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HIGH MORTALITY DURING SETTLEMENT IS A POPULATION BOTTLENECK FOR A TROPICAL SURGEONFISH

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Abstract. Replenishment of benthic marine populations typically involves ''settlement'' from pelagic larval to benthic juvenile habitats. Mortality during this transition has been unknown because of the difficulty of measuring propagule supply in open water. For three weeks, we compared the nocturnal passage of presettlement fishes across the barrier reef encircling Moorea Island (French Polynesia) with the abundance of benthic recruits in the back-reef lagoon on the following morning. During this time, $>$40,000 presettlement unicornfish, *Naso unicornis* entered our study area of $\sim$1 km^2 with half arriving on just two nights. Using coupled Beverton-Holt functions to describe the decay of each cohort, we were able to predict the daily abundance of recruits and their final age structure from the presettlement inputs. The best model estimated that $\sim$61% of the potential settlers were lost between their nocturnal arrival and the following morning, independent of cohort size. Postsettlement mortality was density dependent, varying between 9% and 20% per day. We attribute all mortality to predation and suggest that high risk associated with settlement has shaped colonization strategies. Because fishing targets the survivors of this population bottleneck, aquarium fisheries may be more sustainable when sourced from pelagic juveniles.

Key words: crest nets; density-dependent-independent mortality rates; French Polynesia; larval supply; metamorphosis; Naso unicornis; *pelagic benthic juveniles; piscivores; predation; underwater visual census.*

Introduction

Complex life cycles, involving multiple life stages, are common among aquatic invertebrates and demersal fishes (Roughgarden et al. 1988), the simplest expression being the alternation between dispersive pelagic propagules and sessile or sedentary benthic juveniles. Ontogenetic habitat transitions are ''critical periods'' that may determine the abundance of the next life stage. For fecund species, small variations in mortality rate during the early life history can have a dramatic impact upon the abundance of propagules reaching juvenile nurseries (Fogarty et al. 1991), where resources and predators may impose further bottlenecks on replenishment of the adult population (Myers and Cadigan 1993).

For invertebrates, settlement at the end of the larval period often involves radical restructuring of the body plan. While the metamorphosis of demersal fish is subtler (McCormick et al. 2002), it is nonetheless a critical period in their life cycle (Kaufman et al. 1992), involving rapid changes in behavior, morphology, and ecology (Leis and McCormick 2002). Our best understanding of these changes comes from coral reef species, which are among the easiest marine fish to study in natural settings (Bolker et al. 2002). Close observation has shown that all species studied have very high mortality immediately after settlement as they are adapting to their new surroundings and lifestyles (Sale and Ferrell 1988, Hixon and Webster 2002). Mortality at this time involves complex interactions between guilds of predators (Hixon and Carr 1997), competitors (Carr et al. 2002), shelter (Anderson 2001), and alternative prey (Webster and Almany 2002), and can uncouple the linkage between larval supply and recruitment (Steele and Forrester 2002). Since postsettlement mortality rates can decelerate rapidly as new recruits gain more experience (Doherty and Sale 1986), it is reasonable to suppose that the time of greatest risk is settlement (Hixon 1991).

For most systems, it is impossible to measure losses during settlement because of the difficulty of sampling

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presettlement abundance (''larval supply'') in an unconstrained water column (Choat et al. 1993). The enclosed lagoons of coral reef atolls and oceanic islands encircled by barrier reefs provide a rare exception. Dufour (1991) showed that fish populations in Moorea Lagoon, French Polynesia, are replenished by a nocturnal flux of presettlement fish across the shallow barrier reef (Dufour and Galzin 1993, Dufour et al. 1996) that can be sampled accurately with stationary nets (Appendix A). We used this approach to quantify pelagic inputs into benthic populations and compared these inputs with daily counts of recruitment to estimate mortality during and after settlement.

