Survival dynamics of scleractinian coral larvae and implications for dispersal

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Abstract Survival of pelagic marine larvae is an important determinant of dispersal potential. Despite this, few estimates of larval survival are available. For scleractinian corals, few studies of larval survival are long enough to provide accurate estimates of longevity. Moreover, changes in mortality rates during larval life, expected on theoretical grounds, have implications for the degree of connectivity among reefs and have not been quantified for any coral species. This study quantified the survival of larvae from five broadcast-spawning scleractinian corals (*Acropora latistella*, *Favia pallida*, *Pectinia paeonia*, *Goniastrea aspera*, and *Montastraea magnistellata*) to estimate larval longevity, and to test for changes in mortality rates as larvae age. Maximum lifespans ranged from 195-244 d. These longevities substantially exceed those documented previously for coral larvae that lack zooxanthellae, and they exceed predictions based on metabolic rates prevailing early in larval life. In addition, larval mortality rates exhibited strong patterns of variation throughout the larval stage. Three periods were identified in four species: high initial rates of mortality; followed by a low, approximately constant rate of mortality; and finally, progressively increasing mortality after approximately 100 d. The lifetimes observed in this study suggest that the potential for long-distance dispersal may be substantially greater than previously thought. Indeed, detection of increasing mortality rates late in life suggests that energy reserves do not reach critically low levels until approximately 100 d after spawning. Conversely, increased mortality rates early in life decrease the likelihood that larvae transported away from their natal reef will survive to reach nearby reefs, and thus decrease connectivity at regional scales. These results show how variation in larval survivorship with age may help to explain the seeming paradox of high genetic structure at metapopulation scales, coupled with the maintenance of extensive geographic ranges observed in many coral species.

Introduction

Larval dispersal affects the distribution and abundance of marine organisms, enabling replenishment of populations, colonization of new habitats, and expansion of geographic ranges (Strathmann et al. 2002). Patterns of dispersal also have important consequences for the genetic structure of populations, affecting gene flow, local genetic diversity and population differentiation, and rates of speciation and extinction (Slatkin 1987; Nathan et al. 2003). Consequently, determining the dispersal potential of marine organisms is fundamental to understanding their ecology and evolution. However, significant controversy exists about the scale of dispersal, in particular whether marine populations are mostly self-seeded (i.e., most successful larvae recruit to their natal reef) or are maintained principally by recruits arriving from nearby or even distant reefs (e.g., Cowen et al. 2000; Strathmann et al. 2002).

The dispersal potential of planktonic larvae depends on oceanographic factors transporting the larvae, the acquisition of competence to settle, the length of time spent in the plankton, and the survival of larvae during dispersal (Pechenik 1990). Major sources of mortality in the plankton include starvation (Strathmann 1985), predation (Thorson 1950), physiological stress due to suboptimal environmental conditions (Pechenik 1987), genetic abnormalities, and disease (Rumrill 1990). Although mortality in the plankton is assumed to be high, accurate empirical estimates of mortality are difficult, if not impossible, to obtain in the field for pelagic marine larvae (Levin 1990). Estimates of larval mortality from laboratory cultures, however, are more feasible. Although the latter are likely to overestimate survival in the field (because many potential sources of mortality, such as predation, have been removed), they can

nonetheless be useful in understanding survival. In particular, the energetic constraints on larval survival can be readily examined under laboratory conditions.

For scleractinian corals, knowledge about the survival dynamics of larvae, even under laboratory conditions, is sparse. Most of the studies conducted to date have focused on testing for differences in larval survival under different environmental conditions (e.g., temperature: Edmunds et al. 2001; Bassim and Sammarco 2003; Brooke and Young 2005; Baird et al. 2006; salinity: Vermeij et al. 2006; and UV radiation: Wellington and Fitt 2003), or on estimating median survival time (i.e., the point at which 50% of the cohort have died) (e.g., Harii et al. 2002; Nishikawa and Sakai 2005; Nozawa and Harrison 2005). Few studies have specifically focused on the estimation of longevity, and thus cohorts are rarely followed until all larvae have died (but see Ben-David-Zaslow and Benayahu 1996, 1998 for soft coral examples). Consequently, accurate estimates of longevity (i.e., maximum lifespans) are lacking. In addition, no known studies have formally tested for changes in mortality rates as larvae age, changes that may have important implications for the demography, evolution, and biogeography of corals.

