LETTERS
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Increased local retention of reef coral larvae as a result of ocean warming

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Climate change will alter many aspects of the ecology of organisms, including dispersal patterns and population connectivity[1]. Understanding these changes is essential to predict future species distributions, estimate potential for adaptation, and design effective networks of protected areas[2]. In marine environments, dispersal is often accomplished by larvae. At higher temperatures, larvae develop faster[3–5], but suffer higher mortality[4–6], making the effect of temperature on dispersal difficult to predict. Here, we experimentally calibrate the effect of temperature on larval survival and settlement in a dynamic model of coral dispersal. Our findings imply that most reefs globally will experience several-fold increases in local retention of larvae due to ocean warming. This increase will be particularly pronounced for reefs with mean water residence times comparable to the time required for species to become competent to settle. Higher local retention rates strengthen the link between abundance and recruitment at the reef scale, suggesting that populations will be more responsive to local conservation actions. Higher rates of local retention and mortality will weaken connectivity between populations, and thus potentially retard recovery following severe disturbances that substantially deplete local populations. Conversely, on isolated reefs that are dependent on replenishment from local broodstock, increases in local retention may hasten recovery.

Organisms experience natural and anthropogenic disturbances, such as storms, overexploitation and pollution, that cause destruction of habitat and fragment metapopulations[7]. Recovery from disturbance relies heavily on the success of subsequent recruitment events to the disturbed site[8]. Recruits can originate locally through reproduction of the surviving individuals, or disperse from other locations to the affected areas[9]. For most marine species whose adults are sessile or relatively sedentary, the degree of local retention and dispersal depends on the hydrodynamic regime and the survival and development rates of propagules, such as larvae[10,11]. Larval survival and development depend on temperature[12]. Temperature increases the activity of enzymes, accelerating fundamental biochemical processes and consequently metabolic rates[13]. Increased metabolic rates hasten larval development, potentially reducing the time larvae spend in the plankton and thereby increasing the likelihood that larvae will settle before being flushed from their natal reef[3–5]. However, increased metabolic rates are also likely to increase mortality during larval development, reducing overall recruitment success, including recruitment back to the natal reef as well as successful dispersal elsewhere[4–6]. Thus, whether rising temperatures will strengthen or weaken local retention is not obvious. To determine how ocean warming will influence such patterns, the temperature dependence of the larval mortality rate–development rate trade-off must be quantified.

Here, we extended a dynamic model of coral larval dispersal[14] to characterize how temperature affects the survival and acquisition of competence to settle, and calibrated our models by conducting a series of experiments testing the effects of temperature on larval survival and competence. We then integrated our calibrated survival and competence models with a model of larval retention[15] to project temperature-induced changes in the proportion of larvae produced on a reef that successfully become competent to settle while retained on that natal reef (that is, the number of larvae settling on a reef as a proportion of the total number produced on that reef, hereafter termed local retention). We selected three scleractinian coral species (*Cyphastrea japonica*, *Favites stylifera* and *Acropora millepora*) to evaluate the effect of temperature (27–31 °C) on survival and competence dynamics. These species have lecithotrophic (aposymbiotic) larvae and span an almost twofold range in egg diameter (296.8 ± 2.6, 453.6 ± 4.8 and 541 ± 5.9 μm, respectively). Recent work suggests that broadcast-spawning coral species with smaller eggs acquire the capacity to settle more quickly than species with larger eggs[11]. Consequently, we expect these differences in egg size to systematically affect the influence of temperature on competence dynamics.

We find that, across all temperatures, our models characterize competence and survival dynamics of broadcasting coral larvae extremely well (Fig. 1); in particular, model selection by AIC (Akaike's information criterion) revealed the consistently earlier rate of acquisition of competence at warmer temperatures, and, for *C. japonica* and *A. millepora*, the higher mortality rates at warmer temperatures (Fig. 1 and Supplementary Tables 1–3). Together, the temperature dependence of survival and competence dynamics implies that ocean warming will boost local retention of broadcasting coral larvae on reefs with mean residence times of about 5 days or less (Fig. 2 and Supplementary Fig. 2). This encompasses most fringing and patch reefs worldwide, whose estimated mean residence times typically range from a few hours to about 5 days (Supplementary Information).

