

Post-settlement movement of coral reef fishes and bias in survival estimates

Jennifer L. Frederick*

Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, USA

ABSTRACT: Most coral reef fish have a bipartite life-history characterized by a pelagic larval phase followed by transformation and settlement into a benthic existence. There is increasing interest among marine ecologists in determining the importance of post-settlement processes to reef fish demography. This study distinguishes movement as an important post-settlement phenomenon affecting estimates of early survivorship of juvenile coral reef fishes. Individuals settling onto artificial patch habitats were collected, marked, released and monitored by visual census over 2 systems of isolated artificial patch habitats. Some recently settled juvenile fish moved as much as 100 m over open sand. Probability of movement was dependent on species; size was a significant factor among species, but not among conspecifics. Survivorship calculated from observations of uniquely marked individuals was contrasted with survivorship estimated by comparing the initial number of newly settled individuals at a site with the number of individuals there after a given time interval. The comparison revealed that new settlers and immigrants can mask the loss of individuals included in the original census and thereby inflate estimates of survivorship. Comparing survival estimates with and without accounting for movement demonstrated that survivorship can be underestimated when new settlers subsequently emigrate and survive at another site, but are unwittingly recorded as lost due to mortality. Significant differences were observed in survival experiences for different species and size classes. Where significant differences were found in survival times of mobile individuals versus sedentary, those that moved survived longer.

KEY WORDS: Coral reef fishes · Recruitment · Survival · Mortality · Movement · Artificial reefs

INTRODUCTION

Confronted with the discordant results drawn from 2 decades of ecological research, many marine ecologists now concede that no single factor model adequately explains the distribution and abundance of marine organisms with complex life histories. Rather, the cumulative effects of a number of interacting factors cause pre-settlement losses of larvae and post-settlement losses of juveniles (Doherty 1991, Jones 1991, Doherty & Fowler 1994). For reef fishes, researchers have demonstrated that stochastic variation in larval success can affect recruitment strength (Williams & Sale 1981, Sale et al. 1984a, Doherty 1987), but that high juvenile mortality can also modify recruitment patterns (Doherty & Sale 1985, Victor 1986a, Eckert

1987, Shulman & Ogden 1987, Meekan 1988, Robertson 1988, Sale & Ferrell 1988).

There is continued interest among coral reef fish ecologists in evaluating the importance for early survivorship of the effects of post-settlement processes, e.g. predation (Carr & Hixon 1995), ontogenetic habitat shifts (Lirman 1994, Eggleston 1995), habitat selection (Sweatman & St. John 1990, Wellington 1992), habitat associations (Connell & Jones 1991, Booth & Beretta 1994), and intraspecific competition (Forrester 1990, 1995). A few researchers have inferred that early post-settlement movement of juveniles is an important process shaping observed patterns in juvenile abundance (Shulman 1985, Robertson 1988). However, few have attempted to directly measure movement of juveniles as an important post-settlement phenomenon that might affect estimates of early survivorship. Most studies designed to measure early survival of juveniles have assumed that significant losses from the study site

*E-mail: jfrederi@hpu.edu

were due to mortality, while losses due to emigration to other habitats were unlikely, or at most, negligible (Williams 1980, Aldenhoven 1986, Victor 1986a, Eckert 1987, Jones 1987a, b, 1988, Sale & Ferrell 1988, Booth & Beretta 1994). Yet when losses are due to movement, survival in some other habitat is possible and would have population consequences entirely different from mortality.

The primary obstacle in distinguishing post-settlement losses due to mortality from losses due to successful movement has been one of identifying individuals that have successfully moved. In attempts to overcome this obstacle, some researchers have implicitly used immigration rates to a study site as an estimate for emigration rates from a study site (Victor 1986a, Eckert 1987, Sale & Ferrell 1988, Connell & Jones 1991). Others have assumed that distances of open sand habitat ranging from a few meters (Williams & Sale 1981, Sale et al. 1984b, Doherty 1987) to a few hundred meters (Carr & Hixon 1995) were adequate to minimize successful movement from their study site (in most cases a natural or artificial patch reef) to other suitable habitats. Presumably, at sufficiently isolated sites, the effects of movement and local mortality are indistinguishable because any attempts at movement would end in mortality.

However, the minimum area of open sand habitat that 'sufficiently isolates' a patch habitat and prevents successful movement of juveniles has not been experimentally verified. Given the wide range of existing estimates of what distance of open sand minimizes successful movement, early survivorship may have been underestimated frequently at study sites from which fish moved successfully and survived at another site, but were erroneously recorded as lost due to mortality. If successful movement of early or late juveniles to other suitable habitat can moderate mortality or at least increase the probability of recruitment, it may be an important post-settlement process. Early post-settlement movement should be quantified in survivorship models rather than remain masked within 'mortality'.

