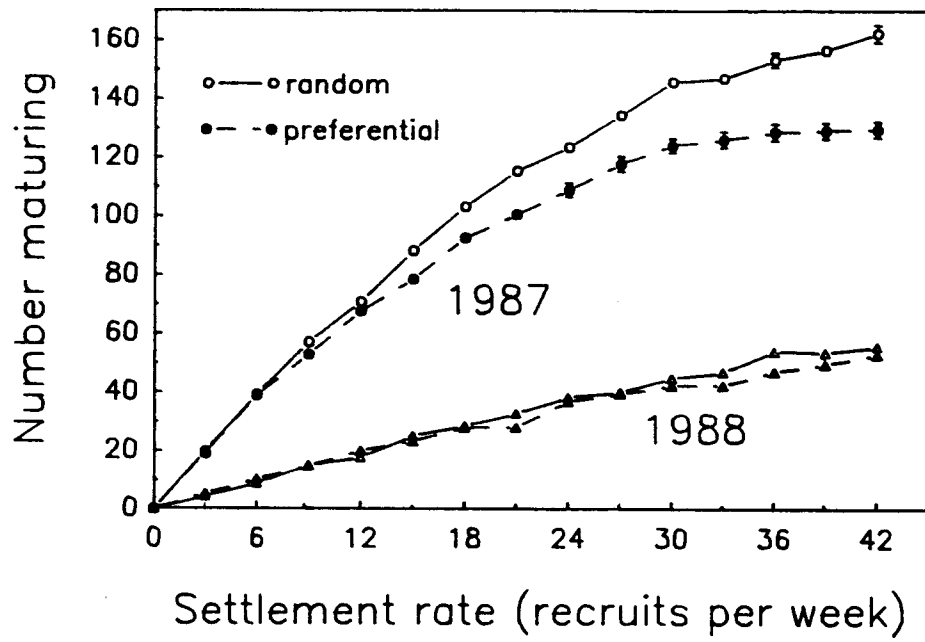
**Figure 4.2:** Percentage of new recruits reaching maturity after 100 weeks as a function of settlement rate for 1987 and 1988. Each point gives the mean  $\pm$  standard error for 20 simulations. "Preferential" refers to settlement preferences for larger groups.