Variation in mortality rates with age typically takes one of a small number of forms, which have different implications for dispersal and population structure. Most models of larval dispersal assume that mortality rate is constant with age (Type II survival (e.g., Hill 1991; Cowen et al. 2000; Armsworth et al. 2001), and thus cohort abundance declines at a constant proportional rate. However, mortality rate may increase with age (Type I survival), so that a large proportion of the cohort remains alive initially, and this proportion decreases markedly as mortality rates increase. Such increases in mortality restrict the extent of long distance dispersal by placing an upper bound on larval lifetimes. Alternatively, mortality risk may be very high initially, and

decrease with increasing age (Type III survival), so that most of the cohort dies early, but those that survive this initial period tend to persist for a relatively long time. This implies that most of the larvae that do not settle quickly (i.e., within or close to their natal habitat patch) will die before reaching other suitable habitat, but those that do survive can disperse very long distances. A combination of Type I and III survival curves can also occur, when mortality rates are elevated both early and late in life. Which of these survival patterns are exhibited by larvae has the potential to influence, for instance, the potential consequences of habitat fragmentation; the rate at which populations can recover from localized disturbances; the efficacy of marine protected areas (and their optimal size and spacing); the genetic structure of populations, and consequent capacity for local adaptation and gene flow; and the potential for range expansion or speciation via founding of peripheral, isolated populations.

The aim of this study was to obtain quantitative estimates of median and maximum lifetimes for five broadcast spawning scleractinian corals, and to test for and estimate changes in mortality rates during the dispersal phase. Survival was quantified for an extended period (until all larvae died, > 200 d) to obtain more accurate estimates of maximum life span than are presently available for corals. In addition, a parametric survival analysis was applied to test for changes in mortality rates as larvae age, and thereby to determine the shape of the survival curve for each species.

Materials and methods

Study site and species

Gametes from five scleractinian corals from three families were collected over three spawning events at two locations on the central Great Barrier Reef, Magnetic Island (19°9′ S, 146°51′ E) and Orpheus Island (18°46′ S, 146°15′ E): *Acropora latistella*

(Family Acroporidae); *Montastraea magnistellata, Favia pallida, Goniastrea aspera* (Family Faviidae); and *Pectinia paeonia* (Family Pectiniidae). Several adult colonies, separated by at least 20 m to minimize the chances of multiple colonies belonging to the same genet, were collected a few days prior to predicted spawning and placed in outdoor aquaria with continuously running filtered seawater at ambient light and temperature. In 2006, spawning occurred on 9th October for *A. latistella* on Magnetic Island, and 10th November for *M. magnistellata, F. pallida, and P. paeonia*, and 9th December for *G. aspera* on Orpheus Island.

Larval cultures

Prior to sunset, colonies were separated by species, placed in separate outdoor aquaria, and monitored for setting behaviour that indicates imminent spawning. Larvae were cultured using a modification of the methods of Babcock et al. (2003). Once the colonies had released most of their gametes, positively buoyant egg and sperm bundles were skimmed off the water surface, mixed, and concentrated into one l larval culturing bowls with high densities of sperm to maximize fertilization rates. Within one to two h, at the start of cleavage, the sperm were diluted to prevent polyspermy, which may affect larval development (Oliver and Babcock 1992). Developing embryos were then transferred at densities of approximately one larva ml^{-1} into 20 l larval rearing buckets containing 0.2 μm filtered seawater (FSW) to minimize the risk of bacterial contamination. Motile larvae developed between 24-48 h after being transferred into the buckets. Three to four d after spawning, the larvae were concentrated into 1.5-2.5 l plastic jars for transport to James Cook University.

Data collection

Upon returning from the field, for each species, five replicates of 100 randomly selected larvae were placed in 70 ml plastic specimen jars containing FSW. Throughout the experiment, the cohorts were maintained at 25-26˚C in a temperature-controlled room with a photoperiod of 12 h light and 12 h dark. Species whose larvae lack zooxanthellae were chosen in order to determine the endogenous energetic capacity lecithotrophic coral larvae have to survive. Initially, at three d intervals, the larvae were counted and transferred into clean jars with fresh FSW. Since it had no noticeable effect on water quality, in order to minimize handling, the sampling interval was lengthened to two weeks as mortality rates stabilized. Because coral larvae typically lyse within 24 h of death, there was no need to distinguish between live and dead larvae, i.e., the larvae remaining at each interval were assumed alive (Baird et al. 2006). The number of surviving larvae at each census was recorded for survival analysis. Accidental spillage of one of the *F. pallida* replicates left only four replicates for analysis.

Analysis

Survival time data have unique properties that make traditional statistical methods inappropriate. The distribution of survival times tends to be right skewed, with some individuals surviving a relatively long time (Collett 1994). This violates the assumption of normality common to many statistical models, and requires use of alternative methods. Many survival models are also formulated specifically to allow for survival data that are "interval-censored." This means that the time of death of each larva is not known exactly. Instead, larvae are censused at fixed intervals; therefore, one knows only how many larvae died between each pair of census times. Data were analyzed using the 'survival' library in R, version 2.4.1.