Over this range of mean residence times, the additional number of larvae expected to acquire competence before leaving the reef outweighs the increase in mortality due to higher temperatures (Fig. 3). Specifically, reefs with shorter residence times have a larger relative increase in local retention (that is, the estimated local retention under climate change as a fraction of local retention under present conditions: Fig. 2). In contrast, the absolute change in local retention (that is, the difference between climate change and present-day scenarios in the proportion of the initial cohort that is retained) peaks at intermediate mean residence times that

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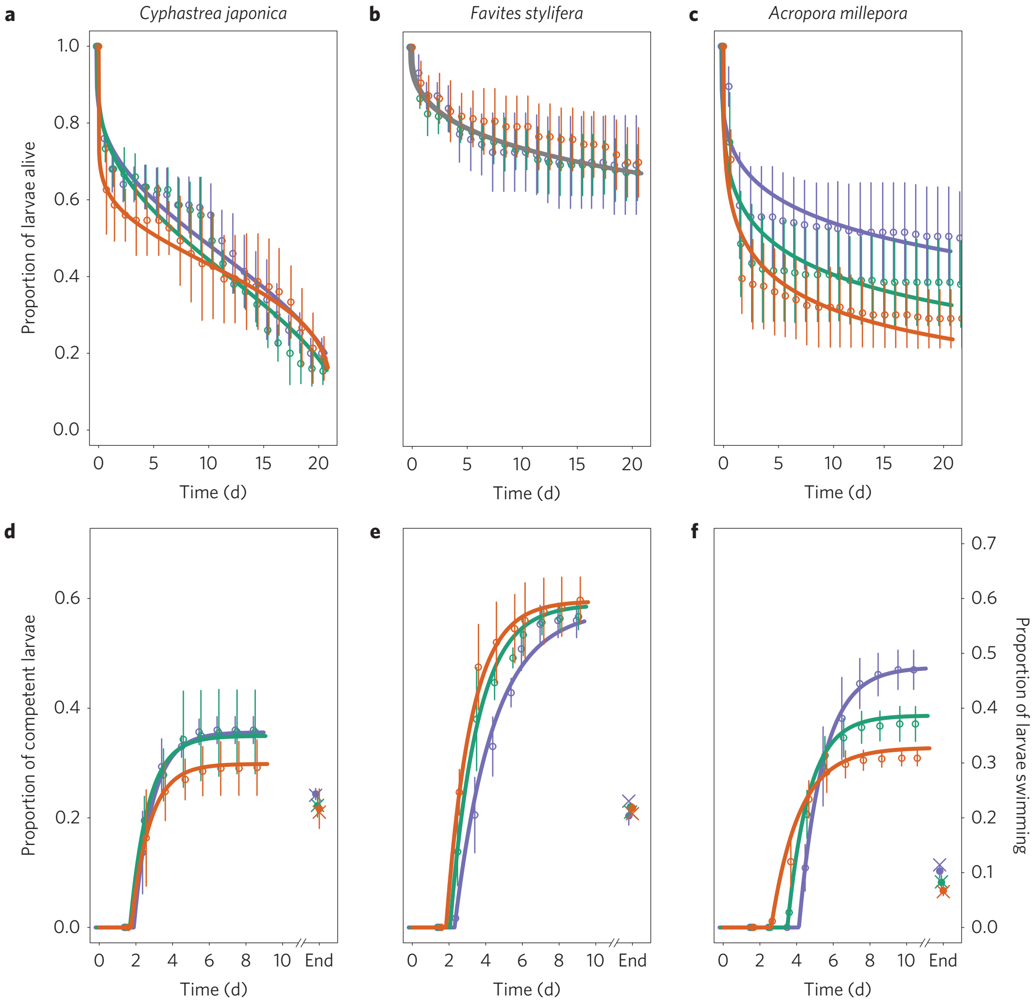