Many early mortality estimates based on net losses of fish from a study site over time may have been confounded by the appearance of new individuals indistinguishable from previously censused individuals. When individuals, or at least cohorts, cannot be distinguished, there is a high degree of uncertainty in survivorship estimates that are based on comparing the initial number of newly settled individuals with the number of individuals present after a known time interval. This is particularly critical when census intervals are short (e.g. daily) compared to the time scale over which developmental changes might allow individuals or at least cohorts to be distinguished.

This purpose of this study was to clearly demonstrate the movement capabilities of juvenile fishes between patch habitats by making direct field observations of marked individuals dispersing over an array of artificial reefs. Within the model system of artificial reefs, I tested 2 specific hypotheses: (1) survival can be underestimated when successful emigration from a study site to a new habitat is not accounted for in survivorship models; and (2) mortality can be underestimated when losses of individuals that are replaced between censuses by new, indistinguishable conspecifics remain undetected.

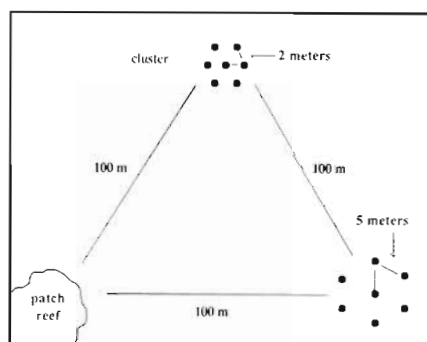
MATERIALS AND METHODS

Movement between artificial patch reefs. To investigate movement patterns, 4 artificial reef clusters were deployed at 2 sand sites in Hanalei Bay, Kaua'i, Hawaii, isolated by at least 100 m or 350 m from the nearest natural or artificial reef and at a depth of approximately 10 m. Underwater visibility varied from <1 m to 15 m. Artificial reef units were constructed of 4 orthogonally stacked and cemented concrete blocks (each block 10 × 20 × 40 cm with 2 holes 3 × 15 × 20 cm). Polypropylene rope streamers were tied to the blocks and unraveled so that 1 m of fringe extended into the water column above the reef unit (as in Gorham & Alevison 1989). This design provided numerous small holes for safe refuge for juvenile fishes and yet was easy to census. Each cluster consisted of a central reef unit or units encircled equidistantly by evenly spaced perimeter reef units. Each of the 4 clusters differed in the radial distance of open sand between central and perimeter reefs (Fig. 1).

The first 2 clusters were assembled concurrently, with radii of 2 m or 5 m, and were isolated by 100 m of sand habitat from each other and the nearest natural reef (Site I). Because substantial movement between clusters was observed, a new site isolated from the nearest natural reef by 350 m was chosen for the third and fourth clusters (Site II). These were assembled consecutively and had a radius of 50 m, or 2 radii of 20 and 50 m, respectively. For clusters with smaller radii (i.e. 2 m and 5 m), adjacent outer reefs in a cluster were equidistant from the central reef and each other. Adjacent outer reefs of clusters with larger radii (i.e. 20 m and 50 m) were spaced 10 to 20 m apart so that fishes moving in any direction were likely to encounter a suitable habitat (Fig. 1).

Between 27 June and 30 August 1994, 286 recently settled fishes of 6 species from 8 to 57 mm standard length (SL) (Table 1) were collected from all perimeter reef units, individually marked using fluorescent elastomer injection (Frederick in press), and released at

SITE I



SITE II

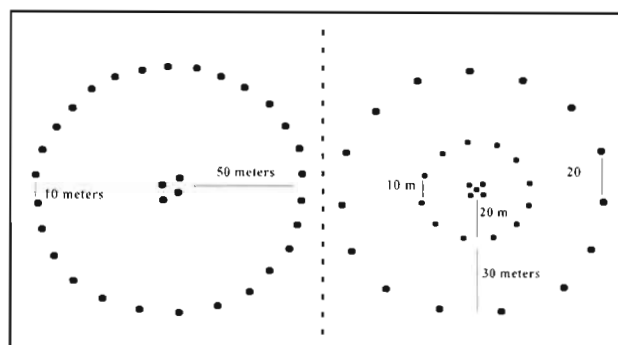


Fig. 1 Artificial reef site configurations in Hanalei Bay. Two clusters of artificial reefs (2 m or 5 m radii) isolated by 100 m from each other and the nearest natural reef were monitored simultaneously at Site I. Two clusters (50 m or 20 and 50 m radii) isolated by at least 350 m from any other reef were monitored consecutively at Site II