Our study required at least one species that could be identified unambiguously from the mostly transparent presettlement stages caught by crest nets, as well as being counted reliably by underwater visual surveys. Both criteria were satisfied with the pulsed settlement of a unicornfish, *Naso unicornis* (Forsskål 1775; family Acanthuridae) that was uncommon at the start of our study. Juveniles of this surgeonfish settle in shallow lagoons and migrate later to outer reef slopes where they spawn (R. Galzin, *personal observation*). The resultant propagules have a presettlement phase of more than two months. During this time, they grow to 4–5 cm standard length (Appendix B) in the ocean before returning across reef crests to their nursery habitat on the lagoon floor.

All of these features facilitated study of the linkage between larval supply and population replenishment, where the cost of settlement was calculated from the difference between the changes observed in the abundance of young benthic juveniles in the lagoon and the changes expected if all fish crossing the reef at night had settled without loss (i.e., only postsettlement mortality is significant).

METHODS

Larval supply

Potential settlement was estimated from seven crest nets spaced equally along 1200 m of gently curving reef crest on the northwest margin of Moorea (Appendix C). Each net was 1.8 m wide and 1 m high, which was high enough to always filter the full height of the water column over the reef. Of the seven nets used in the study, two fished from 17 February 1998, two from 18 February, and all from 19 February onward. Codends were attached to the nets in the afternoon to minimize the catch of debris during the daylight hours when fish do not settle (Dufour 1991) and detached in the early morning to remove the overnight catch. At this time, live fish were transferred to aquaria to determine the fraction of competent settlers, defined by color changes. Collections ended on 5 March yielding quantitative estimates of potential settlement from 16 consecutive nights.

Recruitment

Successful settlement (recruitment) was monitored on six fixed transects measuring ~1 km each and spanning the lagoon from reef crest to shore (Appendix C). Depths along the transects seldom exceeded 2 m. Starting 17 February, all transects were swum each morning by six experienced fish counters, who rotated among transects daily. Each snorkeler carried a T-bar that could be held against the bottom to delineate a strip transect exactly 1 m wide. Only fish first seen inside this strip and considered to be new recruits were counted. Surveys ended on 5 March yielding 15 estimates of benthic densities from 17 consecutive days.

Mortality

Schmitt et al. (1999) showed that a modified Beverton-Holt recruitment function was an appropriate model to describe the decline of a single cohort of reef damselfish. Osenberg et al. (2002) reformulated this approach into a continuous-time version, which we adopted to deal with the decay of multiple daily cohorts followed over different time periods. The equation for this model is

$$N_t = \frac{e^{-\alpha t} N_0}{1 + \dfrac{\beta(1 - e^{-\alpha t}) N_0}{\alpha}} \qquad (1)$$

where α is the density-independent mortality rate, β is the density-dependent mortality rate (both measured as per capita effects), and N is the cohort density.

Age structures

Otoliths (ear bones) were extracted from 220 juveniles collected from the lagoon at the end of the study. Daily rings deposited in these structures were interpreted following standard protocols (Wilson and McCormick 1999) to back-calculate the dates of birth and settlement, and size at settlement for each individual. Every otolith was read twice in blind trials and those differing by more than three days were read a third time seeking consensus (tolerance of two days) with one of the earlier readings. This process yielded 181 fish with settlement dates assigned between 18 February and 1 March 1998.

The same aging protocols were applied to 146 presettlement *Naso* retained from the crest nets to determine the age structure of incoming settlers. Individual-based selection was tested by comparing this initial distribution with the distribution of ages at settlement back-calculated from survivors taken at the end of the study, following the approach used in recent demonstrations of postsettlement selection in reef fishes (Searcy and Sponaugle 2001, Vigliola and Meekan 2002).

Modeling

Our study area was approximately 1 × 1 km (Appendix C) so estimates of potential settlement and re-

