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## Caging experiment to examine mortality during metamorphosis of coral reef fish larvae

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**Abstract** All previous attempts to estimate early post-settlement mortality of coral reef fishes using either caging experiments or disappearance of new recruits have examined fish that had already settled, and therefore did not include the metamorphosis process. Crest nets capture unharmed transparent larvae during their migration from the open ocean to lagoon reefs before metamorphosis. We released these presettlement larvae at night into cages surrounding patch reefs and measured larval survivorship after two nights. This caging experiment involved cages enclosing the natural resident fish fauna, including predators, and others cleared of fish before releasing the larvae. The analyses of variance showed that (1) there was no difference in survivorship between the seven trials, (2) there was a significant difference between cleared and uncleared cages, and (3) there were significant differences between larval species tested. For the seven species that had a significant difference in survivorship between cleared and uncleared cages, average mortality of the larvae was 14% (range 0–26%) in cleared cages and 67% (range 29–76%) in cages with predators. The difference in mortality between species was related to the size of the larvae, as larger species exhibited reduced mortality compared to smaller

species. Mortality was related to the abundance of resident fish that could act as predators or competitors. Predation can have a significant impact on the survival of metamorphosing fish larvae on coral reefs.

**Keywords** Coral reef fishes · Survivorship · Recruiting larvae · Predation · Caging experiment

### Introduction

Many marine organisms, including fishes, have larvae that undergo a pelagic dispersive phase before settling in their adult habitat. The sedentary and conspicuous nature of many newly settled reef fishes allows field workers to observe the replenishment process. Most research to date has attempted to estimate the rate of settlement by focusing on the smallest juveniles that can be found on the reef, assuming that they represent recent larval influx. This approach is the basis of a large literature describing spatial and temporal patterns of recruitment (review in Doherty 1991). While recruitment surveys still have much to offer for the understanding of why fish numbers vary, there may be limits to how well the question of mortality during the settlement process can be resolved using visual surveys of new recruits. This limitation arises because of the possibility of significant early postsettlement mortality (review in Jones 1991).

There are very few data available on mortality of settling larvae. However, between 30 and 78% of newly settled coral reef fishes (Doherty and Sale 1985; Victor 1986; Booth 1991; Carr and Hixon 1995; Hixon and Carr 1997) and between 25 and 90% of newly settled temperate fishes (Van der Veer and Bergman 1987; Tanaka et al. 1989; Planes et al. 1998) may disappear within the first 7 days following their first sighting in coastal environments. Historically, there has been little choice in using recently settled fish to estimate the abundance of presettlement fishes. The recent development of crest nets in French Polynesia provides good

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estimates of the abundance of fish larvae passing over the reef into the lagoon (Dufour and Galzin 1993).

Predation appears to be the major cause of mortality of reef-associated fishes, especially new recruits (Shulman and Ogden 1987; Hixon 1991; Caley 1993; Hixon and Beets 1993; Carr and Hixon 1995; Hixon and Carr 1997). Predation has been shown to influence community structure (Talbot et al. 1978; Hixon 1986; Hixon and Menge 1991). A variety of predators are abundant on most reefs (Williams and Hatcher 1983; review in Hixon 1991), and disappearance of newly settled fish has been demonstrated experimentally to be caused by predation (Doherty and Sale 1985; Caley 1993; Carr and Hixon 1995; Hixon and Carr 1997). In the experiments by Doherty and Sale (1985), Carr and Hixon (1995), and Hixon and Carr (1997), predators were controlled using caging, while Caley's (1993) survey was based on removal of predators from patch reefs sufficiently isolated to limit recolonization. All four studies demonstrated a significant measurable effect of predation observed within a week to a month after settlement. However, these experiments involved already metamorphosed and settled new recruits, and consequently did not take into account mortality occurring during the metamorphosis stage.