Figure 4.2



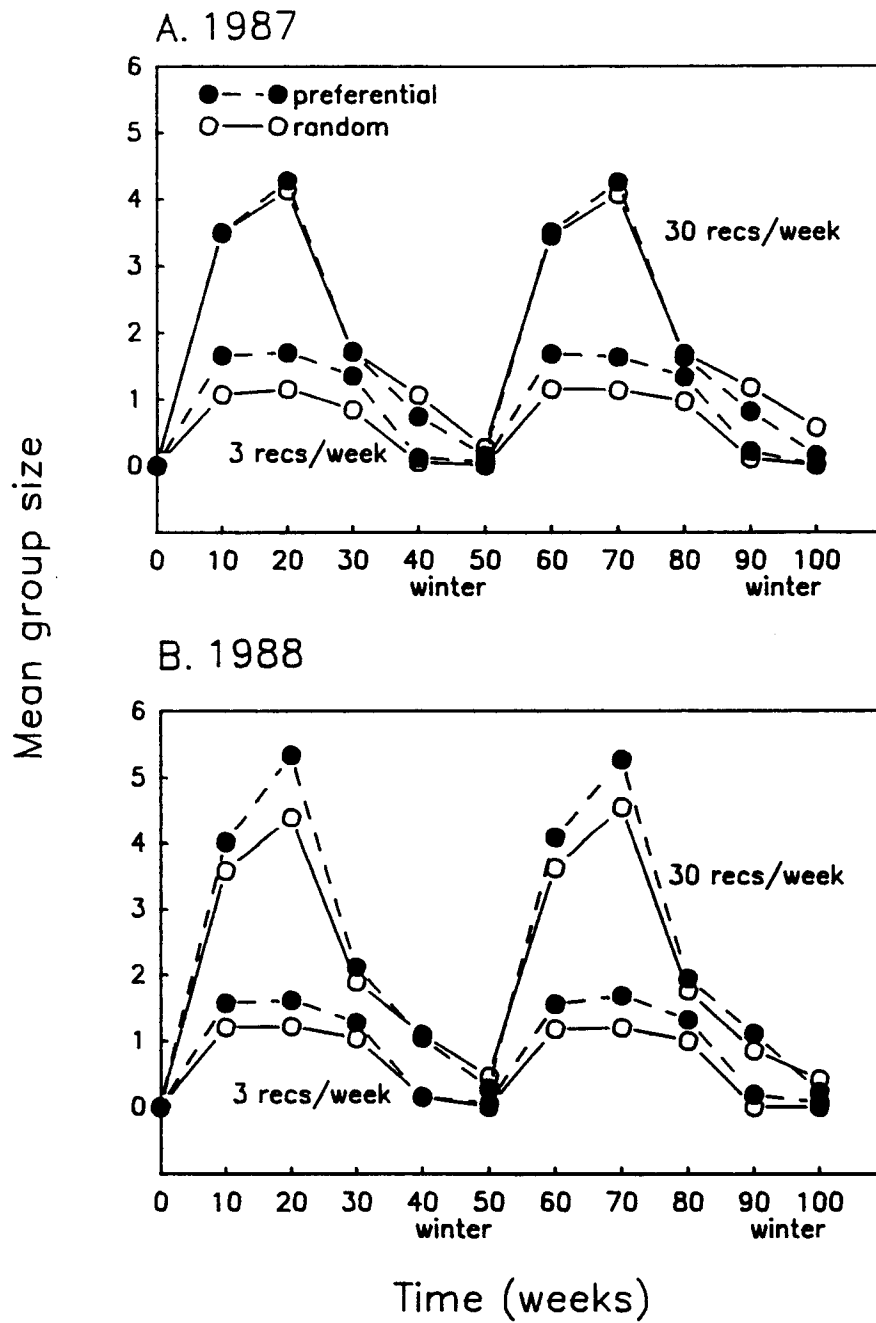
**Figure 4.3:** Number of juveniles maturing after 100 weeks as a function of settlement rate for 1987 and 1988. Each point gives the mean  $\pm$  standard error for 20 simulations. "Preferential" refers to settlement preferences for larger groups.

Figure 4.3



**Figure 4.4:** Predicted seasonal patterns in juvenile group size at settlement rates of 3 and 30 recruits per week, in 1987 and 1988. Each point gives the mean  $\pm$  standard error for 20 simulations. "Preferential" refers to settlement preferences for larger groups.