the central reef units to a maximum density of 70 fish (mean = 41 fish). At Site I, fishes were collected within 8 d of colonizing the reefs; at Site II fishes were collected within 2 d of colonizing the reefs, many of these fish having little or no pigmentation. Movement and survivorship of marked juveniles were monitored by visual census of all reef units in the artificial reef clusters at daily intervals (or as often as feasible). Regular observation periods for individuals ranged from 2 to 48 d; some individuals were censused after the completion of the study up to 133 d after release. The fate of each marked individual was recorded: survival on the central reef unit, movement to a perimeter reef unit, or assumed mortality if it could not be located on the reef cluster. Because individuals could have emigrated beyond the radius of the experimental reef clusters and survived on natural reefs more than 100 m or 350 m away, reported survival is a minimum estimate.

Analysis of survival data. Analysis of survival data required several special considerations. First, survival measurements were confounded by time. That is, whether or not death was observed was influenced by the length of the observation period for the individual and the conditions during that period. Because new individuals were continually added to the study and were followed over various time intervals, the period that each individual was followed was taken into account by stratifying the analysis by the shortest time interval over which differences in survival were measured (daily). Second, over 40% of the fishes outlived the study. This led to right-censored observations;

Table 1. At each site for each species of fish used in movement experiments, total number of individuals marked, number lost from study area during period of monitoring, mean, minimum and maximum size (mm SL), and proportion of all individuals marked and released on a cluster with a given radius that were observed to make at least one movement. Distances are meters traveled over open sand between patch habitats. The category 20 m includes movements observed between the central reefs and the 20 m inner ring and between the central reefs and the 50 m outer ring of the cluster with both radii. Thus, the conservative assumption was made that movements to the outer ring were made in a stepping stone progression

Family	Species	Total	Lost	Size (mm SL)		Movements		
				Mean \pm SD	Min – max	2 m	5 m	100 m
Site I								
Acanthuridae	<i>Acanthurus blochii</i>	9	7	43 \pm 2.3	40 – 48	0/0	9/9	0/9
Apogonidae	<i>Apogon</i> sp.	4	4	14 \pm 7.1	9 – 24	0/3	0/1	1/4
Pomacentridae	<i>Dascyllus albisella</i>	14	13	15 \pm 5.1	8 – 21	1/6	4/8	0/14
Chaetodontidae	<i>Heniochus diphreutes</i>	22	8	43 \pm 2.4	38 – 47	5/5	17/17	3/22
Lutjanidae	<i>Lutjanus kasmira</i>	5	4	46 \pm 4.5	40 – 52	0/0	5/5	2/5
						20 m	50 m	
Site II								
Acanthuridae	<i>Acanthurus blochii</i>	87	65	32 \pm 6.9	20 – 42	0/40	3/47	
Chaetodontidae	<i>Chaetodon miliaris</i>	14	7	26 \pm 2.1	22 – 31	0/0	1/14	
	<i>Heniochus diphreutes</i>	71	34	38 \pm 5.9	26 – 57	0/43	0/28	
Lutjanidae	<i>Lutjanus kasmira</i>	60	26	32 \pm 3.8	20 – 38	25/44	1/16	

that is, the outcome for these individuals was unknown. Omitting these data would underestimate survival, because it was usually the most long-lived individuals that were right-censored. To take into account the time that these individuals were alive, without knowing the exact time of death, I computed survival as a cumulative probability function: probability of survival over the time interval given that the individual had survived up until that time interval (Lee 1992). Finally, survival data did not follow a normal distribution, because of the high early mortality (Type III mortality curve) typical of many marine animals. I used the SAS procedure LIFETEST, which can analyze survival data involving these sorts of special considerations (SAS 1990).

To examine survival as it varied among species, sites, mobile versus sedentary individuals and size classes, I used a modified non-parametric log rank test (Mantel-Haenszel procedure) with time stratified by day (Everitt 1994). This test compares the observed number of deaths occurring among groups at each particular time point with the number expected if the survival experiences of the groups were the same. It is fairly robust to a non-constant hazard ratio (age-specific mortality rate), which frequently occurs when time of origin in a treatment is not the same and when censoring occurs (Pyke & Thompson 1986).