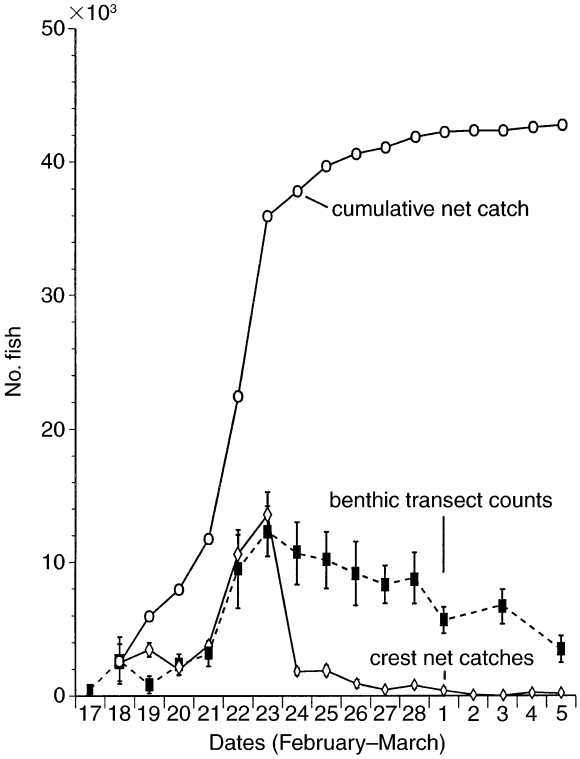

FIG. 1. Nocturnal input of presettlement *Naso unicornis* (mean ± 1 SE) estimated by seven crest nets and average abundance of benthic juveniles estimated by six transects. Both data series and the cumulative input to the lagoon are standardized to 1 km of reef crest.

cruitment densities were standardized to this unit area. Catches in the nets were interpolated to estimate the flux of presettlement *Naso* crossing the reef each night, and therefore potentially added to the benthic population in a 1 km wide swathe between the crest and the beach. Because the recruitment surveys included fish of mixed ages (no visual way to distinguish recruits of close ages), we sought to predict both the daily total abundance of juveniles observed in the lagoon, as well as the age structure of recruits found at the end of the study, by applying models of mortality to the observed presettlement inputs.

The local population was modeled in a spreadsheet as a triangular matrix of daily cohort sizes (rows) over time (columns) between entry into the lagoon and the end of the study (Appendix D). Columns in the matrix were summed to yield the abundance and age structure of survivors for any given day predicted from different combinations of the mortality parameters (α and β) in Eq. 1. Best solutions for these parameters were found with a genetic optimization algorithm (Evolver 4.0, Palisade Corporation, Newfield, New York, USA) that recalculated the spreadsheet exhaustively to find the best fit (least squares minimization) between the predicted and observed patterns in either the abundance or the demographic data.

Two alternative mortality scenarios were evaluated. First, each daily cohort was reduced over time by applying Eq. 1 to the initial density of incoming settlers measured by the nets. Although this approach could reproduce the approximate pattern for either abundance or demography, no set of parameters could simultaneously satisfy both requirements (Appendix D). Second, based on the possibility that pre- and postsettlement mortalities could be qualitatively different, each daily cohort was reduced over time by coupled Beverton-Holt functions. In the first step, N_0 (the number of potential settlers crossing the reef) yielded N_s (the predicted number of successful settlers). Since $t = 1$, the first equation estimates an instantaneous loss of potential settlers with density-independent (α_s) and density-dependent (β_s) parameters. In the second step, N_s became the initial cohort density for the calculation of postsettlement mortality (identical equation with independent parameters α_p and β_p) for time periods between $t = 1$ (for the cohort settling on 4 March) and $t = 15$ (for the cohort settling on 18 February 1998).

RESULTS

At the start of the visual surveys on 17 February 1998, new recruits of *Naso unicornis* were uncommon in our study area (Fig. 1). Nonetheless, the few individuals present were highly conspicuous because of their large sizes at settlement, choice of settlement habitat (rubble and holes on open sand), and hovering behavior. Clear water allowed divers to detect these fish at distances up to 10 m.

Shortly after monitoring began, and just prior to the new moon (which occurred on 26 February), the numbers of benthic juveniles in our study area surged to >12 000 individuals. This rapid change in abundance mirrored a pulse of *N. unicornis* in the net catches, which peaked on the night of 22/23 February (Fig. 1). Abundance in the benthic population peaked on the following morning, and then began a steady decline despite continuing settlement over the next seven nights. On converting net catches to cumulative input, it was clear that a large fraction of the >40 000 potential settlers observed entering the lagoon during this period were missing from the benthic surveys. By the morning after peak settlement, the gap represented two-thirds of the incoming settlers, which suggests high losses during the act of settlement. After a further 10 d, the gap had widened to 10-fold, which suggests that postsettlement mortality was also substantial.