The metamorphosis occurring when larvae encounter reefs is often a very rapid process which can be completed within 24 h (McCormick and Shand 1992). The few studies carried out to date suggest that structural and functional changes range from subtle changes in pigmentation to major reorganization of the physiological, somatic, and sensory systems of the fish (Neave 1986; McCormick and Shand 1992). The nature of the structural, physiological, and behavioral changes that occur at metamorphosis has led some researchers to refer to this stage as a "crucial period" (Blaxter 1988; Browman 1989).

Our goal was to estimate the extent of mortality that could be experienced by fish larvae during the first two nights of settlement, when incoming larval fishes undergo metamorphosis from pelagic to demersal life and find a suitable habitat in which to settle. We accomplished this objective by comparing survivorship of settling larvae on caged patch reefs in the presence and absence of resident predatory fishes. The relevance of the rates of larval mortality observed using caging experiments is discussed in relation to rates of mortality that could occur naturally.

## Materials and methods

### Study site

Experiments were conducted in the western lagoon of Moorea Island (French Polynesia). Moorea lagoon shows a typical reef structure for Pacific volcanic islands, with a reef crest that protects the lagoon area made up of a barrier reef, channel, and fringing reef. Our study site was located at the boundary between the fringing reef and the channel, in an area characterized by

isolated patch reefs lying on sand-dominated substrata. The lagoon depth varies between 1.5 and 2.5 m in this area and the current is moderate. Such a habitat seems favorable for new recruits and they have been found there in abundance (Planes et al. 1993).

### Experimental design

We released settling larvae into enclosed areas and measured the mortality during the first two nights. Mortality values were compared between cleared cages (all fish removed using rotenone poisoning) and cages retaining the resident fish fauna (uncleared cages). Each enclosure was made of a circular frame, 3 m in diameter, of fine mesh net (stretched mesh, 4 mm). The net was suspended within 15 cm of sea level by an inflated annular buoy and was sealed to the sandy lagoon floor by riveted heavy metal sheets. A total of six stakes secured the metal sheets to the sand to ensure perfect sealing of the cage to the bottom. Four extra stakes anchored the annular buoy in order to limit the effect of winds and currents. The total volume of water enclosed varied between 10.5 and 18 m<sup>3</sup> depending on the depth. Cages occupied a surface of 7.1 m<sup>2</sup> in which enclosed patch reefs varied between 3 and 5 m<sup>2</sup> and between 0.8 and 1.5 m high. Patch reefs included dead coral covered with macroalgae and live coral, mainly represented by species of *Porites*, *Acropora*, and *Montipora*.

Seven experimental trials were conducted. Each experimental trial used six cages: (1) three cages were cleared of resident fish, using rotenone poisoning (on the afternoon before the night of release), and were used as controls to survey mortality as a result of manipulation of young fish, and (2) the other three cages were maintained untouched with their natural resident fish faunas. In order to ensure independence of experimental trials, each trial used three new patch reefs (for the cages with resident fish fauna) and three from the previous experiment (the cleared reefs). Cleared reefs therefore varied from one experimental trial to the next. Because cages were moved and cleaned every 3 days, we did not encounter problems with algal fouling. A total of 24 patch reefs have been used over the seven experimental trials: six for the first trial and three new reefs for each of the six successive trials. We were concerned that this approach required rotenone poisoning coral patches in order to compare survival of larvae in natural habitats with and without resident fish. We minimized the number of patch reefs poisoned and each patch reef head was used twice: first as a habitat with resident fish fauna and second as a habitat cleared of resident fish.

The experimental protocol was composed of five steps:

1. During the first night, settling larvae were caught using crest nets.
2. In the early morning, larvae were sorted and kept alive in white drums of about 300 l, empty of any substratum in order to stop the process of metamorphosis. Larvae could then be maintained transparent over 24 h.
3. The second night (after larvae remained 24 h in the white drums without being fed), transparent larvae were released at around 11:00 p.m. in the cages as if they had colonized the reef one night later.
4. The larvae remained caged during the second night, the second day, and the third night. Altogether they remained in the cage for 36 h (two full nights and one full day) for each experimental trial.
5. In the morning of the third day, all cages were rotenone sampled to recover the new recruits that remained, together with the resident fish in the uncleared cages.