Estimation of larval longevities

A Kaplan-Meier product-limit analysis was used to obtain nonparametric estimates of the shape of the survivorship curves for each species. The Kaplan-Meier method estimates the survival probabilities at any time, $\hat{S}(t)$, as the product of the conditional probabilities, p_i, of larval survival between all censuses up to time, t:

$$\hat{S}(t) = p_1 \times p_2 \times \ldots p_t \qquad (1)$$

At the first census, all larvae are at risk of mortality, and the survival probability is calculated as the total number of deaths divided by the total number of larvae. For each additional census time, however, the number of larvae who have already died decreases the number of larvae at risk. The conditional survival probability for the larvae at these census times, given they have survived to the previous census, is calculated as the number of larvae at risk, r_i, minus the number of larvae who died, d_i, divided by the number at risk:

$$p_i = \frac{r_i - d_i}{r_i} \qquad (2)$$

Nonparametric survival analyses, like Kaplan-Meier, cannot explicitly accommodate interval-censored observations (i.e., they assume the death of the larva occurred at the exact time recorded). Depending on whether the last time the larva was observed alive or the first time when the larva was observed dead is used in the analysis leads to either an underestimate or overestimate of survival respectively, by one census. In this paper, the census times at which the larvae were last observed alive were used as the time of death. This means that estimates of survival times will be slightly conservative (i.e., low). In addition, nonparametric survival analyses cannot explicitly incorporate information from replication, such as differences in survival among replicate jars.

Therefore, larvae were pooled across replicate jars to estimate overall survival curves for each species, but replicate jars were also analyzed separately to determine the degree of variability in survival among replicates.

Tests for variation in mortality rates

A parametric survival analysis was conducted to investigate the overall shape of the survival curve for each species. Parametric survival analyses can accommodate interval censoring, as well as additional survival information provided by replication. In particular, variation in survival times of larvae between replicates could occur due to differential handling effects, or interactions among larvae within jars (e.g., transmission of a pathogen between larvae in the same jar). Such effects can be explicitly incorporated in parametric models in a manner analogous to random effects in standard linear statistical models (Hosmer and Lemeshow 1999). The exponential and Weibull distributions were fitted separately to the observed survival times to determine whether mortality was constant or changed with cohort age. The exponential distribution is the simplest model for survival times and assumes that mortality rate is constant over time:

$$h(t) = \lambda, \qquad (3)$$

where the mortality rate, λ, is a positive constant. This model corresponds to Deevey's (1947) Type II survival curve. If mortality rate is not constant, then the Weibull distribution is often used. The Weibull distribution can accommodate the three basic survival curves with constant, monotonically increasing or monotonically decreasing mortality (Pinder et al. 1978). For the Weibull distribution, mortality rate is modeled as:

$$h(t) = \lambda\alpha(\lambda t)^{\alpha-1}, \qquad (4)$$

where the scale parameter, λ, and shape parameter, α, are positive constants. The shape parameter of the Weibull distribution defines the shape of the survival curve (Pinder et al. 1978). If α=1, the Weibull distribution is identical to the exponential distribution (i.e., Type II survival). When α>1, mortality rate increases with age (Type I survival); if α<1, mortality rate decreases with age (Type III survival).

Although the Weibull distribution can accommodate the three basic types of survival, it is inappropriate when the mortality rate is not monotonic (i.e., not consistently increasing or decreasing through time), such as for a bathtub shaped hazard function. Therefore, to test for such survival patterns (e.g., Type III survival early in life and Type I late in life), the time series were divided into early and late phases, and the exponential and Weibull distributions were fitted separately to each part.

Maximum likelihood methods implemented in 'survreg' were used to find the best-fit parameter estimates and associated likelihood for the exponential and Weibull models fitted to each species. To compare the likelihoods and select the model with the best fit to the observed survival times, Akaike's Information Criterion (AIC) was used. AIC is a measure of goodness of model fit (i.e., the maximum likelihood achieved for the model), with a penalty term for the number of parameters:

$$AIC_i = -2MLL_i + 2p_i, \qquad (5)$$

where MLL_i is the maximized log-likelihood for model *i*, and p_i is the number of estimated parameters for that model. The model with the lowest AIC is the estimated best model. Akaike weights were then calculated to quantify the uncertainty associated with the model selection. The Akaike weight can be considered an estimate of the probability that a model is the best model in a set of alternatives (Burnham and Anderson 2002).