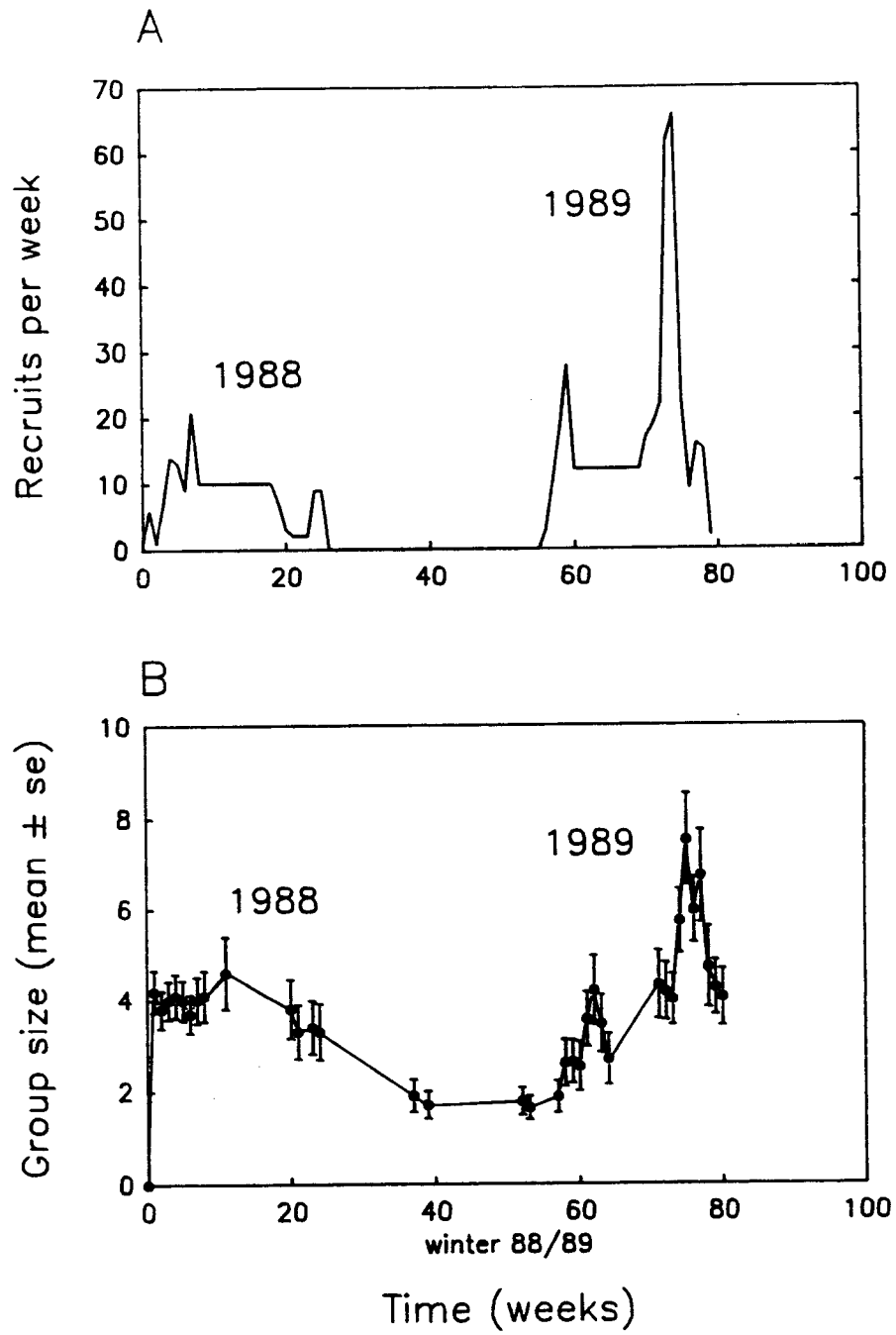
Figure 4.4



**Figure 4.5:** (a) Actual weekly settlement rate in 1988 and 1989.

(b) Actual seasonal fluctuations in mean group size during 1988 and 1989.