Fish larvae released in each cage varied in species composition and number of individuals between experimental trials due to variation in catch of the crest nets. Catches of seven crest nets were grouped to give enough larvae for each experimental trial. Assemblages of ten different species with different abundance were tested in the trials, with the same number of individuals and

species composition used in all cages within an experimental trial. (See Appendix available as electronic supplementary material on the web at <http://link.springer.de/link/service/journals/00338/tocs.htm>.) Species composition and abundance of settling larvae could not be homogenized between experimental trials because they depended on the availability of larvae from the crest nets. In the analysis of correlation between mortality and resident predators, we defined two size classes for the fish larvae (small ones as species with larvae up to 20 mm total length, and large ones for larvae longer than 20 mm) because predators vary according to the size of the prey.

Each experimental trial ended with the removal of fish (recruits with or without resident fish) from all six cages. Cages having only larvae and lacking a resident fish fauna permit an estimate of mortality resulting from the manipulation. Cages having larvae and a resident fish fauna allow estimation of the impact of resident potential predators. We defined potential predators as carnivorous species (Legendre et al. 1997) that were at least two times longer (total length) than the settling larvae released. We defined two categories of potential predators: (1) potential predators longer than 35 mm (total length) that could feed on larvae smaller than 20 mm, and (2) potential predators longer than 70 mm that could feed on even larger larvae.

#### Data analysis

Three-factor analysis of variance was used to test for differences in survivorship between larval species, treatments (caged reefs with resident fish removed [F-] vs. caged reefs with resident fish present [F+]), and experimental trials (seven). In addition, one-factor analysis of variance was calculated in order to test for differences between treatments for each species separately. In both sets of analyses, use of ANOVA was justified on the basis that Bartlett's tests showed the row data to be homogeneous ( $p > 0.05$ ). Finally, regression analyses were calculated in order to look at the relationship between the survivorship of settling larvae and the abundance of potential predators.

## Results

Larval catches in the crest nets were sufficient for ten species to be included in the experiments. Among the ten species, only two were tested in all seven experimental trials (*Stegastes nigricans* and *Acanthurus triostegus*), while two others were only involved in one trial (*Cephalopholis argus* and *Chaetodon auriga*). Finally, the six other species (*Chromis viridis*, *Chrysiptera leucopoma*, *Chaetodon citrinellus*, *Zebbrasoma scopas*, *Naso unicornis*, and *Rhinecanthus aculeatus*) were used in 6, 4, 4, 5, 3, and 3 trials respectively. The difference in the number of experimental trials for each species arose from the variability in catch of the crest nets (a consequence of the variability in recruitment between 18 February and 3

March 1998). In addition, four cages (trial 5, cage 1; trial 6, cages 2 and 6; trial 7, cage 3) were damaged due to high current conditions. Overall, a total of 20 caged reefs with the resident fish present and 19 caged reefs with resident fish removed were tested with various assemblages of settling larvae (see Appendix).

Mean survivorship for all species varied between 47.1%  $\pm$  3.4 SE in the presence of resident fish and 83.3%  $\pm$  3.0 SE in their absence. The ANOVA showed that most of the significant variance was explained by the difference between treatments (71.3% of the total variance), between species (10.6% of the total variance), and between species within cleared or uncleared cages (4.7% of the total variance) (Table 1). The analysis of variance indicated that variance between experimental trials was not significant, suggesting that the seven experimental trials were comparable despite the lack of similarity between patch reefs and also the variability of the resident fish fauna.