RESULTS

Movement between artificial patch reefs

Movement between patch reefs was observed for all 6 species. Over all species and cluster configurations, approximately 25% of marked fishes were observed to move at least once over distances of open sand ranging from 2 to 100 m (Table 1). Of the 41 individuals that moved, approximately 30% made multiple movements. Some were observed to move 3 or 4 times, most often back to reefs that they had already visited. Four additional 100 m movements were observed for the butterflyfish *Heniochus diphreutes*: 1 individual moved between reef clusters twice, and 3 other individuals moved to the 5 m cluster after their 2 m cluster was dismantled. Fifteen additional movements were observed for the snapper *Lutjanus kasmira* representing repeated movements of 9 individuals over distances of 10, 20 and 30 m.

Factors associated with movement

Probability of movement was dependent on species (Fisher's exact test, $n = 286$, $p < 0.001$) (Table 1). How-

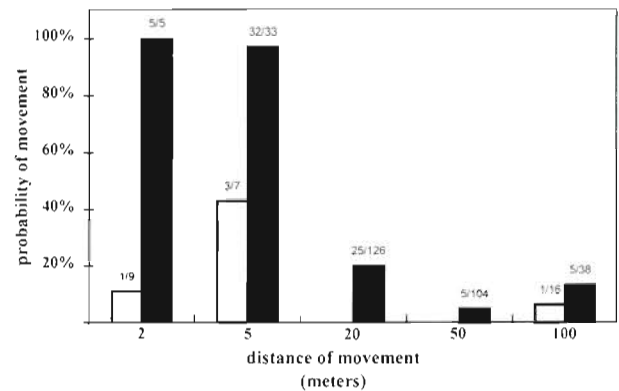


Fig. 2. For 2 size classes, probability of movement over a given distance of open sand between patch habitats (radii of reef clusters). Probabilities represent the percent of all individuals marked and released on a cluster with a given radius that were observed to make at least one movement. Size classes are ≤ 20 mm SL (white bars) and > 20 mm SL (black bars). The distance 20 m includes movements observed between the central reefs and the 20 m inner ring and between the central reefs and the 50 m outer ring of the cluster with both radii. This accommodates the conservative assumption that movements to the outer ring were made in a stepping-stone progression. No data are available for fishes ≤ 20 mm SL moving 20 m or 50 m.

ever, at Site I (2 m and 5 m radii clusters), the species effect was confounded by fish size. Most fishes ≤ 20 mm SL were apogonids and pomacentrids, and most fishes > 20 mm SL were acanthurids, chaetodontids, and lutjanids. Species of the smaller size class moved less frequently than those of the larger (Fisher's exact test, $n = 54$, $p < 0.001$) (Fig. 2). For mobile fishes > 20 mm SL (acanthurids, chaetodontids, lutjanids), larger individuals traveled longer distances (Kendall's tau = 0.317, $n = 35$, normal approximation $p = 0.004$). Pomacentrids and apogonids were not included in this test because none were monitored at Site II (20 m and 50 m radii clusters), where potentially longer movements could have been measured. Among conspecifics, there was no significant difference in sizes (SL) of mobile and sedentary individuals (Rank sum tests, $p > 0.17$, except among *Dascyllus albisella*, $p = 0.083$). The weakly significant difference for *D. albisella* may be due to lower overall survival for smaller individuals that resulted in less opportunity for movement.

Factors associated with survival

The survival experiences of the 6 species in this study were significantly different [Mantel-Haenszel (log rank) test, $p = 0.0001$]; therefore, further analysis was stratified by species. Survival data from Sites I and

II were pooled for analysis, because no significant differences in survival time were found for species measured at the 2 sites ($p \geq 0.16$). For 4 species, there was no significant difference in the survival time of mobile versus sedentary individuals ($p \geq 0.18$). Where more significant differences were found (*Apogon* sp. $p = 0.08$; *Dascyllus albisella* $p = 0.0006$), mobile individuals survived longer than those that remained sedentary. *Acanthurus blochii*, *Heniochus diphreutes* and *Lutjanus kasmira* showed highly significant differences in survival between size classes ($p < 0.001$). Other species showed no differences ($p > 0.4$). Where significant differences were found, smaller size classes generally showed lower survival. Among fishes that moved, there were no significant differences in survival (1) by distance of movement ($p > 0.3$) or (2) by the time between release and movement ($p > 0.8$).