The coupled Beverton-Holt equations were able to closely predict the observed abundance of benthic juveniles during the 16-d period (Fig. 2A). Table 1 shows the four per capita mortality rates producing this result, revealing qualitative differences between the first and subsequent d. In the best fit between predicted and observed abundance, $\beta_s = 0$ meaning that settlement losses were the result of density-independent mortality of ~61% of the potential settlers. A plot of residuals

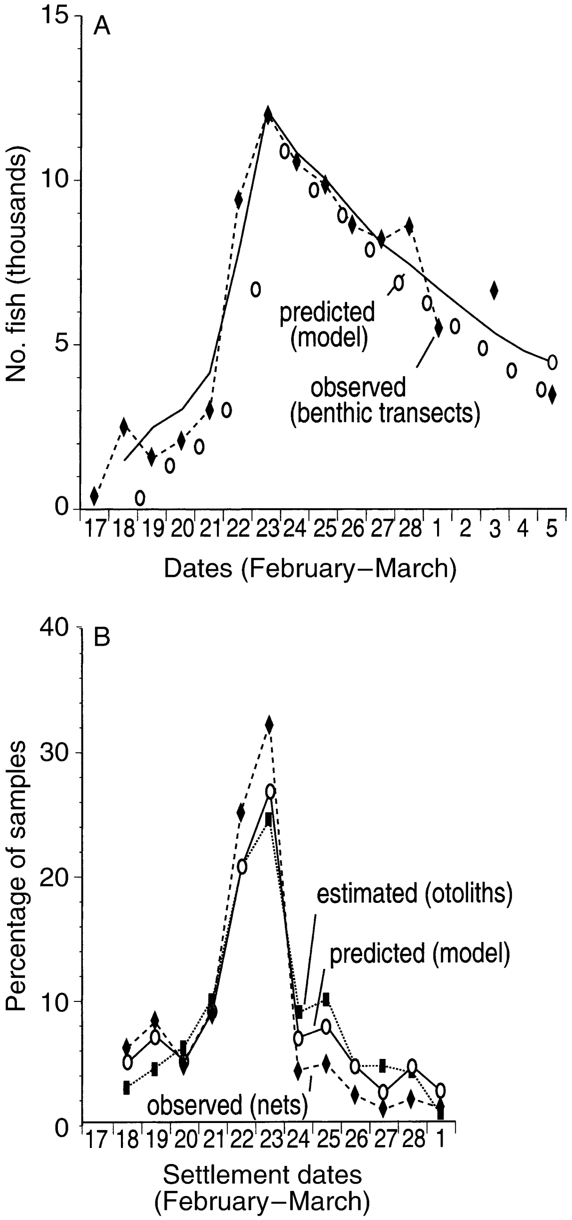

FIG. 2. (A) Predicted and observed numbers of benthic juveniles in the back-reef lagoon based upon the best model fit to abundance; mortality parameters are shown in Table 1. (B) Age structure (settlement dates) predicted for 4 March 1998 by the same model and observed in the otoliths of benthic juveniles collected on that date. The initial inputs (crest net catches) are shown for illustrative purposes.

from this fit showed no trend against initial cohort strength ($r^2 = 0.03$), consistent with density-independent loss. In the following two weeks, however, postsettlement mortalities included a density-dependent component ($\beta_p > 0$) and ranged from 9% to 20% on the first day for different daily cohorts.

The same model solution also closely reproduced the age structure of the population found at the end of the study (Fig. 2B). A slightly better fit was achieved for the latter, when optimized on this variable alone. The resultant model, however, estimated a lower value for the instantaneous loss of settlers (43%) and overestimated juvenile abundance, albeit not to the degree shown by the single application of Eq. 1 (Appendix D). This result is probably artifactual because aging error is known to smear and flatten peaks in an age distribution (Worthington et al. 1995). When a soft constraint was added to this optimization, requiring a match with the maximum density observed on 23 February, the best model based upon age had almost identical parameters to the unconstrained model based upon abundance (Table 1).