Because survivorship varied significantly between species ( $p < 0.001$ ) (Table 1), we computed one-factor analyses of variance for each single species, comparing survivorship in the presence and absence of resident fish (Table 2; Fig. 1). Seven species showed significant differences between treatments (*Acanthurus triostegus*, *Chaetodon citrinellus*, *Chromis viridis*, *Chrysiptera leucopoma*, *Rhinecanthus aculeatus*, *Stegastes nigricans*, and *Zebbrasoma scopas*). The three species that did not show significant differences in survivorship between treatments (*Cephalopholis argus*, *Chaetodon auriga*, and *Naso unicornis*) were the ones that were tested the least often (one, one, and three experimental trials, respectively), suggesting that it is the weaker tests that have failed to yield a significant result. In subsequent analyses, we removed the three species (*Cephalopholis argus*, *Chaetodon auriga*, and *Naso unicornis*) that did not show significant differences since we assumed that these results were affected by the smaller data sets arising from testing in only one to three experimental trials (cf. Appendix in electronic supplementary material on the web).

Variability of survivorship among species was correlated to the mean sizes of the settling larvae introduced in the cages (Fig. 2). These relationships were calculated separately for larvae in the presence and absence of resident fish. Larval survivorship was significantly correlated with larval size in the absence of resident fish ( $R^2 = 0.78$ ;  $p = 0.009$ ). In uncleared cages,

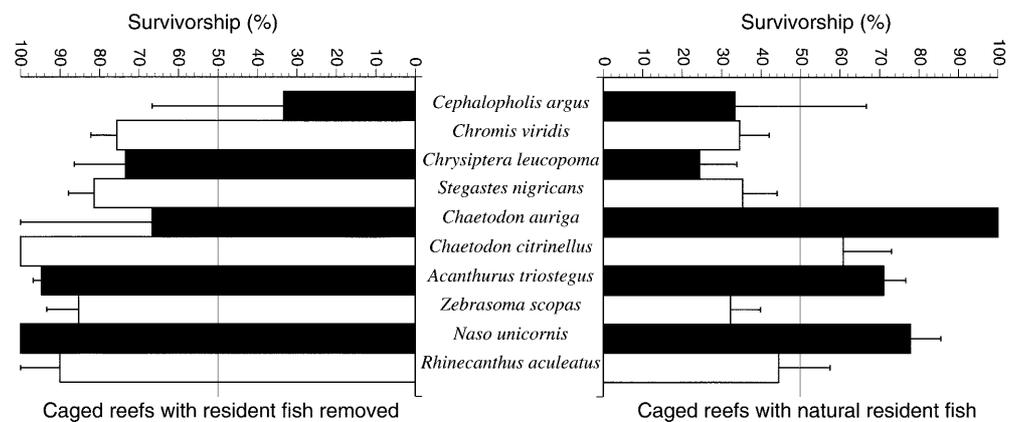
**Table 1** Three-factor ANOVA testing survivorship between species, treatments ([F-] vs. [F+]), and the seven successive experimental trials. *Underlined numbers* indicate significant values

Source of variance	df	Mean square	F	<i>p</i>
Species	9	4,592.82	4.72	< <u>0.001</u>
Treatments	1	30,812.59	31.66	< <u>0.001</u>
Experimental trials	6	1,589.99	1.63	<u>0.143</u>
Species $\times$ treatments	9	2,051.74	2.11	<u>0.033</u>
Species $\times$ experimental trials	26	842.92	0.87	<u>0.654</u>
Treatments $\times$ experimental trials	6	1,535.14	1.58	0.158
Species $\times$ treatments $\times$ experimental trials	26	817.97	0.84	0.688
Residual	131	973.04		