Figure 4.5

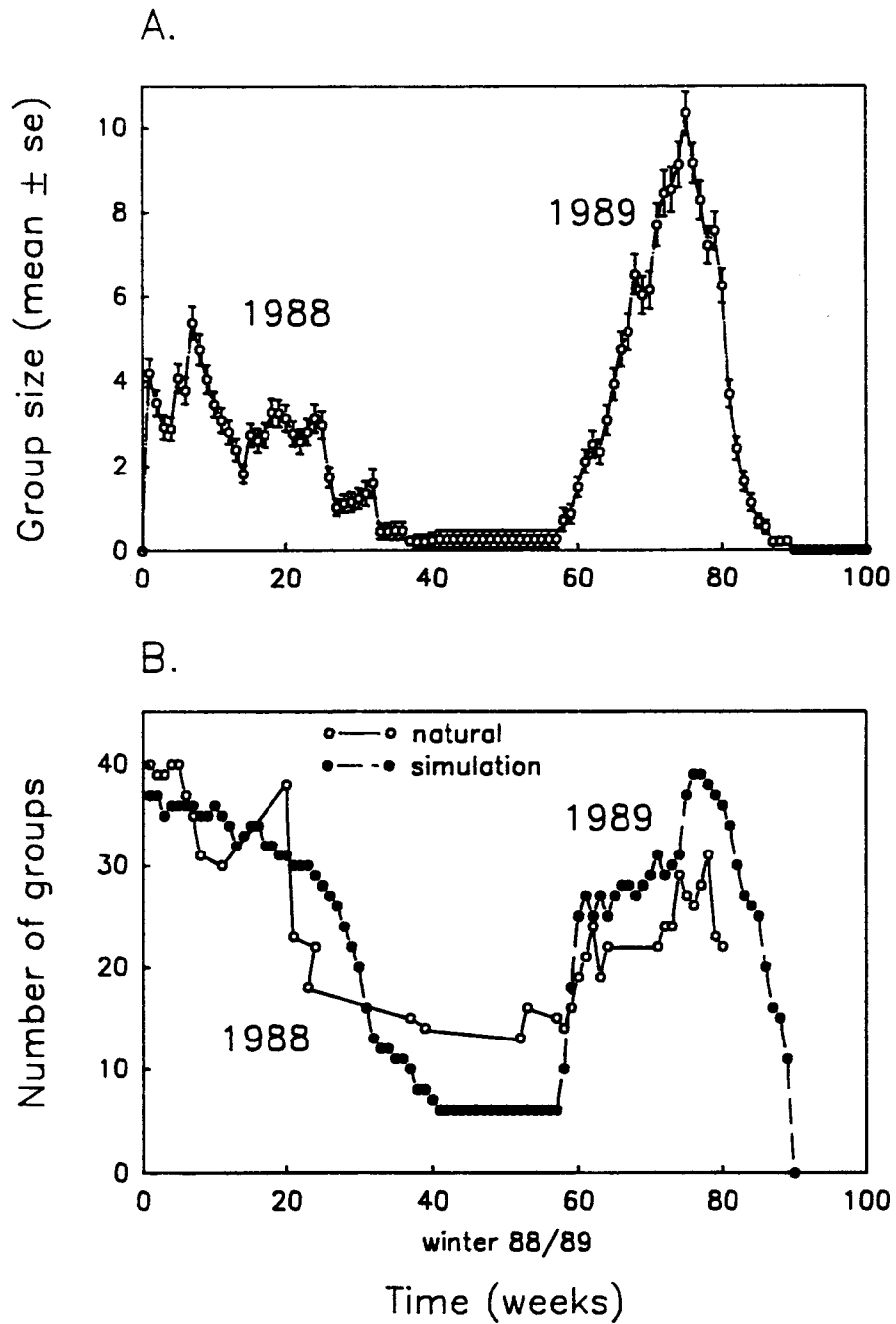




**Figure 4.6:** (a) Seasonal fluctuations in group size in 1988 and 1989 predicted from the simulation model using actual weekly settlement (Fig. 5a, above) during 1988 and 1989, and juvenile growth and survival data for 1988.

(b) Seasonal fluctuations in number of coral heads (of 40 total) supporting 1 or more fish.

Figure 4.6



## Summary and Conclusions

### 1. Summary of findings:

- a) Best estimates of larval settlement rates were obtained under a protocol of daily censuses where recruits were counted and removed during each census.
- b) Most larvae settled onto coral heads at night (between dusk and dawn), irrespective of tidal direction, suggesting that larval dispersal onto reefs has an active component.
- c) Larval settlement occurred predominantly from April to October, with peaks of settlement from May to mid-June and from late-August to mid-September in 1989.
- d) Seasonal patterns of larval settlement were synchronous among 5 sites in and around Kaneohe Bay during 1989.
- e) On a natural patch reef and an experimental grid of coral heads, larvae settled more often on coral heads supporting groups of conspecifics than on empty coral heads. Other possible factors such as coral head size, isolation, rugosity and location on the reef did not generally influence settlement rate.
- f) Binary choice experiments in the field and in an aquarium confirmed that larvae exhibited settlement preferences for groups of conspecifics, and that such preferences may be mediated through visual cues.
- g) Juveniles living in groups were part of a linear dominance hierarchy, with the largest fish being socially

dominant. This was established through monitoring aggressive chases between pairs of fish. A chase almost always consisted of a larger (higher-ranked) fish chasing a smaller fish.