The distribution of pelagic larval durations recovered from potential settlers revealed the long (median 75 d) and variable (range 30 d) ages typical of surgeonfishes (Fig. 3). The right-skewed distribution of ages suggests that *N. unicornis* is able to delay its final metamorphosis until it finds the right conditions for settlement (McCormick 1999). The similarity of the age distributions at settlement observed in potential settlers (net catches) and recovered from survivors (benthic juveniles) does not support selection against individuals from either edge of the distribution, consistent with random mortality.

DISCUSSION

Although this is far from the first study to measure postsettlement mortality of coral reef fishes, few have tracked the decay of natural cohorts from settlement (Hixon and Webster 2002). No previous study has tracked the decay of cohorts from presettlement abundance in a quantitative manner, although some have attempted to track temporal changes in relative abundance to link larval supply with replenishment (Milicich et al. 1992).

This linkage is of fundamental importance to marine ecologists interested in mechanisms of population dynamics and scientists tasked with managing marine fish harvests. In the last 20 yr, ecologists studying coral reef fishes have debated the relative importance of density-independent vs. density-dependent mortality following settlement (Hixon 1998, Doherty 2002, Hixon and Webster 2002). In a recent review, Hixon and Webster (2002) found that 17 of 20 species experienced density-dependent per capita mortality at some time and place, usually shortly after settlement. In a meta-analysis of 71 studies, Osenberg et al. (2002) found no consistent difference in the per capita strength of density dependence (β) when all were reanalyzed in a common framework using the time-continuous Beverton-Holt recruitment function (Eq. 1). Instead, they found that the emphasis placed on density dependence vs. density independence reflected the different population densities of the various species being studied (see also Doherty 2002). In other words, it is often difficult if not impossible to detect density dependence at low densities where the outcomes will be indistinguishable

TABLE 1. Per capita mortality rates (α_s, β_s, α_p, β_p) in the two-step model calculated from least-squares fits of model outputs to observed patterns of total abundance (first row) and observed age-structure at the end of the study (second row), constrained by abundance (see *Results*).

	Settlement loss			Postsettlement mortality		
Variables	α_s	β_s	Loss (%)	α_p	β_p	Daily loss (%)
Abundance	0.9362	0	60.8	0.0933	2.67×10^{-5}	19.8
Age structure	0.9358	0	60.8	0.0966	2.67×10^{-5}	20.0

Note: The loss column (far right) shows the initial decline of the largest cohort with a presettlement strength of 13 571 fish/km^2.

from density independence. We make this point to emphasize the utility of the Beverton-Holt function to provide a common quantitative framework for future comparisons. However, this approach can be data intensive, so simpler approaches are also useful (Hixon and Webster 2002).

Our use of the Beverton-Holt function adds to other successful applications (Shima and Osenberg 2003) and goes a step further to show a rapid change in per capita mortality rates at the ontogenetic transition between larval and juvenile habitats. The unique aspect of our study is that we were able to estimate cohort strength just prior to settlement, which allowed us to match larval supply with the replenishment of benthic populations. Our first discovery was that simply applying Eq. 1 to the presettlement inputs did not reproduce the patterns that we observed in abundance and age structure of the benthic population over 16 d (Appendix D). The superior performance of the coupled model provides strong circumstantial evidence that mortality during settlement was both qualitatively and quantitatively different to that on settled fishes.

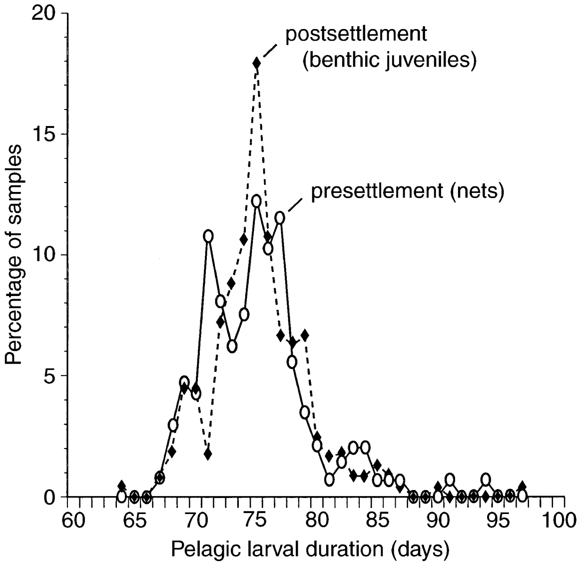

FIG. 3. Ages at settlement of fish collected by crest nets and back-calculated from the otoliths of benthic juveniles surviving on 4 March 1998.