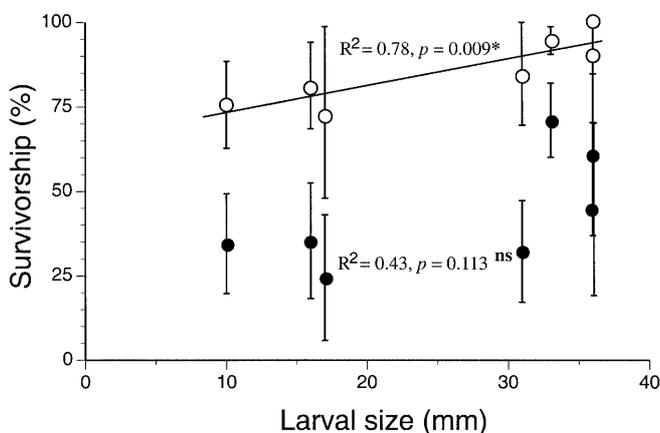
**Table 2** One-factor ANOVA testing treatment effects ([F−] vs. [F+]) for each species. *Underlined numbers indicate significant values*

Species	Mean square (df)		F	p
	Treatment	Residual		
<i>Acanthurus triostegus</i>	4,881.27 (1)	414.71 (34)	11.77	<u>0.002</u>
<i>Cephalopholis argus</i>	< 0.001 (1)	3,333.33 (4)	< 0.001	1.000
<i>Chaetodon auriga</i>	1,666.67 (1)	1,666.67 (4)	1.00	0.374
<i>Chaetodon citrinellus</i>	7,363.33 (1)	1,094.00 (18)	6.73	<u>0.018</u>
<i>Chromis viridis</i>	12,760.35 (1)	828.54 (29)	15.40	< <u>0.001</u>
<i>Chrysiptera leucopoma</i>	14,406.00 (1)	1,462.09 (23)	9.77	<u>0.005</u>
<i>Naso unicornis</i>	1,367.52 (1)	391.41 (11)	3.49	0.088
<i>Rhinecanthus aculeatus</i>	6,670.64 (1)	1,185.19 (12)	5.63	<u>0.035</u>
<i>Stegastes nigricans</i>	18,515.00 (1)	1,204.76 (34)	15.37	< <u>0.001</u>
<i>Zebrasoma scopas</i>	19,642.26 (1)	860.05 (26)	22.84	< <u>0.001</u>

**Fig. 1** Mean percent survivorship (with standard error) of larvae of ten reef fish species released during seven experimental trials in cages with resident fish removed and in cages with the natural resident fish fauna



the relationship was not significant ( $R^2 = 0.43$ ;  $p = 0.113$ ) despite species with larger larvae ( $> 20$  mm in total length) showing higher survivorship than species with smaller larvae (52.1 vs. 31.4%). The lack of significance in the relationship between survivorship and larval size in cages with resident fish comes from the fact that of the four species with large larvae, two exhibited low



**Fig. 2** Relationship between mean percent survivorship ( $\pm$ SE) and size of settling larvae released in the cages with resident fish removed (*open circles*) and cages with the natural resident fish fauna (*dark circles*). Only the seven species showing significant differences between the two treatments are included (see text for details)

mean survivorship (*Rhinecanthus aculeatus* and *Zebrasoma scopas*). On the other hand, species with smaller larvae (*Chromis viridis*, *Chrysiptera leucopoma*, and *Stegastes nigricans*) showed homogeneous low survivorship.

Survivorship data in the presence of resident fish were compared with the number of potential predators per caged patch reef for the seven experimental trials (Fig. 3). For all seven species combined, survivorship was only significantly correlated with the number of large predators ( $> 70$  mm in total length) ( $R^2 = 0.393$ ). Survivorship declined with greater numbers of potential predators. Considering species with large ( $> 20$  mm total length) and small ( $< 20$  mm) larvae separately, the number of predators of at least 70 mm total length was significantly correlated with survivorship of both large and small larvae ( $R^2 = 0.190$  and  $R^2 = 0.390$  respectively). The total number of potential predators ( $> 35$  mm total length) was significantly correlated with survivorship of small larvae ( $< 20$  mm) ( $R^2 = 0.340$ ), suggesting that predation on these larvae is independent of predator size.