h) Juvenile growth was retarded in larger groups in both 1987 and 1988, although growth rates were generally lower in 1988. Higher-ranked fish also grew faster than lower-ranked fish. Therefore, slower growth represents a cost to living in larger groups.

i) Survivorship, especially of new recruits, was enhanced in larger groups, probably due to reduced risk of predation. For recruits, survivorship was positively related to group size and recruit length. Therefore, increased survivorship represents a benefit to living in larger groups.

j) Simulation models incorporating growth and survival data predicted that recruits would reach mature size more quickly in smaller groups in both 1987 and 1988. However, the probability that a recruit would reach maturity increased with group size in 1987 and was unrelated to group size in 1988.

k) A demographic model using data collected on larval settlement and juvenile growth and survival showed that larval settlement preferences affected juvenile group sizes and the number of juveniles reaching maturity. Number of fish maturing was positively related to larval settlement rate over most settlement rates in 1987 and 1988,

suggesting that primary recruitment limitation may be operating. Differences in results between years indicated that secondary recruitment limitation was also occurring.

## **2. Conclusions:**

My results suggest that larval advection (arrival) at reefs has an active component, and that they are generally preferring to settle with conspecific groups on branching coral heads. This suggests the existence of some net benefit to living in groups for incoming larvae. While a benefit exists in the form of enhanced survivorship of new recruits, growth is slower in larger groups and so a longer time elapses in larger groups before maturity is reached. However, the increased probability of surviving to mature size in larger groups, albiet the increased time to reach maturity, may account for the strong settlement preferences demonstrated for conspecific groups.

My study highlights the ability of settling larvae to discriminate among settlement sites. Also, it demonstrates that considerable variability in the net benefit of living in large groups exists both between and within years. This variability has seldom been considered in studies of animal ecology, and may be an important element in determining the adaptive value of animal behavior.

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## **APPENDICES**

**Appendix 1: Coral cover on patch reefs in Kaneohe Bay**

**Aim:** To determine the extent of coral cover on the slopes of natural patch reefs in Kaneohe Bay.

**Methods:** On two occasions (27 August, 1987: Reefs 21, 22, 23 of Roy 1970, and 30 September, 1990: Reef 23 only), I estimated coral cover using the following method: At each of four compass directions on a patch reef ( $0^{\circ}$ ,  $90^{\circ}$ ,  $180^{\circ}$  and  $270^{\circ}$ ), a tape measure was extended directly down the reef slope from the reef crest. At depths of 3, 6 and 9 metres, a tape measure was extended horizontally along the face of the reef slope. At 50cm intervals along this tape measure, I recorded the substrate directly beneath, as one of:

- (a) Live *Porites compressa* ("P")
- (b) Live *Montipora verrucosa* ("M")
- (c) Rubble (dead coral skeletons) ("R")
- (d) Sand substrate ("S")
- (e) Bubble algae (*Dictyosphaeria* sp.) ("D").

Therefore, on each date for each reef surveyed, I collected data from 4 transects at each of three water depths.