Our major finding is that ~61% of potential nocturnal settlers had disappeared by the following morning and that this huge loss was unrelated to size or composition of the incoming cohort (i.e., density-independent mortality). In contrast, postsettlement mortality was density dependent, with total losses on the first day varying between 9% and 20% depending upon daily cohort strength. These rates are consistent with published values for mortality of newly settled reef fishes (Hixon and Webster 2002). Similarly, our estimate for the density-dependent parameter β_p ($\sim 3 \times 10^{-5}$) falls within the confidence limits calculated by Osenberg et al. (2002) in their meta-analysis.

We are confident that the density-independent loss (α_s) that we have associated with the act of settlement represents mortality and not simply failure to settle within our study area. Moorea lagoon is encircled by shallow fringing barrier reef with breaking waves except for deep passes that allow lagoon water to return to the ocean. Our study area was the middle of a 6-km^2 segment of lagoon bounded by passes, and extensive searches for *Naso* recruits throughout this larger area did not find higher densities elsewhere. Under typical conditions, it is physically impossible for presettlement fish to return to the ocean after crossing the barrier reef by swimming against the surf. The only other route back to the ocean was a 2–3 km swim to the passes, which seems improbable given the abundance of habitat along the way suitable for settlement. While we cannot exclude the entry of additional settlers through these passes (Sancho et al. 1997), we rely upon the fact that all live fish transferred from the crest nets to experimental arenas survived well (Planes and Lecaillon 2001) as evidence that we did not overestimate larval supply to our study area. Based on previous studies, predation is the most parsimonious explanation of the large fraction of potential settlers that were missing at the first benthic census (Hixon 1991, Hixon and Webster 2002, Webster 2002). Indeed, nocturnal observations during our study revealed various small groupers actively foraging just inside the reef crest.

Predation that is capable of reducing a cohort by more than half in less than a day must have profound impacts on population dynamics (Steele and Forrester 2002) and will exert strong selection on individual traits of settling reef fishes (Searcy and Sponaugle 2001). There are many features of settling reef fishes (timing, coloration, and behavior) that appear to be coadapted traits reducing the risk of predation during the transition between pelagic and benthic habitats (Leis and McCormick 2002). Additionally, mass nocturnal arrival, as observed in our study, must confer a degree of predator swamping. We suggest that the high risk settlement period deserves further study while acknowledging that it will not be easy because of the complex interactions between predator guilds (Hixon and Carr 1997), competitors (Carr et al. 2002), and multispecies prey (Webster and Almany 2002). However, there is no choice because processes acting rapidly at settlement can impose lasting influences on populations (Webster 2002).

Our finding of high mortality during the settlement of a species with a large agile presettlement stage has practical outcomes for the management of reef fish resources. On one hand, it challenges the notion of restocking coral reefs with hatchery-reared juveniles for all but the most depleted systems. Since there is so much functional redundancy at the piscivore level in coral reef systems (Hixon 1991), restocking may require a degree of predator swamping that is prohibitive. On the other hand, high mortality during the colonization of reefs provides a strong argument to shift the harvest of ornamental species toward presettlement individuals (Hair et al. 2002).

Our study also has application to the understanding of other complex life cycles. Most marine invertebrates share the same bipartite life histories as reef fishes, and settlement is also a crucial transition in these populations (Gosselin and Qian 1996, Hunt and Scheibling 1997). Studies of age-specific mortality in marine invertebrates, like those on fishes, often reveal extreme mortality during the juvenile stage that is particularly intense immediately after settlement (Gosselin and Qian 1997, Pineda et al. 2002). Mortality during settlement of marine invertebrates has not been measured, and may be higher given their very different body sizes, sensory systems, and swimming abilities. Our message is to document the previously undescribed loss of reef fish during the act of settlement and to recommend further work in both groups on this crucial life history event.