Figure 1 | Experimental survival and competence dynamics. **a**–**f**, Proportion of surviving larvae in the absence of settlement cues (**a**–**c**), and proportion of larvae settled (**d**–**f**, left axis) and swimming at the end of the experiment (**d**–**f**, right axis) in the presence of settlement cues for *Cyphastrea japonica*, *Favites stylifera* and *Acropora millepora* at 27 °C (purple), 29 °C (green) and 31 °C (orange). Lines show best-fit models, open circles are average (±s.e.) survival (**a**–**c**) and settlement (**d**–**f**), filled circles are average (±s.e.) proportion of larvae swimming at the end of the experiment, and crosses are the corresponding model predictions. To enhance readability, points and model fits for 27 °C and 29 °C were shifted $-0.2\,\mathrm{d}^{-1}$ and $-0.1\,\mathrm{d}^{-1}$, respectively, along the *x* axis.

are comparable to or slightly less than the present pre-competent period of these species (Supplementary Fig. 2). In reefs with very short residence times (<0.5 days), the relative increase in local retention can be extremely high, but the corresponding absolute increase is low (Supplementary Fig. 1). Nonetheless, even small absolute increases are likely to be important, especially on isolated reefs where a large proportion of the settlers are likely to be of local origin. In contrast, for relatively dense matrices of reefs with substantial larval exchange between subpopulations, small absolute increases in local retention may be less important.

On reefs with long mean residence times (that is, more than 5 days, for example, large lagoons and atolls), the more rapid acquisition of competence does not compensate for potentially higher rates of larval mortality at higher temperature. Thus, changes to levels of local retention in reefs with long mean residence times mainly depend on how larval mortality rates are affected by higher temperatures. Within each reef (that is, among species), the relative increase in local retention is greater for species with larger eggs and longer pre-competent times (Fig. 2); however, the absolute change in local retention was highest for the species with the lowest mortality rate, *F. stylifera* (Supplementary Fig. 2). This suggests that species with longer development (that is, bigger eggs[11]) will probably experience a greater relative increase in local retention; however, absolute changes in local retention also benefit from low baseline mortality rates, because more larvae are alive to benefit from earlier acquisition of competence.

The effects of temperature on local retention occur because of differences in the way that changes in competence acquisition and mortality interact with flushing rates on reefs. One can conceptualize how temperature-induced changes in the minimum pre-competence period (t_c) and mortality rates influence local retention by considering how the proportion of larvae that are alive and not yet flushed from a reef (that is, the pool of potential settlers) changes over time, for reefs with different mean residence times (Fig. 3). Note that absolute changes in local retention scale approximately with changes in the proportion of potential settlers (Fig. 3a,c), whereas relative changes scale approximately with changes in the logarithm of the proportion of potential settlers (Fig. 3b,d). Reductions in t_c have the greatest absolute effect for intermediate mean residence times (Fig. 3a) but, in relative terms, have progressively larger effects as mean residence times decrease (Fig. 3b). Specifically, when mean residence time is very long, larvae are flushed from the reef at a slow rate, so a reduction from t_{c27} to t_{c31} has a small effect in both absolute and relative terms (Fig. 3a,b, green lines). When mean residence time is intermediate, a reduction in t_c leads to a larger (absolute and relative) increase in the pool of