**Results:****(a) By water depth:**

Date	Reef #	Depth (m)	% cover (mean of 4 dirns)				
			P	M	R	S	D
1987	21	3	13	4	12	14	57
		6	6	2	7	40	45
		9	4	1	19	70	6
	22	3	26	3	5	15	51
		6	10	0	10	39	41
		9	5	2	5	30	59
	23	3	23	0	13	21	43
		6	11	0	16	21	52
		9	6	4	4	77	9
1989	23	3	6	0	14	16	64
		6	9	0	29	17	45
		9	1	5	13	76	5

**(b) By compass direction:**

Date	Reef #	Direction (degrees)	% cover (mean of 3 depths)				
			P	M	R	S	D
1987	21	0	3	2	16	44	35
		90	8	5	13	37	37
		180	5	2	9	49	35
		270	13	2	16	37	32
	22	0	5	1	5	30	59
		90	5	0	21	65	9
		180	17	2	5	41	35
		270	32	3	0	38	27
	23	0	13	2	8	33	44
		90	8	0	13	49	30
		180	20	2	19	38	21
		270	11	2	2	40	45
1989	23	0	2	3	17	38	40
		90	8	0	11	40	41
		180	9	2	19	35	35
		270	3	2	26	32	37

**Conclusions:**

1. Overall coral cover (not including coral overgrown by bubble algae) was low, ranging from 0 to 32%.
2. *Porites* cover generally decreased with depth, while *Montipora* cover was negligible in 3m and 6m transects.
3. Coral cover was reasonably even with direction on all reefs.
4. Reef 23 cover patterns were very similar between years, except that *Porites* cover at 3m dropped from 23% to 9% from 1987 to 1989.

**Appendix 2: Analysis of storage lipids in *Dascyllus albisella* tissue**

**Aim:** To determine whether the percentage of body tissue comprising storage lipid was related to juvenile group size, social rank, body length, or growth in length of fish.

**Methods:** All fish analysed were captured from patch reefs 21, 22 and 23 during September, 1986. At capture, I recorded the group size and social rank of each individual, and placed each specimen temporarily on ice while in the field prior to transport to Hawaii Intitute of Marine Biology. There, I obtained the wet weight of each fish, and froze them in water. The specimens were transported, packed in dry ice, to Oregon State University, where each was thawed and had its stomach contents removed (Appendix 3). The carcass was dried to constant weight at 60°C and reweighed (dry weight: Appendix 4). The sample was then reduced to a homogeneous coarse powder using mortar and pestle and a "Wiggle-Bug" shaker. Two subsamples of the powder were separated and their lipid concentration determined using the Folch et. al (1957) chloroform/methanol extraction method, which removes polar and non-polar lipid fractions that are not membrane-bound. Lipid concentration was then expressed as a percent of total dry body weight for each fish.

**Results:**

Multiple regression model with percent lipid (100 X (gms per gm dry weight of tissue)) as dependent variable.

\*:  $p < .05$ ,  $n = 40$ .

Variable	t-value	R <sup>2</sup>	p-value
group size	-.029	.050	.778
social rank	-2.19	.026	.042*
length	4.01	.507	.001*
growth	3.56	.200	.002*
water	1.03	.334	.318

**Conclusions:** Lipid content of fish increased with fish length and growth rate (mm/day, see Chapter 3), and was positively-related to social status. The use of water content as an estimate of % lipid would not be justified for this species.

**Appendix 3: Analysis of diets of juvenile *D. albisella***

**Aim:** To determine the diets of juvenile *D. albisella*, and to determine whether the size of prey items ingested by fish were related to fish length, group size, or social rank of individuals.

**Methods:** During the course of collection and processing of specimens for lipid analysis (Appendix 2), I examined gut contents of 23 fish, ranging in total length from 20 to 63mm, and caught on patch reefs 21, 22 and 23 in September 1987. For each, I measured the maximum dimension (mm) of the largest prey item found in the gut of each fish, and identified the main components (by volume) of the stomach.