Results

Species differed substantially in their survival dynamics (Fig. 1). For *A. latistella*, survival declined sharply during the first few weeks after spawning, although the degree of this decline varied considerably among replicates (Fig. 1a). However, for all replicates, survivorship stabilized during the second month (i.e., slopes of the survival curves became shallow and parallel), and this second phase of very low mortality lasted until approximately 100 d, at which point survival began to decline again. *F. pallida* survival also appeared to exhibit this three-phase pattern, although the initial decrease was not as steep or as protracted as for *A. latistella*, nor did survivorship stabilize to the same degree during the second phase (~50-100 d, Fig. 1b, solid line). As with *A. latistella*, there was substantial variation among replicates in the initial rate of decline in survival, with some replicates showing steep initial declines in survivorship and others showing little difference between early and late phases (Fig. 1b, dashed lines). *P. paeonia* also showed initially steep declines in survival followed by more stable survival; however, both the initial period of high mortality and the second phase of stable survival appeared to end sooner than for *A. latistella* and *F. pallida*. In contrast to these species, *G. aspera* and *M. magnistellata* survival did not noticeably decline during the first few weeks (Fig. 1d-e). In fact, survival remained relatively high until after 100 d, when, again, survival began to decline increasingly sharply. The variation among replicates for both *G. aspera* and *M. magnistellata* was smaller in magnitude than for the other three species, particularly during the early period of high survival.

Despite substantial differences in shapes of survival curves, all species were extremely long-lived, with maximum lifespans ranging from 195-244 d (Table 1). Median lifetimes were less consistent among species (Table 1): species exhibiting steep declines in initial survival had substantially shorter median lifetimes than those with

high initial survival (e.g., 4 d for *A. latistella* vs. 138 d for *G. aspera*). However, due to the variation in replicates within species, there was also considerable variation between the median estimates of the individual replicates and the pooled data. These differences in median survival between replicates ranged from 28 d for *A. latistella* and *G. aspera*, up to 90 d for *F. pallida* (Table 1).

The parametric analyses provided strong support for variation in mortality rates across species, despite the variability in initial survival among replicates (which the parametric models incorporate as random effects). Specifically, for all species, the Weibull model provided a better fit to the observed survival times than the exponential model, confirming that larval mortality rates indeed vary over time (Table 2). The support for the Weibull model was strong for both early and late phases of the time series for *A. latistella*, *P. paeonia*, *M. magnistellata* and *G. aspera* (>96% support in each case, relative to the exponential model), and the late phase for *F. pallida* (>99% support). Although the Weibull model was also favoured for the first phase of the time series for *F. pallida*, the exponential model's fit was nearly as good (52% and 48% support respectively). For four of the species, the division of survival data into two parts provided strong evidence for decreasing mortality rates ($\alpha<1$: Type III survival) in the initial weeks following spawning, and increasing mortality rates ($\alpha>1$: Type I survival) as larvae aged (Fig. 2a-d). In contrast, for *M. magnistellata*, age-specific mortality increased monotonically during both early and late phses of larval life ($\alpha<1$: Type I survival), although this effect was more pronounced during the latter half of the experiment (Fig. 2e, Table 2). Remarkably, senescence began at approximately the same age in all species, 100 d after spawning (see the downward bend in survival curves in Fig. 2).

Discussion

The broadcast spawning coral larvae studied here, which lack maternally inherited zooxanthellae, have lifespans far exceeding expectations for lecithotrophic larvae. Previously, the longest reported life span for an azooxanthellate coral larva was 130 d for *Acropora valida* (Baird 2001). All of the coral species in this study had maximum larval lifetimes exceeding this by 50% to 80%. In fact, the larvae lived almost twice as long as generally reported for scleractinian coral larvae (Table 3), and nearly an order of magnitude longer than values typically used in numerical models of dispersal distances in corals (e.g., Williams et al. 1984). In addition, the majority of species in this study had median lifetimes that exceed previous estimates for broadcast spawning corals by as much as threefold (Table 3). This finding is probably the result of the exclusive focus in this study on larval survival, whereas previous studies frequently have had other aims, and stopped the experiment before the death of all larvae (e.g., Babcock 1984; Nishikawa et al. 2003; Nishikawa and Sakai 2005; Nozawa and Harrison 2005).

These results highlight the need to re-evaluate the current understanding of larval energetics. To date, there has been only one attempt to estimate the energetic limits on the dispersal of coral larvae that lack zooxanthellae. Specifically, Richmond (1988) measured the energy content and metabolic rate (i.e., respiration) of recently developed larvae. He then predicted the length of the competency period (i.e., the duration over which larvae maintain the ability to settle and metamorphose) to be 20 d in *Acropora tenuis* larvae, assuming that coral larvae are competent until approximately 1/3 of their initial size. Using the same approach, but removing this competence assumption, the model predicts 30 d as an upper bound on larval lifetimes. Although these calculations are based on a different species than the ones in this study, it is

striking that all five species studied here have maximum lifespans exceeding this estimate by nearly an order of magnitude.