## Discussion

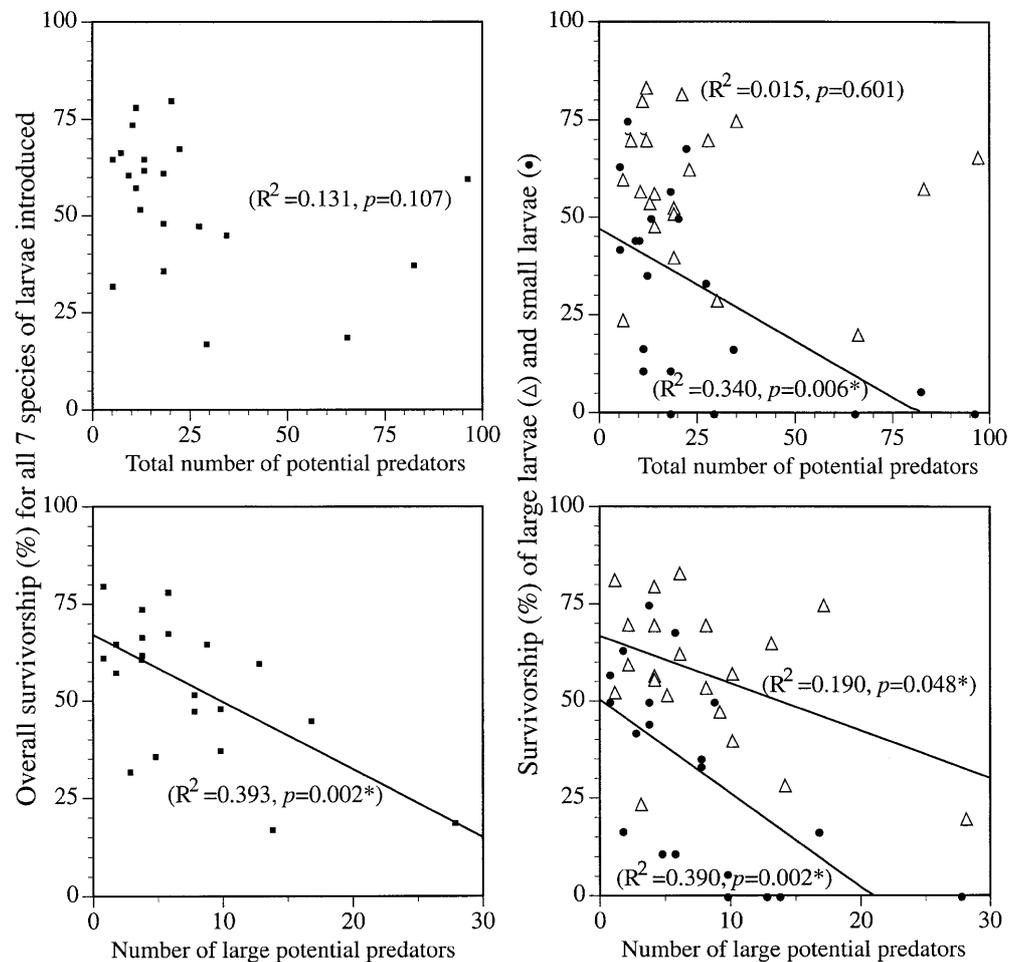
For the seven species that showed significant differences in survivorship between cleared and uncleared cages, mortality of larvae during the metamorphosis averaged

67% when transparent larvae were released at night in caged reefs with resident fish. Such a value cannot be generalized as an unbiased estimate of mortality that would occur naturally, but it represents the highest instantaneous rate of loss yet documented for recruited fish. Our control of caged reefs, which were cleared of the resident fish fauna, showed mortality averaging 14% (for these seven species). This figure was significantly different from the mortality in cages with resident fish present. The difference between the caged reefs cleared of resident fish and uncleared caged reefs gives a net mortality due to predation and possibly competition of 53% of the introduced settling larvae over a 36-h period. When looking at each species separately, the mortality varied between species with a maximum of 76% for *Chrysiptera leucopoma* and a minimum of 29% for *Acanthurus triostegus*.