Survival estimates and the effect of successful movement

Using results of repeated censuses of the clusters, survivorship was calculated using 2 models. The first model (Model 1) provided a survival rate based on the losses of marked fishes from the central reef over time. By attributing all losses to mortality and ignoring movement, Model 1 underestimated survivorship. The second model (Model 2) used the marking program to allow recognition of migrators, whose survival could be measured after emigration from the central reef. Model 2 produced more accurate survival rates, because real mortality was not inflated by losses due to movement. Non-parametric estimates of Model 1 and Model 2 survival functions were generated using the life table method of SAS LIFETEST. Comparing the curves for each species observed to move within or between reef clusters at Site I (Fig. 3) and within clusters at Site II (Fig. 4) demonstrates the importance of movement as a source of post-settlement loss.

The blue-striped snapper *Lutjanus kasmira* demonstrated the greatest tendency for post-settlement movement. After 8 d of observations at Site I (Fig. 3B), survival was twice as high in the model which included individuals moving 100 m (Model 2), a difference maintained through Day 35 of observations. At Site II (Fig. 4A), where 43% of *L. kasmira* emigrated 20, 30 or 50 m from the central census site, survival was about twice as great in Model 2 for most of the 48 d period of observations.

The Hawaiian domino damselfish *Dascyllus albisella* was the smallest species studied; marked individuals were as small as 8 mm SL. Unlike other fishes in this study, young *D. albisella* remained inconspicuously hidden within holes of the reefs during censusing and

were not observed to roam far from shelter. However, movement of marked individuals between patch reefs did occur, creating striking differences in survival curves. Half of all fish marked at the 5 m radius cluster moved from the central reef to a perimeter reef; only 1 of 6 fish moved at the 2 m radius cluster, but overall survival was very low. Without knowledge of these movements, survival would appear to plummet to zero after only 4 d (Fig. 3C), when in fact survival was greater than zero for at least 35 d.

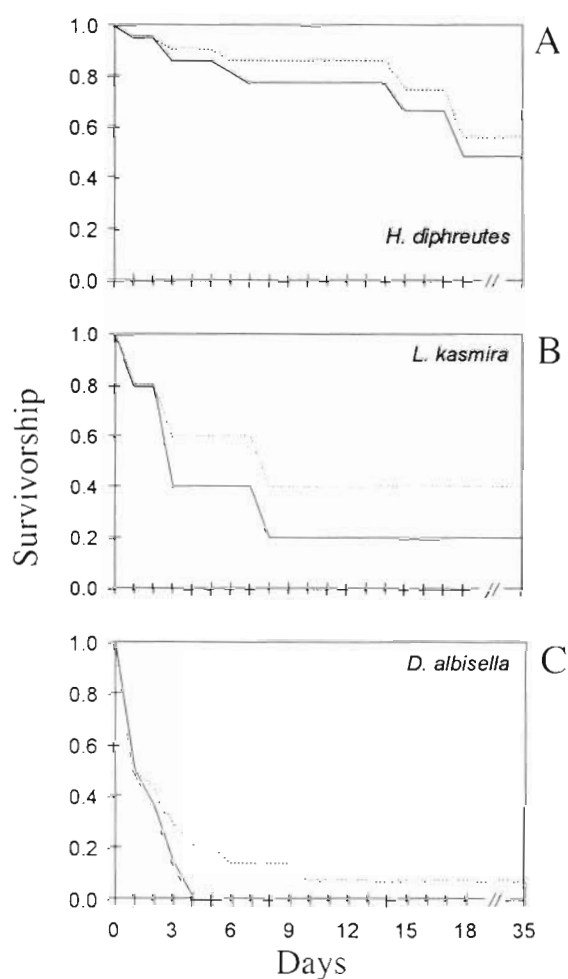


Fig. 3. Survival for 3 species at Site I. Model 1 (—) is the survival estimate based on losses from the central reefs. Model 2 (---) is the survival estimate based on losses of individuals over the entire site and includes survival of mobile individuals. Differences between Model 1 and Model 2 survivorship represent the survival of individuals moving 100 m between reef clusters for *Heniochus diphreutes* (A) and *Lutjanus kasmira* (B), which schooled freely over the 2 and 5 m radius clusters. For *Dascyllus albisella* (C), the difference between Model 1 and Model 2 survivorship represents the survival of individuals moving 2 m or 5 m within clusters. Number of migrators: A = 3, B = 2, C = 5. Total number of individuals monitored: A = 22, B = 5, C = 14