In principle, for lecithotrophic coral larvae, survival times will be determined by maternally provided endogenous reserves and the rate at which larvae utilize these resources (Morgan 1995). To survive for long periods of time, larvae must begin life with large energy reserves, be able to supplement their endogenous reserves during larval life, or be able to control their metabolic rates. Eggs and larvae of most coral species examined to date contain high concentrations of lipids (60-85% by weight), which may be indicative of large energy reserves (Richmond 1987; Arai et al.1993; Wellington and Fitt 2003; Harii et al. 2007). Coral larvae of some species, like *P. damicornis*, may be able to supplement these resources with energy translocated from symbiotic zooxanthellae (Richmond 1987). However, the majority of broadcasting spawning species, including the ones studied here, produce larvae that lack zooxanthellae (Harrison and Wallace 1990). Although many larvae can be induced to take up zooxanthellae under experimental conditions (Krupp 1983), including *Acropora* (Nishikawa et al. 2003; Baird et al. 2006), and *Goniastrea* (Nozawa and Harrison 2005), it is not yet known whether larvae regularly acquire zooxanthellae during the planktonic phase. In any case, however, this could not explain the extended survival times observed in this study, which were measured in culture in the absence of zooxanthellae. Another possible source of energy suggested for marine larvae is the assimilation of dissolved organic matter (DOM) from seawater (e.g., Manahan 1990; Hoegh-Guldberg 1994; Shilling et al. 1996). Although the uptake of DOM has not been confirmed for coral planulae, it is possible that assimilation of DOM contributed to the survival of larvae in this study.

An alternative explanation for the high survival observed here is that larvae changed their energetic expenditure as they aged. Larvae of some planktotrophic taxa can enter a no-growth, energetic steady state in which net energy intake balances basic metabolic demand (Pechenik 1980). For lecithotrophic larvae, especially ones that do not grow during the planktonic phase, it seems unlikely that larvae could enter a comparable steady state. However, other non-feeding larvae do cease active swimming after prolonged periods of time in the laboratory, and this may be a means of conserving energy (e.g., Bryozoa: Jaeckle 1994; Wendt 1996). Indeed, in this study, the larvae of most species were observed to decrease or cease swimming within the first month after spawning. Dahan and Benayahu (1998) noted a similar decrease in larval movement of the soft coral *Dendronephthya hemprichi* after 40 d.

It is important to note that the extended lifetimes reported here, as well as in previous studies, are almost certainly overestimates of actual survival times in the field, due to the benign conditions in culture. Temperature, salinity, and light levels were constant throughout the experiment, sterile conditions minimized bacterial contamination, and there were no predators. In the field, larvae are subject to fluctuations in physical, chemical, and biological conditions, and additional sources of mortality, such as predation and bacterial infection, that can shorten the realized lifetimes of larvae (Olson and McPherson 1987; Eckman 1996). Nevertheless, given that previous estimates of survival also come from benign culture conditions, the present study does show that coral larvae can survive much longer than previous data have suggested.

Age-dependent mortality rates

Larval mortality rates changed throughout the duration of the planktonic phase in this study. In particular, for most species, the data provide strong support for increased mortality risk both early and late in the life of coral larvae. This type of survival, a combination of Type III and Type I survival curves, occurs in many species; however, this is the first documentation of such a pattern for the larval phase alone: such patterns are usually evident only when the complete life history from birth to death is considered (Paranjpe and Rajarshi 1986; Tanner 2001).

High initial rates of mortality may be due to developmental failure in a proportion of the larval cohort, unequal provisioning of offspring by parents, or density dependent mortality. Were developmental failure the cause, one would expect the period of high mortality to coincide with the pre-competent larval period, when larval development is most pronounced. However, most larvae acquire competence within a few days of spawning (Baird 2001, Miller and Mundy 2003), whereas the high mortality observed here lasted for at least a month. This discrepancy argues against developmental failure as a likely explanation for these results. Alternatively, unequal provisioning of larvae could have led to elevated mortality early in the experiment, as poorly-provisioned larvae died, while more well-provisioned larvae survived longer. Although inequality in larval provisioning has been quantified for some taxa, (e.g. fishes: Gagliano and McCormick 2007), whether it is great enough in corals to explain the observed rapid, early declines in survival is presently unknown. A third possibility is that mortality is density dependent, i.e., mortality rates are greater at the higher densities found early in the experiment. Plausible mechanisms for this exist: for instance, as larvae die, they lyse into lipid masses that can entrap other larvae, which could lead to further mortality. This hypothesis could be tested in future experiments by manipulating water volume as larvae die to keep densities approximately constant.