In natural habitats, disappearance of new recruits is the result of both predation and migration. When aiming to estimate the impact of predation on new recruits, the main difficulty is to segregate it from movement. The objective of the caging protocol was to control for migration and to be able to ensure that losses are due to mortality rather than migration. In such a perspective, our cleared cages provide a control

which evaluates mortality that may result from handling, while cages enclosing natural fauna, aimed at estimating the mortality in the presence of competitors and predators. Whatever the experimental design, the main problem with the use of cages is that any effect observed may be confounded by effects of the cages themselves, due to reduced water flow, increased shading, chemical pollution, exclusion of transient fish, and potential change in the behavior of resident fish and/or introduced larvae (Doherty and Sale 1985; Steele 1996; Connell 1997). For all these factors, which have the potential to affect the disappearance of introduced larvae, we distinguished physical factors such as the change in water flow, shading, and behavioral effects. Regarding the structure of the cages and the experimental design, we consider that the direct effect of physical factors is negligible since both treatments are affected by change in water flow, shading, and also because the cages are very large compared to the size of the larvae. This only implies that larvae are under similar conditions in both treatments, and how these treatments modify behavior of both larvae and predators remains difficult to test. In fact, larval behavior could be modified because larvae were not fed during 24 h while being held, they did not find the appropriate

**Fig. 3** Relationship between mean survivorship of settling larvae and number of potential fish predators on the caged patch reef. Survivorship was calculated in each experimental trial for larvae of all seven species showing significant differences in survivorship between the two treatments (*dark squares*) and separately for the four species with large larvae (*open triangles*, > 20 mm total length), and the three species with small larvae (*dark circles*, < 20 mm total length). Potential predators are defined as carnivorous species with individuals longer than 35 mm in total length. Large potential predators are defined as those longer than 70 mm in total length



habitat in the patch reef caged, they were released with conspecifics, and because we did not match the experimental density with the natural density in the cages. Some of these confounding effects seem not to have affected our experiment. For example, the total number of larvae introduced in the cages varied from 20 to 40, but we did not observe any significant relationship between the number of larvae introduced and the rate of losses (neither in cleared nor uncleared caged), suggesting that the density of larvae in the cages did not affect their mortality. Beside behavior of the larvae, behavior of predators is also likely to be affected by the limited foraging space in which they are confined, and the availability of the numerous preys released. Further, there is no question that cages enclose the sedentary fish fauna and exclude the transient fish, therefore limiting the mortality compared to the natural environment. Finally, individual species of larvae or predators may be affected to different degrees by caging effects. All these considerations make it impossible to directly compare the disappearance of larvae observed in cages with the rate that would occur naturally. These problems have been emphasized in previous caging experiments (Doherty and Sale 1985; Kennelly 1991; Connell 1997), leading to the reputation of exclusion cages as being unreliable for producing data in reef fish ecology. Nevertheless, this technique is often the only method available to determine whether disappearance of fish is due to mortality or movement.

Despite the problems that result from using caging protocols, the present work is unique because all previous surveys were made on already metamorphosed larvae and consequently dismissed the critical period of metamorphosis and the time spent looking for a suitable habitat. However, several studies have attempted to estimate mortality of new recruits (Sale and Ferrell 1988). Estimates of mortality of new recruits during the first month following their first observation in reefs varied among species; 54 to 90% in *Chromis cyanea* (Booth and Beretta 1994; Carr and Hixon 1995), 18 to 57% in *Thalassoma bifasciatum* (Hunt von Herbing and Hunte 1991; Carr and Hixon 1995), and 90% in *Haemulon flavolineatum* (Shulman and Ogden 1987). Our estimates of mortality over 36 h (29 to 76% for seven species) are of a similar range to those observed previously for new recruits over a 1-month period. Daily counts of new recruits of *Thalassoma bifasciatum* showed similar trends with higher mortality in the first day (11.5%), with a sharp decrease in this mortality in the next 2 days, declining to an average of 1% per day (Victor 1986). Such a pattern was described for several groups of species with mortality of at least 25% during their first 5 days, while less than 15% were lost during the next 5 days and almost no fish disappeared during the last 5 days (Doherty and Sale 1985). Our results are consistent with previous surveys mentioned above and reinforce the idea that the rates of mortality of young coral reef fishes are greater during the first days following their arrival. A similar result was recently found