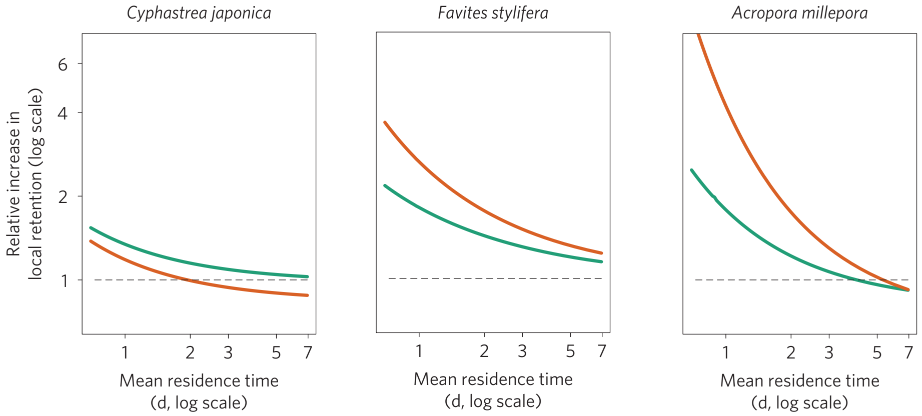

Figure 2 | Relative increase in the proportion of larvae that attain competence while retained on the natal reef over a realistic range of mean residence times around a reef with a 2 °C increase (29 °C, green line) and 4 °C increase (31 °C, orange line). The dashed line represents values of local retention equivalent to present temperature at the time of spawning; thus, values above the dashed line represent an increase in local retention relative to present temperature (27 °C), whereas values below the dashed line represent a decrease in local retention (see relative increase in local retention for reefs with shorter retention times in Supplementary Fig. 1).

potential settlers (Fig. 3a,b: dark blue lines). When mean residence time is very short, the absolute increase in local retention is small, because most larvae have already been flushed from the reef before t_{c31}, but the relative increase is large, because the increase in the pool of potential settlers is on top of very low baseline local retention (Fig. 3a,b, light blue line). An increase in mortality rates imposes a proportional reduction in the number of larvae available to settle. Consequently, in absolute terms, this effect is larger for longer mean residence times, because the proportional reduction is imposed on a larger pool of larvae not yet flushed from the reef (Fig. 3c). However, this same proportionality of the effect of mortality makes its relative reduction in the number of settlers independent of mean residence time (Fig. 3d).

Our results suggest that reef recovery will become more dependent on locally produced larvae than at present, for two reasons. First, a larger proportion of locally produced larvae will settle back onto their natal reefs. Second, a smaller proportion of larvae produced are likely to immigrate from reefs elsewhere, because a smaller fraction of those larvae will be exported from their natal reefs, and those that do may experience higher mortality during dispersal. Populations that rely on local retention for persistence[16,17], such as those on isolated reefs[18], are likely to benefit from the projected increases in local retention caused by ocean warming. Increased local retention will also benefit persistence because more larvae will recruit to favourable habitats[19], reducing potential phenotype–environment mismatches[20,21] and thereby increasing post-settlement survivorship.

An increase in local retention also implies a stronger link between the abundance of adults and recruits at the reef scale. This has the potential to make populations more responsive to local management initiatives, such as limits on the use of destructive fishing gear[19,22]. However, higher rates of local retention and increased mortality during dispersal also imply reduced connectivity among populations. Such reduced connectivity could adversely affect populations that depend on larval exchange for persistence, if these network persistence effects are not outweighed by the higher settlement of locally produced larvae[16–18].

The consequences of higher local retention and reduced connectivity should vary with the spatial distribution of habitat patches[23] and disturbance severity. For populations in relatively continuous reef systems over a latitudinal gradient (for example, Great Barrier Reef), weaker connectivity implies lower rates at which warm-adapted genotypes could migrate to higher latitudes in response to warming environments[24,25]. Conversely, on more isolated reef systems (for example, Hawaii or French Polynesia), higher local retention would increase the capacity of the population to recover from minor disturbances, but would also increase the time lag in recovery (owing to stock-recruitment effects) when reef-scale disturbance is severe[8].