In addition to the biological mechanisms noted above, handling effects may have contributed to the high initial mortality that we observed. Despite efforts to minimize handling effects (e.g., sterilization techniques, minimal handling and transport), there may still have been detrimental effects of handling on larval survival, such as bacterial infection, or damage in transport. However, handling protocol remained the same for the duration of the study, except for a decrease in census frequency (see Methods), and transport of larvae occurred only in the first week. The fact that larvae were obtained during three different spawning events up to two months apart argues against a change in the culture environment (e.g., temporary contamination of filtered seawater), because the high mortality phase occurred at different times for different species. It is not clear why handling effects would continue to impact larvae for several weeks after spawning, and then go away. Nevertheless, the possibility that handling effects contributed to the high initial mortality rates cannot be ruled out.

Although it is difficult to determine conclusively the cause of the high early mortality, depletion of energy reserves as larvae age appears to be the only plausible cause of increased mortality late in life. Handling effects are unlikely to explain this part of the survival pattern because it followed months of high survival, and the same handling protocol was followed throughout, with larvae manipulated every second week. Similarly, a change in the culture environment is an unlikely explanation, because the onset of increased mortality rates (~100 days after spawning in all species) occurred at different times because the larval cohorts were produced during spawning events up to 60 d apart.

Implications for dispersal

Because coral larvae are relatively poor swimmers, their dispersal distances will largely depend on the duration of the pelagic phase and the speed and direction of water currents transporting the larvae (Scheltema 1986). Long-lived larvae are generally thought to have a higher capacity to disperse widely simply because of the increased time in the plankton (Williams et al. 1984; Richmond 1987; Babcock 1988). Results reported here show that larval longevities are much greater than previously reported, and should be sufficient to allow very long distance dispersal. For example, Harrison et al. (1984) concluded a larval duration of only 91 d (less than half the maximum lifespan of all species examined here) was long enough to support the recruitment of *Acropora* species to the Hawaiian Islands from the Johnston atoll 729 km away. Remarkably, the onset of senescence occurred approximately 100 d after spawning for all species, suggesting very similar potential for long distance dispersal, despite substantial differences in median lifetimes.

However, high early mortality suggests that while the potential for rare long distance dispersal events exists, most larvae do not survive long enough to be transported very far. Thus, the majority of successful recruitment is likely to involve settlement on natal or neighbouring reefs, particularly given that most larvae become competent to settle quickly, within a few days after spawning (Baird 2001; Miller and Mundy 2003). Although the potential for handling effects to have contributed to this high early mortality cannot be ruled out, this inference is consistent with genetic studies that have found high genetic structure at local scales (Ayre and Hughes 2000). Moreover, sources of mortality excluded from the laboratory, such as predation, have the potential to amplify this early steep decline in survival. The findings reported here suggest that genetic structure is likely to be higher for species such as *A. latistella*,

whose survival declines rapidly early in life, and lower for species such as *G. aspera* and *M. magnistellata*, which do not exhibit this early phase of high mortality.

This study rigorously documents changes in mortality rates as larvae age; it also reveals that coral larvae can remain alive far longer than either previous observations, or projections based on estimates of larval metabolic rates, would suggest. Observations of larvae in culture during this study suggest that larvae substantially reduce active swimming after the first few weeks of life, although many remained neutrally buoyant and resumed active swimming when agitated. Thus, the long lifespans documented here may be due to a capacity to ration energy expenditure, a hypothesis that warrants further investigation. Regardless of the proximate mechanism, however, larval lifespans on the order of 200 or more days suggest that corals are able to maintain energy reserves longer than previously thought, and thus potentially to disperse very long distances, a fact that may partly explain the extraordinarily large geographic ranges of many corals (Hughes et al. 2002). Despite the potential for long life and long distance dispersal, however, high mortality early in life for some species suggests that connectivity between reefs may well decline very rapidly over even relatively short distances. However, because this high initial mortality differs substantially in its magnitude among species, the extent to which population dynamics are coupled among reefs at regional scales may well be expected to vary substantially among species. This hypothesis has important implications for how relative abundances of coral species may change in response to habitat fragmentation or changes in disturbance regimes, and thus warrants further investigation.