in Moorea (French Polynesia) by comparing larval flow entering the lagoon and visual census of newly settled recruits. About 90% of the settling larvae of *Naso unicornis* and *Naso lituratus* disappeared within 10 days (Dufour 1998). The range in mortality found in our study (from 29% for *Acanthurus triostegus* to 76% for *Chrysiptera leucopoma*) is certainly much higher than previously proposed because earlier studies could only consider the settled larval stage.

Analysis of survivorship in relation to the abundance of potential predators in uncleared caged reefs at the end of each experimental trial showed that mortality of settling larvae was related to the abundance of potential fish predators. In addition, we looked at size selection of predation by separating both potential predators (>35 and >70 mm in total length) and settling larvae (>20 and <20 mm in total length) into different size classes. Correlation analysis showed that large predators feed on either small or large settling larvae, while small predators feed only on small settling larvae (Fig. 3; significant relationship between number of large predators and survivorship of both large and small settling larvae, and significant relationship between total number of predators and small larvae). The second relationship was expected since predators are usually larger than their prey, while the first one shows that larger predators are opportunist for the size classes of their prey (Coates 1980). Such a relationship explains the difference in survivorship that we found between large and small settling larvae.

Small settling larvae (*Chromis viridis*, *Chrysiptera leucopoma*, and *Stegastes nigricans*) showed lower survivorship than species with large settling larvae (*Acanthurus triostegus*, *Zebrasoma scopas*, *Chaetodon citrinellus*, and *Rhinecanthus aculeatus*). Considering that predators are opportunist for the size classes on which they feed, small larvae will have more predators on the reef than larger ones, resulting in lower survivorship. This could also be an artifact of the caging experimental design which focused on the effect of sedentary predators, which are usually smaller than transient ones.

Finally, among the large settling larvae caged, we observed one group with lower survivorship (*Zebrasoma scopas* and *Rhinecanthus aculeatus*) compared to the other group of *Chaetodon citrinellus* and *Acanthurus triostegus*. Behavior of the settling larvae is also different between the two groups, with the first two species being more cryptic in corals while the last two occur in the water column around corals. Consequently, *Zebrasoma scopas* and *Rhinecanthus aculeatus* will be more accessible to sedentary cryptic predators while *Chaetodon citrinellus* and *Acanthurus triostegus* will be more vulnerable to transient predators. Expressed in a different fashion, one could hypothesize that there should be some counter-selective processes in having large and noncryptic recruiting larvae, otherwise all species would have favored this strategy through evolutionary time. Cages have modified the environment by removing

transient predators which contribute also to larval mortality (Carr and Hixon 1995). Change in the predatory fish fauna through caging may have favored survivorship of large and noncryptic settling larvae. On the other hand, if predator success is enhanced by the confined foraging area of a cage, larval survivorship may be lower than natural conditions. Because of all the possible artifacts of caging experiments, it is difficult to draw firm conclusions on the overall effect of predation on settling larvae in the wild.

An average net mortality of 53% during the first two nights on the reef is certainly the highest rate of loss ever observed over such a short time period for a fish population. While this figure is not an accurate estimate of natural larval mortality, it confirms the importance of predation on larval survival in the metamorphosis stage. Our results suggest that metamorphosis (i.e. the time between arrival on the reef and location of an appropriate habitat) is a critical period in the demographic regulation of populations. Further, since larval mortality during the settling differed more than two-fold between species, this demographic process may have varying importance among co-occurring species.

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