Laboratory experiments have played a key role in understanding how organisms respond to higher temperatures, including on coral reefs[26,27]. However, populations in nature are subject to additional factors that are not simulated in the laboratory. For instance, it is unclear how much populations will be able to adapt to increasing ocean temperatures. Ectotherms consistently develop faster where temperatures are warmer, and the relative shift in competence time documented here (20–40% reduction in the minimum time to competence over 4 °C) is comparable to changes in larval development rates observed along geographical temperature gradients[28]. This suggests that our calibrated changes to competence dynamics are likely to be relatively robust to any decadal-scale local thermal adaptation that may occur. Conversely, mortality rates are often more similar between populations adapted to different temperatures, than within a single population that is experimentally subjected to different temperatures[29,30]; thus, local thermal adaptation could ameliorate the increased mortality documented here, which could amplify the projected increases in local retention. In addition, larval mortality in the plankton may be influenced by factors other than temperature, such as predation, that are not present in the laboratory (although they may not be influenced by factors that are potentially important in the laboratory, such as experimental handling). To investigate the robustness of our results to such factors, we evaluated the sensitivity of our estimates to overall levels of mortality. This analysis indicates that overall mortality levels had a relatively small impact on how the effect of temperature on local retention changed with reef residence time (Supplementary Fig. 3).

Persistence of coral populations under climate change will depend on the responses of a range of demographic variables, such as, lifetime fecundity, larval survival and dispersal (local retention and connectivity), post-settlement survival and growth[16,17,31], to both warming and acidification. So far, most attempts to evaluate such population-level implications have focused on responses at the adult and juvenile stages[32–34]. The present study shows that temperature-induced changes to larval competence dynamics will also alter metapopulation dynamics by systematically changing local retention. These effects are likely to vary predictably among locations depending on how hydrodynamics and reef