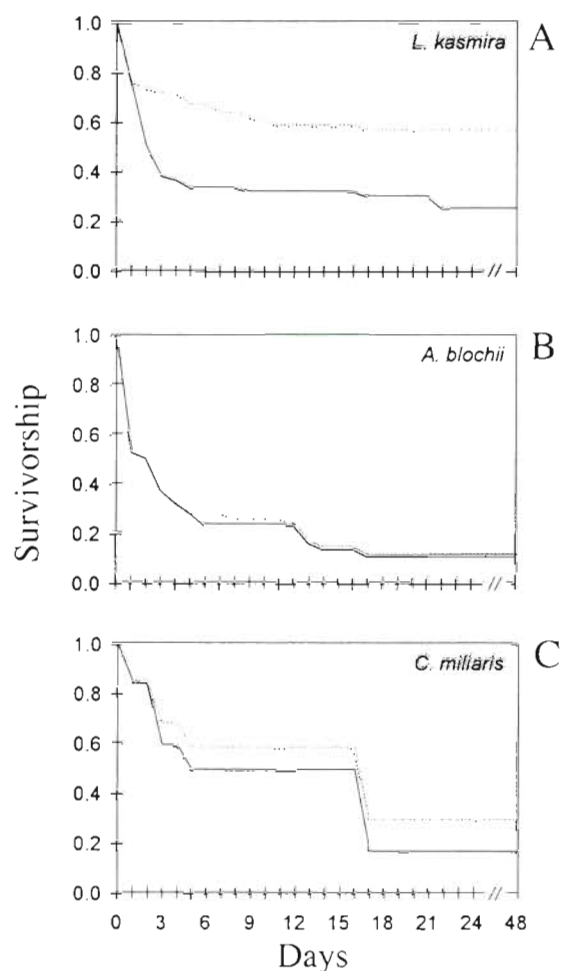


Fig. 4. Survival for 3 species at Site II. Model 1 (—) is the survival estimate based on losses from the central reefs. Model 2 (.....) is the survival estimate based on losses of individuals over the entire site and includes survival of individuals moving 20 m or 50 m. Number of migrators: A = 26, B = 3, C = 1. Total number of individuals monitored: A = 60, B = 87, C = 14

Mortality estimates and the effect of undetected loss and replacement

To measure the bias in mortality estimates from new indistinguishable colonizers replacing previously censused individuals, the population flux at the central reefs of the clusters at Site II was monitored by repeated censuses. At each census, loss from the central reef for the period between censuses was estimated by 2 methods: net loss and actual loss. Net loss was computed as the difference between a count of the total number of individuals present on the central reef and the count of the previous census. Because this method did not keep track of individuals, it did not distinguish new individuals that had colonized between

censuses. Net loss was contrasted with actual loss, which was computed as the number of marked individuals that were present on the central reef at the previous census and absent at the current census.

A comparison of the 2 'mortality rates' showed that unrecognized new colonizers could replace previously censused individuals and mask actual losses. In 74 % of censuses where actual loss of marked individuals was measured, net loss underestimated actual loss (Fig. 5). For censuses where net loss was less than actual loss, replacement of previously censused fish by new fish would have gone undetected but for the marking of individuals. In other cases, when colonization numbers were large, resulting in an apparent net gain of fish, replacement would likely have been suspected. However, without accurate identification of individuals, the total amount of mortality that had occurred between censuses would remain unknown. Neither net loss nor actual loss in the examples of Fig. 5 is corrected for successful, monitored emigrations from the central reef to perimeter reefs (as in Figs. 3 & 4).

Evaluation of effects of marking and transplantation on movement patterns

All newly marked fish were held and observed underwater for 2 hours before release. Based on laboratory observations, signs of imminent mortality (e.g. increased reaction time and loss of equilibrium) could be detected within that time (Frederick in press). Among fishes >20 mm SL ($n = 270$), no signs of stress or imminent mortality were observed. For fishes <20 mm SL ($n = 16$), 2 individuals appeared negatively affected and were assumed to have died shortly thereafter. This level of mortality was not significantly greater than zero (Fisher's exact test; 1-sided, $p = 0.276$). In this experiment, designed to test for emigration by marking and monitoring individuals, it would not have been possible to accurately identify and follow a control group of unmarked fishes.