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APPENDIX A

A photograph of a crest net similar to the ones used in this study is available in ESA's Electronic Data Archive: *Ecological Archives* E085-071-A1.

APPENDIX B

A photograph of *Naso unicornis* showing the development of juvenile pigmentation is available in ESA's Electronic Data Archive: *Ecological Archives* E085-071-A2.

APPENDIX C

An aerial map of the study area is available in ESA's Electronic Data Archive: *Ecological Archives* E085-071-A3.

APPENDIX D

A triangular matrix of the decay of daily cohorts by days for *Naso* crossing the reef top and graphical output for the best solutions derived from a single application of Eq. 1 is available in ESA's Electronic Data Archive: *Ecological Archives* E085-071-A4.

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ERRATUM

In the paper by P. H. Doherty, V. Dufour, R. Galzin, M. A. Hixon, M. G. Meekan, and S. Planes (2004), "High mortality during settlement is a population bottleneck for a tropical surgeonfish," *Ecology* **85**(9):2422–2428, an incorrect version of Fig. 2A was published, with some of the symbols displaced from the trendline. The corrected figure is presented below.

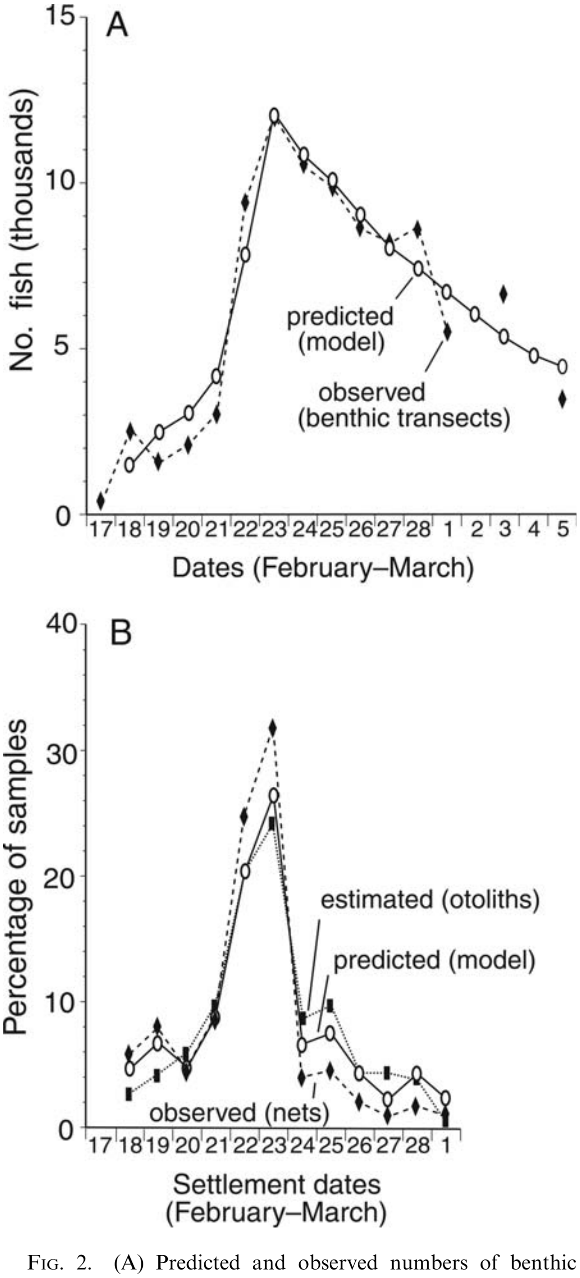

FIG. 2. (A) Predicted and observed numbers of benthic juveniles in the back-reef lagoon based upon the best model fit to abundance; mortality parameters are shown in Table 1. (B) Age structure (settlement dates) predicted for 4 March 1998 by the same model and observed in the otoliths of benthic juveniles collected on that date. The initial inputs (crest net catches) are shown for illustrative purposes.