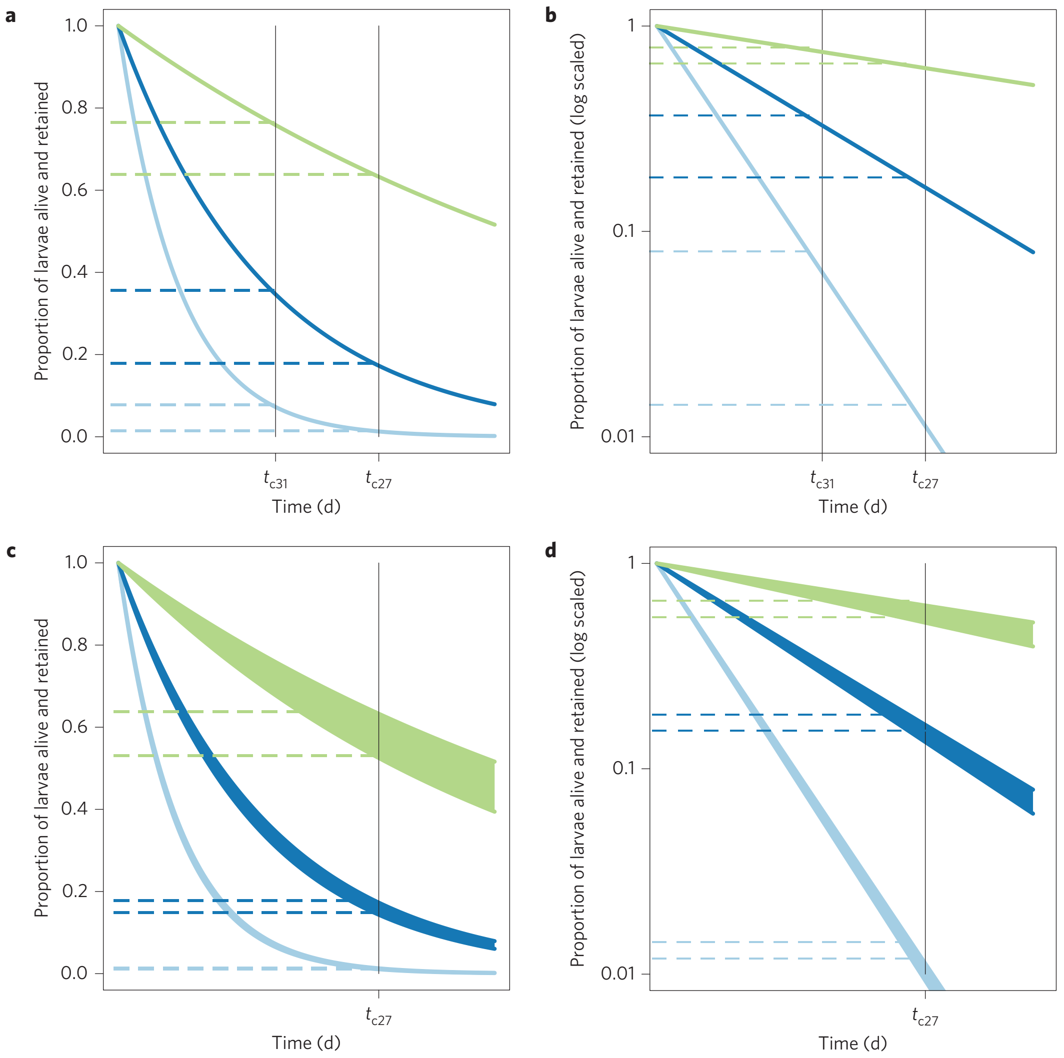

Figure 3 | Proportion of potential settlers (live larvae not yet flushed from the reef) for reefs with short (1 day, light blue), intermediate (2.5 days, dark blue) and long (10 days, green) mean residence times, using estimates for *A. millepora* (Supplementary Table 2). In **a**,**b**, mortality rate is equal for all reefs (λ_{27}), and the vertical distance between the dashed lines represents the increased proportion of potential settlers due to the reduction in the minimum time to competence from t_{c27} to t_{c31}. In **c**,**d**, minimum competence time is fixed at t_{c27}, and mortality rate is low on the top (λ_{27}) and higher on the bottom (λ_{31}) of each shaded band; thus, the vertical distance between the dashed lines shows the reduction in the proportion of potential settlers due to the increased mortality rate λ_{27} (λ_{31}) is the mortality rate parameter at 27 °C (31 °C), respectively.

geomorphology influence residence time, and among species depending on characteristics such as egg size that are correlated with baseline development rates[11]. Such predicted changes to species dispersal patterns present managers of marine resources with both opportunities and challenges. Increased local retention in corals, and other marine organisms with short larval pre-competence periods (such as some fish, snails, crustaceans and echinoderms), suggests that the management of local human impacts will become increasingly effective as a means of mitigating reef degradation. In addition, as connectivity among populations weakens, the spacing of marine protected areas may also need to be reduced to maximize resilience to climate change and effectively protect ecosystems[2,22,23].

Methods

To predict how local retention of corals may be altered by ocean warming, we extended a model of coral larval retention around a reef that incorporates the dynamics of larval survival and acquisition of competence[11,14]. Second, we experimentally calibrated the effect of temperature on the model parameters for three coral species, *Cyphastrea japonica*, *Favites stylifera* and *Acropora millepora*. Finally, we used the calibrated model to estimate the proportion of larvae successfully attaining competence to settle while retained in their natal reef (local retention) at different temperatures (see Supplementary Information for details). The data and code have been deposited at datadryad.org (http://dx.doi.org/10.5061/dryad.7vj03).

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Author contributions

J.F., A.H.B. and S.R.C. designed the experiments. J.F., A.H.B. and S.H. performed the experiments. J.F. and S.R.C. analysed and modelled the data. All authors contributed to writing the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.F.

Competing financial interests

The authors declare no competing financial interests.