Transplantation is commonly employed to manipulate densities of individuals on artificial reefs to examine various post-settlement processes. Some investigators report little difficulty in getting transplants to remain on their host reefs (Jones 1987a, Forrester 1990, 1995, Booth 1991) and no significant differences in the permanence of transplants versus controls (Lirman 1994, Carr & Hixon 1995). Others report spontaneous emigration by pomacentrids, which required repeat transplantation (Ebersole 1985, Jones 1987b, 1988) or special measures to prevent emigration (Sweetman 1985b). The time to first observed movement after manipulation and release was examined to identify possible spontaneous emigration. Immediately

Fig. 6. Number of fish and directional headings of first observed movement in degrees relative to place of collection (home reef) for fish moving from the central reefs to perimeter reefs (i.e. compass bearing of collection reef minus compass bearing of destination reef). Fish moving at a heading of 0° returned to place of collection

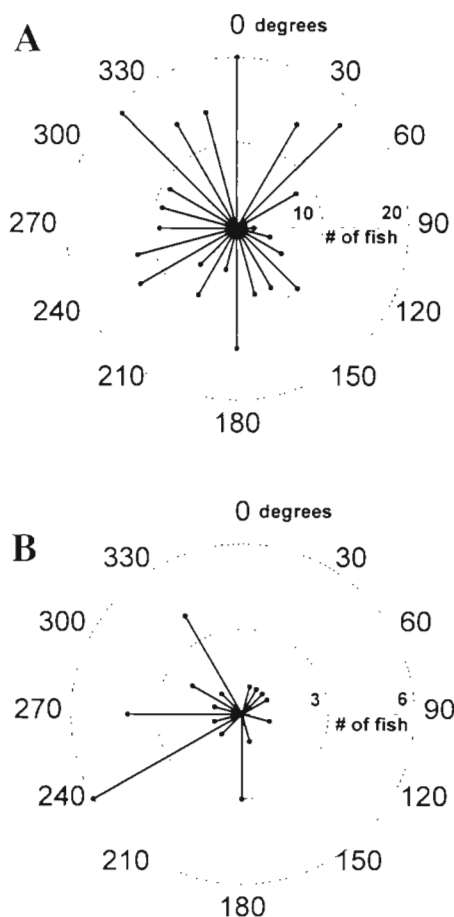


Fig. 7. (A) Number and angular distribution of fish initially colonizing artificial patch reefs at the perimeter of Site II. Dispersion is indicated by compass bearings of perimeter reefs from the center of the circular cluster. Length of rays extending from center are scaled by frequency. (B) Number of fish and directional headings of destination reefs after dispersal from central reef site to perimeter reefs at Site II

DISCUSSION

A large part of the research on early post-settlement processes of coral reef fishes has been conducted with pomacentrids on patch reefs, in part because of their presumed sedentary nature. Although the results obtained in this study are based on limited sample sizes of only 1 species of damselfish, they suggest that early survival of pomacentrids may often have been underestimated because of undetected movements (Jones 1987a, b, 1988, Sale & Ferrell 1988, Booth & Beretta 1994). At least 2 studies exist in which movement of pomacentrids has been directly observed. In a study of *Dascyllus albisella*, Booth (1991) marked 30 new recruits (10 to 15 mm SL) by fin clipping and transplanted them to an array of artificial reefs. One movement was observed between reefs 10 m apart in a

5 × 12 grid of 60 small coral heads, but many marked fish were never resighted. Forrester (1990) manipulated *D. aruanus* juveniles on an array of artificial reefs and measured a 2% movement rate between reefs 20 to 25 m apart. Only juveniles that had grown larger than 25 mm fork length (FL) were marked for individual identification.

Post-settlement movements by juveniles of other taxa are largely unconfirmed in the literature. Brock et al. (1979) inferred substantial post-settlement movement from a recolonization experiment on a patch reef in Kane'ohe Bay, Hawaii, isolated from other reefs by 120 m. The majority of fishes colonizing the patch reef were juveniles well beyond transformation, indicating that they had not arrived from the plankton. In a study of abundances of surgeonfishes on patch reefs in the Caribbean, Robertson (1988) suggested that for some patch reefs receiving few new settlers but supporting large populations of larger size classes, relocation some time after settlement may be the primary source of recruits. Mortality of labrids in the Caribbean and Great Barrier Reef (Victor 1986a, Eckert 1987) was studied on reefs isolated by 10 m of sand or seagrass from other suitable habitats. At both sites, negligible emigration was inferred, because no immigration was observed. Based on estimates of low immigration rates to a temperate reef population of blennies *Forsterygion varium*, Connell & Jones (1991) also inferred that emigration was negligible for new recruits up to 2 mo post-settlement. Forrester (1995) observed movement of marked Caribbean gobies *Coryphopterus glaucofraenum* between natural and artificial reefs located at least 8 m from any other reef, but apparently the event was rare. Results reported here of acanthurids, chaetodontids, and lutjanids moving at least 50 m and sometimes 100 m confirm the possibility that early post-settlement movement occurs with some frequency among some common coral reef species.