**Results:**

**1. Maximum prey size (n= 40 fish):**

Variable	t-value	p-value	R <sup>2</sup>
Group size	1.81	.088	.089
Social rank	-1.29	.073	.099
Body length	1.06	.031*	.411
-----			
Total		.001*	.506



2. Diet composition \* (n=40 fish):

Prey item	number per fish (mean $\pm$ s.e.)	% of fish containing item
Copepods	1.95 $\pm$ .39	72.5
Isopods	.75 $\pm$ .22	30.0
Unidentified crustaceans	.22 $\pm$ .08	22.5
Other	.03	2.5
-----		
TOTAL	3.65 $\pm$ .75	-

\*: All stomachs contained significant amounts of what appeared to be partly decomposed phytoplankton or benthic algae. All stomachs examined were at least half full of food.

**Conclusions:**

Fish length is a reasonable predictor of maximum prey size, although fish of lower social status also have a lower (marginally non-significant,  $p=.073$ ) maximum prey size.

**Appendix 4:** Relationships between morphometric characters for *Dascyllus albisella*

**Aims:** To examine various morphometric measures and determine what relationships existed between them.

Specifically:

(a) Was total length a good predictor of standard length?

(b) Was wet weight a good predictor of dry weight?

(c) What was relationship between gut length and body length?

**Methods:** Total length and standard length were measured to the nearest mm in the field and laboratory. Other measurements were taken from the same fish used in lipid analysis (Appendix 2): wet weight was of lightly blotted fish, dry weight was of the same specimens that had been dried to constant weight at 60° C. % water was derived from wet and dry weights for each fish. I removed alimentary tracts from each fish in the course of diet analysis (Appendix 3)- gut length was defined as its length from the distal end of the buccal cavity to the anus, measured with an ocular eyepiece.

**Results: Correlations between morphometric characters**

(n=40, \*: p&lt;.05)

	tot.l	Std.l	wet wt	dry wt.	%water
Total length(mm)					
Standard len(mm)	.996*				
wet weight (gms)	.969*	.962*			
dry weight (gms)	.963*	.956*	.999*		
water content(%)	-.778*	-.772*	-.754*	-.760*	
gut length (mm)	.955*	.943*	.953*	.946*	-.745*

**Conclusions:**

1. The high positive correlation between total length and standard length allows accurate conversion between these measures of fish length.
2. Wet weight can be accurately converted into dry weight.
3. Gut length is proportional to body length, suggesting that no major ontogenetic dietary changes occur to juvenile fish.

**Appendix 5:** Histological examination of gonadal tissue of *Dascyllus albisella*

**Aims:** To determine the state of sexual maturity of larger juveniles, and to test the hypothesis that maturity occurs at 70mm total length.

**Methods:** Fish were removed from the Sampan coral grid on 8 October 1990. I recorded their group size, social rank, total length, standard length (some) and dissected gonads to Bouin's Fixative for 24 hours, then stored them in 70% EtOH. These gonad samples were stained, sectioned and interpreted by Dr. Maria Rasotto and Dr. D. Shapiro of Dept. of Zoology, Univ. of Puerto Rico.

**Results:**

#	Total Length (mm)	Standard Length (mm)	Rank/Group Size	Wet Weight (gms)	Gonads
1	71.0	-	1/11	11.01	F,I
2	60.5	-	5/11	6.26	M,I
3	63.5	-	3/11	7.53	F?,I
4	66.5	-	2/11	8.69	F,I
5	60.0	-	1/1	6.20	F,I
6	63.5	-	1/4	7.71	F,I
7	59.5	-	1/3	6.63	M,I
8	73.5	-	1/5	11.33	F, vitt
9	62.5	-	2/5	7.19	F,I
10	60.5	47.0	1/4	7.22	F,I
11	56.0	44.0	1/2	5.93	F,I
12	72.0	56.0	1/15	1.22	M,I
13	62.0	48.0	6/15	7.72	F,I
14	70.0	54.0	2/15	10.88	F,I
15	63.5	49.0	5/15	8.65	M?,I
16	60.0	46.0	7/15	6.81	F,I

(Key: see next page)

**Key:**

(M: spermatocytes seen; F: oocytes seen; I: immature- no gametogenesis seen; vitt: vittelogenesis seen i.e. likely mature)

All gonads (except # 13) were filled with oocytes.