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Figure Legends

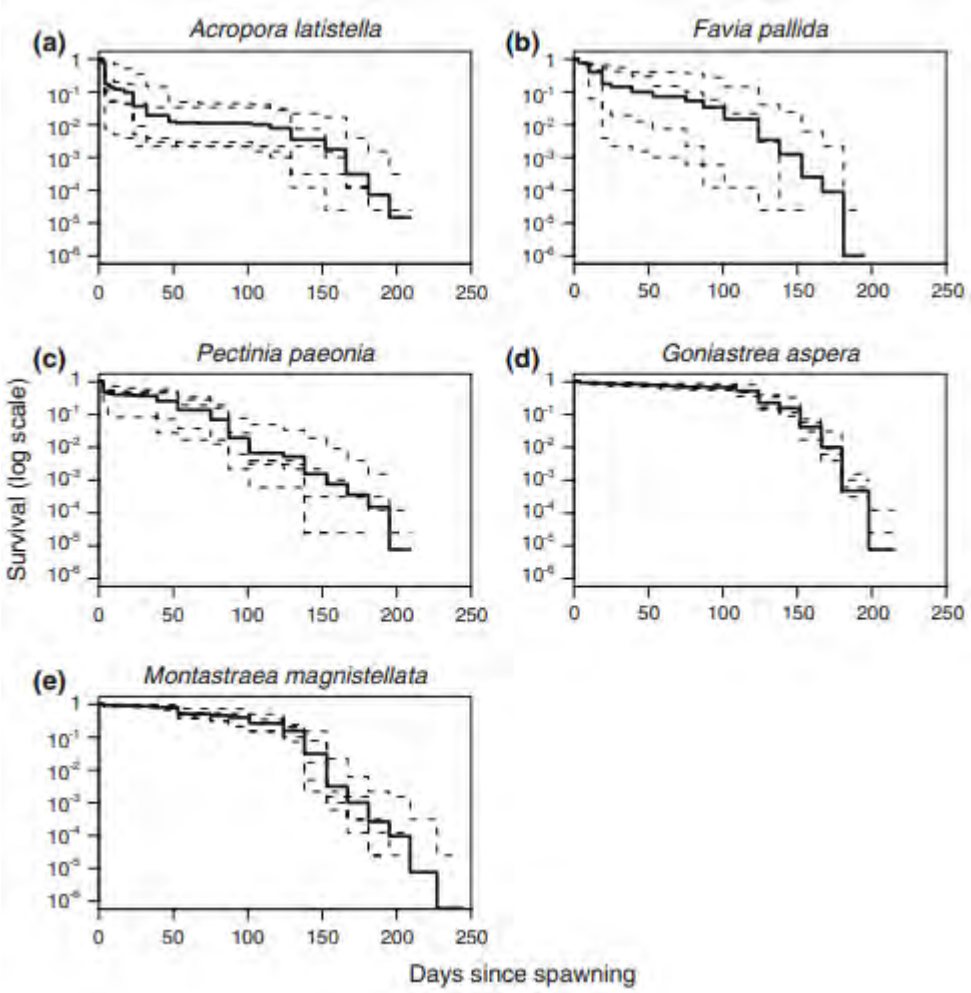

Fig. 1 Kaplan-Meier estimated survival probabilities for all replicates pooled (*solid line*) for each species. Individual replicates are also plotted (*dashed lines*), to illustrate variation among replicates