The demonstrated ability of coral reef fishes to make successful early post-settlement movements between patch habitats has important implications. To determine more accurately how survival of juvenile coral reef fishes is affected by post-settlement processes, we must study the fate of individuals on a larger spatial scale than previously. Knowledge of juvenile movement patterns aids in performing repeated visual census of juveniles over large reef areas where an observer could predict the home range of a particular species at a particular age. Especially when the application of a marking technique may be undesirable or not feasible, recensusing individuals or cohorts based on an *a priori* estimate of their home range can facilitate studying other early life history characteristics. It would also help in designing closed system juvenile demographic studies which utilize systems of patch reefs.

The results of this research suggest that for studies of early survival for which emigration from the census area has remained unaccounted, survival may have been underestimated. This research has shown that individuals can survive and persist after moving at least 100 m to a new site and have a positive effect on survival estimates at least as long as those that remain sedentary. Estimates of survival may have been further confounded by arrival of undetected new colonizers. Mortality rates based on net losses of fish between censuses are common in the literature (Victor 1986a, Eckert 1987), probably because until recently no suitable marking method was available. Based on the present demonstration, early mortality reported can be underestimated due to unrecognized loss and replacement by settlement or immigration. These 2 processes—unobserved migrations and unobserved settlement and replacement—probably create bias in survival estimates simultaneously, so that a wide range of net errors is possible. The observations of this study illustrate the potential effects in a model system. The magnitude of error is probably dependent on strength of local settlement pulses, local predation rates, habitat quality, the frequency of movement, and the time elapsed between censuses.

Making a movement between habitats presents risks to survival, both in the hazards of the journey to another habitat and in the suitability of that destination. It may be assumed that post-settlement movements would only be beneficial if the risk to survival induced by leaving is less than the potential loss of fitness incurred by staying in a habitat with strong negative effects. Therefore, the prevalence of successful post-settlement movement may be an indicator of the relative risks associated with predation and the suitability of various alternative habitats, and thus may be site-specific. Although this study did not attempt to assign motive for the observed movement, it does imply that juvenile coral reef fishes may be equipped with the behavioral flexibility to exercise habitat choice shortly after settlement. Habitat sampling may be a life history tactic for juvenile fish and may confer an advantage to species that make frequent post-settlement movements.

Perhaps marine ecologists have underestimated the abilities of newly settled coral reef fishes. The most recent work of fish biologists suggests that young reef fish have great developmental and behavioral flexibility. While still in the plankton, they may be able to slow their growth and sustain periods of active swimming until suitable settlement habitat is encountered (Victor 1986b, Cowen 1991, Stobutzki & Bellwood 1994). Upon settlement, juvenile fishes have exhibited diel behavioral patterns, sensory cueing and habitat choice (Eckert 1985, Sweatman 1985a, 1988, Sweatman & St. John

1990, Wellington 1992). In fact, Kaufman et al. (1992) used the term 'transition phase' to describe the sequence of events bridging the late larval and early juvenile periods, and suggested that the importance of these events as determinants of population structure has been underestimated. Ontogenetic migration of late juvenile coral reef fishes from sea grass beds and/or mangroves to adjacent reefs is a well-known mechanism for their successful recruitment to adult populations (Shulman 1985, Robertson & Duke 1987, Ogden 1988, Rooker & Dennis 1991, Lirman 1994, Eggleston 1995). If intense competition or local disturbance such as predation or habitat destruction is encountered soon after settlement to the reef, the ability to make early post-settlement movements to alternative habitat would be adaptive.

Acknowledgements. This work benefited from the insightful comments of J. Parrish, R. Kinzie, K. Holland, M. Hixon, R. Buckley and J. Orr, and the patient field assistance of R. DeFelice, A. Friedlander, J. Peterson and L. Ross. Sage statistical advice was offered by A. Taylor. R. Buckley graciously provided technical advice on the marking methodology, and D. Shafer provided unlimited support and encouragement. J. Glynn and the staff at the Hanalei site of the Kauai National Wildlife Refuge Complex, U.S. Fish and Wildlife Service, were helpful and accommodating in providing logistic support. Northwest Marine Technology, Inc., Shaw Island, Washington, generously supplied the marking materials. Partial funding was provided by the Hawaii Cooperative Fishery Research Unit through a grant to J. Parrish from the Hawaii Department of Land and Natural Resources, Division of Aquatic Resources.

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This article was presented by K. Sherman (Senior Editorial Advisor), Narragansett, Rhode Island, USA

Manuscript first received: July 18, 1996

Revised version accepted: February 18, 1997