Specimens prepared and interpreted by Dr. Maria Rasotto.

**Conclusions:**

Only one fish (#8, 73.5mm total length) was considered to contain mature (vittelogenetic) gonads), supporting the hypothesis that the length at maturity was approximately 70mm.

**Appendix 6:** Examination of otolith depositions of recruit  
*Dascyllus albisella*

**Aims: To:**

1. Determine the duration of the planktonic larval stage
2. Determine whether recruits collected on the Sampan coral grid during 1990 were newly settled from the plankton, or had resettled from adjacent reefs.
3. Consider the relationship between larval duration and body length of new recruits. A strong positive correlation would indicate that growth rates in the plankton were not highly variable.
4. Monitor seasonal variation in length of settling larvae.

**Methods:** I collected a sample of 33 new recruits (9.51±0.86 sem, range 7.7-10.7)mm SL on the Sampan grid On 20 September 1989, and frozen in water. These were sent in 90% EtOH to Dr. G. Wellington (Univ. of Houston) for otolith analysis. In addition, I made collections of new recruits from Sampan grid at other times during the summer and measured total lengths of a subsample of fish in each collection.

**Results:**

1. Duration of planktonic larval stage: 25.0±1.8 sem days, n=33 fish, range= 21 to 28 days.
2. All 33 recruits were 0 to 3 days post-settlement.

However, no clear post-settlement otolith daily increments were seen by Dr. Wellington.

3. There was a strong positive relationship between larval duration in days and body length (SL) of recruits ( $r=0.87$ ,  $n=33$ ). 4. Variation in recruit lengths, 1989, Sampan grid:

Date	Mean length	sem	range (mm TL)	N
15 May	13.9	0.18	12.5-16.5	48
17 May	13.7	0.17	12.5-16.5	9
25 May	15.6	0.25	13.5-17.5	20
1 June	15.7	0.17	14.0-17.0	20
7 Sept	13.7	0.20	12.5-15.0	20
20 Sept	13.8	0.22	11.5-15.0	20

Therefore, variation in recruit body length between collection days was similar to that within a day.

#### Conclusions:

1. Recruits sampled on the coral grid were recent settlers.
2. There appears to be little variation in growth rate of larvae while in the plankton, since a strong body length/larval duration relationship was found.
3. Given the strong correlation between body size and planktonic duration, this suggests that mixing of larvae from cohorts hatched several days apart occurs. However, the slightly larger recruits from 25 May and 1 June collections suggests slightly longer larval durations at those times.
4. Larval duration was similar to that reported by Wellington and Victor (1989).

## Appendix 7: Individual differences in growth rate

**Aims:** The unexplained variation in growth rates of fish in multiple regression models (Chapter 3, Table 6) amounted to 45% in 1987 and 63% in 1988. Here, I estimate the amount of this unexplained variation that is due to intrinsic differences in growth rate between individuals.

**Methods:** For tagged individuals that were recaptured on two successive occasions (stanzas), I considered that the strength of the relationship between residual growth (from multiple regression equations in Table 6) in the two successive stanzas would indicate the proportion of unexplained variation attributable to individual differences.

**Results:** Residual growth in one stanza accounted for 39% of the variation in residual growth of fish in the subsequent stanza in 1987, but only 1.5% in 1988 (Table 1).

**Table 1:**

Year	R <sup>2</sup>	p value	N
1987	0.392	0.012*	15
1988	0.014	0.508	45

**Conclusions:** In 1987, individual differences in growth rates (i.e., those not attributable to direct effects of the variables in Table 6) explained a significant



proportion of the variation in growth rate between individuals. However, this was not so in 1988. The low % variation explained by individual differences in 1988 suggests that heritability of growth rate (sensu Falconer 1979) is low for this species. Fish generally exhibit particularly plastic growth, but individual variation in growth can be significant in some species (e.g., medaka: Magnuson 1962; plaice: Purdom 1974).