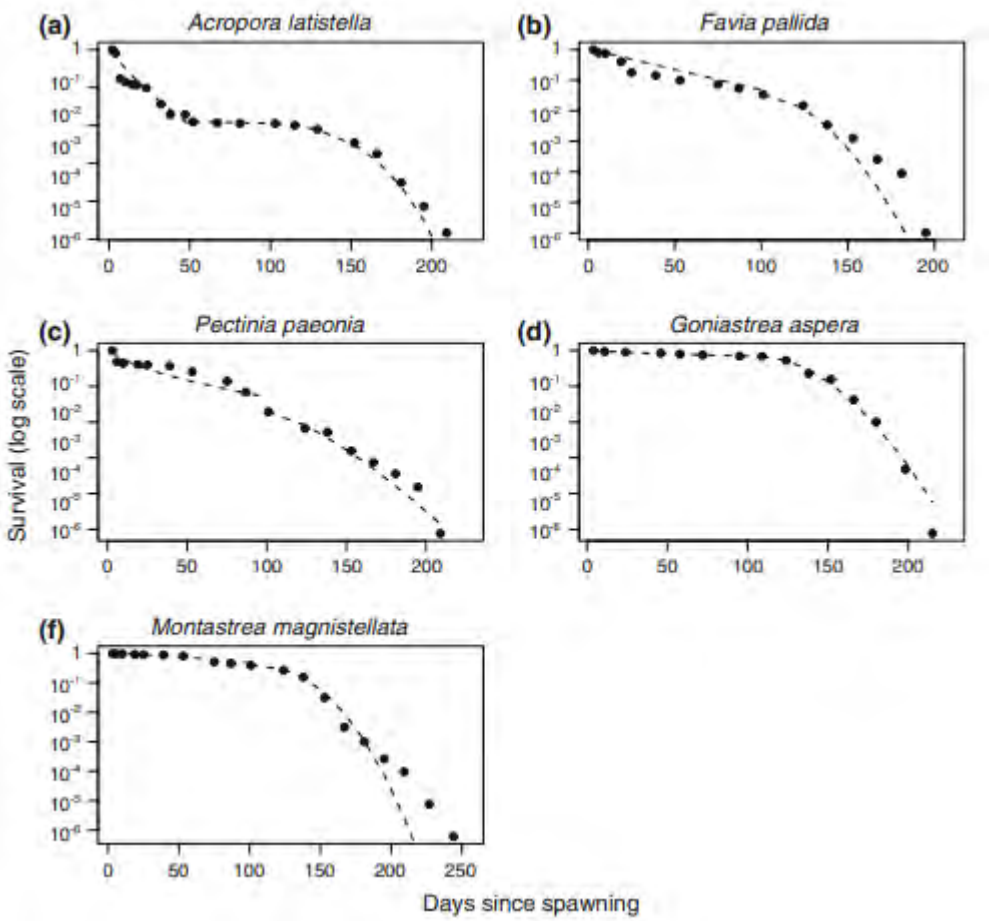

Fig. 2 Estimated parametric survival functions fitted to the empirical data with the Weibull distribution. In all panels, points show the empirical survival pattern, and lines show the best-fit Weibull distribution for the divided time series

Table 1 Longevity and median lifetime estimates for each coral species. *Min* and *Max* refer to the shortest and longest median survival times for the replicates analyzed separately, and *Pooled* refers to the median survival time when data from all replicates were pooled before analysis

Species	Kaplan-Meier Median Estimates (d) Replicates			Maximum Longevity (d)
	Min	Max	Pooled	
Acropora latistella	4	32	4	209
Favia pallida	10	101	19	195
Pectinia paeonia	3	75	53	209
Goniastrea aspera	124	152	138	215
Montastraea magnistellata	101	138	124	244

Table 2 Akaike's Information Criteria (AIC) for the exponential and Weibull models based on maximum likelihood results for the divided time series. Akaike weights (% Support) indicate relative likelihood for each model

Species	Split (d)	Exponential		Weibull			Survival Curve
		AIC	% Support	α	AIC	% Support	
Acropora latistella	< 52	2119	< 1	0.78	2074	> 99	Type III
	> 52	428	< 1	4.10	311	> 99	Type I
Favia pallida	< 101	1596	48	0.96	1596	52	Type III
	> 101	329	< 1	1.83	298	> 99	Type I
Pectinia paeonia	< 101	2419	< 1	0.62	2309	> 99	Type III
	> 101	351	1	1.37	343	99	Type I
Goniastrea aspera	< 109	739	4	0.71	733	96	Type III
	> 109	1780	< 1	1.85	1617	> 99	Type I
Montastraea magnistellata	< 101	1231	< 1	1.42	1216	> 99	Type I
	> 101	1385	< 1	2.32	1155	> 99	Type I

Table 3 Estimates of median and maximum survival times for a range of broadcast spawning scleractinian coral species, sorted by longevity. Plus (+) indicates larvae were still alive at the end of the observation time

Species	50% mortality (d)	Longevity (d)	Reference
Montastraea magnistellata	124	244	This study
Goniastrea aspera	138	215	This study
Acropora latistella	4	209	This study
Pectinia paeonia	53	209	This study
Favia pallida	19	195	This study
Acropora valida	16	130	Baird 2001
Platygyra daedalea		124	Nozawa and Harrison 2000
Acropora millepora	14	110	Baird 2001
Acropora hyacinthus		91	Harrison et al. 1984
Acropora gemmifera	14	90	Baird 2001
Goniastrea retiformis	11	90	Baird 2001
Acanthastrea lordhowensis		78	Wilson and Harrison 1998
*Goniastrea aspera**	14	70	Nozawa and Harrison 2005
Favites chinensis	32	63	Nozawa and Harrison 2005
Goniastrea favulus		60+	Babcock 1984
Acropora tenuis	25	69+	Nishikawa et al. 2003
Goniastrea australiensis		56	Wilson and Harrison 1998
Acropora digitifera	10	45+	Nishikawa and Sakai 2005
Acropora formosa		23	Harrison et al. 1984

**Goniastrea aspera* is shown twice to show previously estimated survival times for this species